Revised phylogenetic analysis of the Aetosauria (Archosauria: Pseudosuchia); assessing the effects of incongruent morphological character sets

William G Parker

Aetosauria is an early-diverging clade of pseudosuchians (crocodile-line archosaurs) that had a global distribution and high species diversity as a key component of various Late Triassic terrestrial faunas. It is one of only two Late Triassic clades of large herbivorous archosaurs, and thus served a critical ecological role. Nonetheless, aetosaur phylogenetic relationships are still poorly understood, owing to an overreliance on osteoderm characters, which are often poorly constructed and suspected to be highly homoplastic. A new phylogenetic analysis of the Aetosauria, comprising 27 taxa and 83 characters, includes more than 40 new characters that focus on better sampling the cranial and endoskeletal regions and represents the most comprenhensive phylogeny of the clade to date. Parsimony analysis recovered three most parsimonious trees; the strict consensus of these trees displays an Aetosauria that is divided into two main clades: Stagonolepoidea, which includes the Desmatosuchinae and the Stagonolepidinae, and Aetosaurinae, which includes the Typothoracinae. The small-bodied aetosaurs, typified by *Aetosaurus ferratus*, are recovered at the base of the Aetosaurinae, consistent with the hypothesis that they may represent juvenile forms of larger typothoracine taxa, which are also recovered within Aetosaurinae. As defined Desmatosuchinae now contains *Neoaetosauroides engaeus* and several taxa that were previously referred to the genus *Stagonolepis*. A new clade, Desmatosuchini, is erected for taxa more closely related to *Desmatosuchus*. Overall support for some clades is still weak, and Partitioned Bremer Support (PBS) is applied for the first time to a strictly morphological dataset and demonstrates that this weak support is partly because of conflict in the phylogenetic signal of cranial versus postcranial characters. PBS helps identify homoplasy among characters from various body regions, presumably the result of convergent evolution within discrete anatomical modules. It is likely that character conflict results from different body regions evolving at different rates, which may be under different selective pressures.

Revised Phylogenetic Analysis of the Aetosauria (Archosauria: Pseudosuchia); Assessing the Effects of Incongruent Morphological Character Sets

William Gibson Parker

[1] Division of Resource Management, Petrified Forest National Park, Petrified Forest, Arizona, USA

[2] Jackson School of Geosciences, The University of Texas at Austin, Austin, Texas, USA

Corresponding Author:

William Parker[1]

1 Park Road, P. O. Box 2217, Petrified Forest, Arizona, 86028, USA

Email address: William_Parker@nps.gov

ABSTRACT

Aetosauria is an early-diverging clade of pseudosuchians (crocodile-line archosaurs) that had a global distribution and high species diversity as a key component of various Late Triassic terrestrial faunas. It is one of only two Late Triassic clades of large herbivorous archosaurs, and thus served a critical ecological role. Nonetheless, aetosaur phylogenetic relationships are still poorly understood, owing to an overreliance on osteoderm characters, which are often poorly constructed and suspected to be highly homoplastic. A new phylogenetic analysis of the Aetosauria, comprising 27 taxa and 83 characters, includes more than 40 new characters that focus on better sampling the cranial and endoskeletal regions and represents the most comprenhensive phylogeny of the clade to date. Parsimony analysis recovered three most parsimonious trees; the strict consensus of these trees displays an Aetosauria that is divided into two main clades: Stagonolepoidea, which includes the Desmatosuchinae and the Stagonolepidinae, and Aetosaurinae, which includes the Typothoracinae. The small-bodied aetosaurs, typified by *Aetosaurus ferratus*, are recovered at the base of the Aetosaurinae, consistent with the hypothesis that they may represent juvenile forms of larger typothoracine taxa, which are also recovered within Aetosaurinae. As defined Desmatosuchinae now contains *Neoaetosauroides engaeus* and several taxa that were previously referred to the genus *Stagonolepis*. A new clade, Desmatosuchini, is erected for taxa more closely related to *Desmatosuchus*. Overall support for some clades is still weak, and Partitioned Bremer Support (PBS) is applied for the first time to a strictly morphological dataset and demonstrates that this weak support is partly because of conflict in the phylogenetic signal of cranial versus postcranial characters. PBS helps identify homoplasy among characters from various body regions, presumably the result of convergent evolution within discrete anatomical modules. It is likely

that character conflict results from different body regions evolving at different rates, which may be under different selective pressures.

INTRODUCTION

The goal of phylogenetic systematics is to determine phylogenetic relationships of organisms based on shared homologous character states, and to use this information to interpret the evolutionary histories of clades, or monophyletic lineages of organisms, as well as the histories of various evolutionary character transformations. This presents special challenges for vertebrate groups with extensive carapaces of dermal armor like those of aetosaurian and ankylosaurid archosaurs, which are comprised of hundreds of individual osteoderms. Whereas these osteoderms may be common in the fossil record, they are generally dissociated from the rest of the skeleton prior to burial. It has been asserted for aetosaurians that osteoderms provide an exhaustive source of phylogenetically informative character data above and beyond that provided by the underlying skeleton (e.g., Long and Ballew, 1985; Heckert and Lucas, 1999; Parker, 2007), but it has also been argued that, while informative, these data may be plagued with phylogenetically confounding homoplasy (Parker, 2007, 2008a). The specific goal of this paper is to confront these assertions analytically, by undertaking an expanded phylogeny of aetosaurian archosaurs based on the largest taxonomic sample yet assembled, and using a suite of characters that samples both osteoderms and endoskeletal characters.

Historical Background

Aetosaurians are quadrupedal, pseudosuchian archosaurs characterized by shortened skulls with upturned snouts, heavy armor carapaces, as well as ventral armor (Figure 1; Walker, 1961; Desojo et al., 2013). They ha~~ve~~ a global distribution during the Late Triassic ~~Epoch~~ and are often used as index fossils for biostratigraphic correlations (Figure 2; Heckert and Lucas, 1999; Desojo et al., 2013). Paramedian osteoderms possess diagnostic surface ornamentation that allow for assignment of material to various taxa, although as previously mentioned some of these characters may be homoplastic (Long and Ballew, 1985; Parker, 2007). Accordingly it has been argued that characters from the lateral osteoderms may be more phylogenetically informative (Parker, 2007).

When Long and Ballew (1985) first proposed a taxonomy of North American aetosaurs based exclusively on osteoderm characters, they considered only four taxa (*Desmatosuchus*, *Typothorax*, *Calyptosuchus*, *Paratypothorax)*. Much new work based upon many new specimens revealed that the particular osteoderm character combinations proposed by Long and Ballew (1985) in fact can occur in many other unique combinations, resulting in the establishment of many new taxa based almost solely on osteoderms (e.g., Zeigler et al., 2003; Martz and Small, 2006; Spielmann et al., 2006; Lucas et al., 2007a, Parker et al., 2008; Heckert et al., 2015). Furthermore, it has been demonstrated that aetosaurs with nearly identical osteoderm character combinations can differ significantly in the other portions of the skeleton, especially in the cranial elements, indicating even more potential taxonomic variation (Desojo and Báez, 2005, 2007; Desojo and Ezcurra, 2011). Finally, aetosaurian osteoderm characters are not intraorganisimally homogeneous (i.e. characters can differ depending on position within the same carapace) and capturing this variation in the construction of phylogenetically informative characters is challenging (Harris et al., 2003; Parker, 2008b).

Although early studies did focus on character change across broadly defined carapace regions such as the cervical and caudal regions (e.g., Long and Ballew, 1985; Heckert and Lucas, 1999), more recent studies have sought to detail variation within th~~o~~se subregions~~ as well, in some cases almost osteoderm row by osteoderm row ~~(Martz, 2002; Parker, 2003; 2008b; Schoch, 2007; Parker and Martz, 2011; Heckert et al., 2015). Potentially further complicating this situation is our general lack of data regarding character transformations affected by ontogenetic variation as well as differences caused by individual and sexual dimorphism. Overall though, the rich source of character data present in aetosaurian osteoderms provides the systematist with a broad canvas on which to construct a detailed phylogenetic hypothesis, presuming of course that the changes in osteoderm characters are indeed phylogenetically informative (Parker, 2007) and that the homology of these characters can be determined (e.g., Harris et al., 2003).

At present we do not have an appropriate sample size to capture all of intraorganisimal character variation that occurs across the aetosaurian carapace. Indeed, many taxa are currently only known ~~by~~ a handful of associated osteoderms, ~~where~~ the current challenge simply ~~lies~~ in determining the proper position of these osteoderms in the carapace (Lucas et al., 2003; Martz and Small, 2006; Spielmann et al., 2006; Parker, 2007; Lucas et al., 2007a). ~~Presumably as~~ more discoveries are made, particularly of associated and articulated specimens, our increased understanding of positional variation ~~will~~ allow for more precise placement of isolated osteoderms leading to stronger determinations of homology of individual osteoderms (Parker and Martz, 2010; Heckert et al., 2015).

For this study all previously published characters used for determination of aetosaurian systematics were reviewed (Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 1999; Parker, 2007; Desojo et al., 2012; Heckert et al., 2015). Characters were discarded if found to be generally uninformative or ambiguously scored. The retained characters as well as new characters have been rewritten to be more descriptive and thus hopefully ~~more comprehensible~~. Although the retention and construction of many characters and associated character states would presumably lead to better resolution and clade support (Hillis et al., 1994), the goal of any phylogenetic analysis is accuracy, and this should not come at the expense of artificial resolution (Slowinski, 1993). Thus, the overarching goal of this project was to recover phylogenetic trees that 'make sense' given our anatomical understanding of aetosaurians, rather than highly resolved and supported trees that appear problematic and nonsensical in these regards. The matrix of Parker (2007), which ~~is currently~~ used as the basis for ~~current~~ phylogenetic analyses (Parker et al., 2008; Desojo et al., 2012, Heckert et al., 2015), is dominated ~~in number~~ by osteoderm characters~~, which~~ is ~~considered to be~~ problematic given the ~~past determinations of~~ large amount~~s~~ of homoplasy in this dataset (Parker, 2007; Desojo et al., 2012) ~~as well as~~ the ~~major~~ assumption that osteoderm characters provide ~~the actual historic~~ phylogenetic signal irrespective of ~~character states occurring throughout~~ the rest of the skeleton (Parker, 2007, 2008b). ~~Therefore~~ this study ~~sought~~ to increase the number of ~~utilized~~ non-osteoderm characters as suggested by Desojo (2005) and Desojo et al. (2012). This ~~was challenging~~ because of the relative infrequency of aetosaurian postcranial remains, which are lacking for many taxa or sometimes ~~covered~~ by articulated carapaces. The best source for aetosaurian postcranial bones is the *Placerias* Quarry in northeastern Arizona (Long and Murry, 1995). However, owing to a lack of association with diagnostic osteoderm material, most of these postcranial elements cannot unequivocally be referred to species-level groups (Parker, 2005a; *contra* Long and Murry, 1995). Fortunately, there is cranial material preserved for many aetosaurian taxa and almost every known skull, with the exception of some elements from the *Placerias* Quarry and the Post

Quarry (Texas), are unambiguously associated with osteoderms allowing for a precise taxonomic referral. Thus, the present analysis was able to significantly expand the number of cranial characters utilized.

The basis for aetosaurian phylogenetic characters and character transformations is a table of information published by Long and Ballew (1985:58) where comparisons are provided between various North American taxa, establishing a key early character-based taxonomic scheme for aetosaurians (also see Walker, 1961). Several of these characters are still utilized in recent phylogenetic analyses. The first computed phylogenetic analysis of aetosaurians (Parrish, 1994) examined 15 characters (six osteoderm, nine non-osteoderm) and eight taxa. Nine of those characters were parsimony-uninformative for the in~~-~~group and there several incorrect scorings and typographical errors that affect the analysis; thus the published tree is neither well-resolved nor accurate in its character state distributions (Harris et al., 2003). Heckert et al. (1996) expanded on Parrish's (1994) work, inflating the matrix to nine taxa and 22 (potentially 23) characters (17 armor, five non-armor). That study was affected by some scoring errors and the lack of a non-aetosaurian outgroup (Harris et al., 2003)~~. But it included~~ many new characters that ~~are still staples of~~ aetosaurian phylogenetic studies ~~to date~~ and have been further corroborated in the present study. Furthermore that study was the first to unambiguously recover the major clades Desmatosuchinae and Typothoracisinae (*sensu* Parker, 2007).

Heckert and Lucas (1999) aimed to expand the matrix of Heckert et al. (1996), in part to determine the phylogenetic relationships of a new taxon, *Coahomasuchus kahleorum*. Their published matrix consists of 13 in-group taxa and 60 characters. However, 26 of these characters are parsimony uninformative and as noted by Harris et al. (2003) the published matrix included several typographical errors. ~~When corrected, produced a tree different from the one published.~~

Harris et al. (2003) were critical of several other aspects of this study, including the *ad hoc* deletion of taxa from the matrix when safe methods to determine appropriate taxon deletion are available (e.g., Wilkinson, 1995a), and character constructions which inflated seemingly non-independent character suites that biased the resulting tree (composite versus reductive coding, Rowe, 1988; Wilkinson, 1995b). Nonetheless, the study by Heckert and Lucas (1999) built further upon the character list of Heckert et al. (1996) and represents a very important progression in our understanding of aetosaurian systematics.

The most recent phylogenetic analysis (Parker, 2007) focused on the lateral osteoderms ~~of aetosaurian~~s, whereas previous~~ly~~ studies had focused more on characters of the paramedian osteoderms (Heckert et al., 1996; Heckert and Lucas, 1999). Parker (2007) noted that aetosaurians could roughly be divided into three groups based on the overall anatomy of the lateral osteoderms. This translated into a phylogenetic analysis (16 in-group taxa, 37 characters) that recovered three distinct clades~~;~~ Aetosaurinae, Desmatosuchinae (Heckert and Lucas, 2000) and Typothoracinae. Whereas support for Desmatosuchinae and Typothoracinae was strong, especially for Paratypothoracini, Aetosaurinae was generally unresolved or weakly supported. This became especially apparent when other taxa were added to the matrix causing significant differences in tree topology and character support (Parker et al., 2008; Desojo et al., 2012). Indeed, a recent study (Desojo et al., 2012) failed to recover Aetosaurinae as a more inclusive clade, with *Aetosaurus ferratus* as the only member. Nonetheless Typothoracinae remains well-supported and resolved, and although Desmatosuchinae is always recovered and well-supported, ~~the constituent taxa~~ are not always fully resolved (Parker et al., 2008). Criticisms of Parker (2007) dataset include the lack of endoskeletal characters as well as scoring errors (Desojo and Ezcurra, 2011; Desojo et al., 2012; Heckert et al., 2015).

Materials and Methods

In order to ~~test~~ these questions about taxon sampling, character independence, and tree topology, the previous matrices have been expanded to include more taxa and characters. An expanded study was necessary to create a robust matrix to not only potentially clarify all in-group relationships, but also to create a baseline matrix that would remain stable for future additions of new taxa and specimens. The new matrix (Appendix A) utilizes 83 characters for 26 in-group taxa. The characters are well-divided between anatomical regions, with endoskeletal characters constituting the majority (34 cranial, 16 axial/appendicular, 33 osteoderm).

The 26 in-group taxa include the majority of aetosaurian taxa currently considered valid (Desojo et al., 2013; Roberto-Da-Silva et al., 2014; Heckert et al., 2015). They are listed below and this study is the first to investigate ~~to~~ phylogenetic positions of *Adamanasuchus eisenhardtae*, *Apachesuchus heckerti*, *Stagonolepis olenkae*, and *Redondasuchus rineharti*. Furthermore, it scores a new taxon, *Scutarx deltatylus gen. et sp. nov.*, and rescores some other taxa (e.g., *Coahomasuchus kahleorum*; *Typothorax coccinarum*) based on new material.

Taxa excluded from this analysis include *Acaenasuchus geoffreyi* Long and Murry, 1995; *Redondasuchus reseri* Hunt and Lucas, 1991; *Typothorax antiquum* Lucas et al., 2003; and *Chilenosuchus forttae* Casamiquela 1980. *Acaenasuchus* and *Chilenosuchus* were excluded because *Chilenosuchus* presently scores as a taxonomic equivalent of *Typothorax coccinarum* (Wilkinson, 1995a), and newly recognized material of *Acaenasuchus* casts doubt on its aetosaurian identify (Parker, unpublished data). *Redondasuchus reseri* is poorly known and presently scores as a taxonomic equivalent of *Redondasuchus rineharti* (Wilkinson, 1995a);

whereas *Typothorax antiquum* represents an ontogenetic stage of *Typothorax coccinarum* (Parker, 2006; Parker and Martz, 2011; Martz et al., 2013).

Revueltosaurus callenderi is included in the analysis as an outgroup because it is currently recovered as the sister taxon of Aetosauria (Nesbitt, 2011). Furthermore, it is known from several specimens, which preserve nearly the entire skeleton. *Postosuchus kirkpatricki* is utilized as an outgroup because it is relatively complete, well-described and illustrated (Weinbaum, 2011, 2013). Furthermore, it represents a more nested clade (Paracrocodylomorpha) within Pseudosuchia providing deeper optimization of character states than can be provided by *Revueltosaurus*. Both of these taxa have been utilized as outgroups in ~~past~~ phylogenetic studies of the Aetosauria (e.g., Heckert and Lucas, 1999; Parker, 2007; Desojo et al., 2012; Heckert et al., 2015). Unfortunately neither *Postosuchus* nor *Revueltosaurus* can presently be scored for lateral osteoderm characters and therefore have been scored as inapplicable for these taxa. Furthermore, most of the paramedian osteoderm characters were scored as inapplicable for *Postosuchus* because even though *Postosuchus* possesses dorsal osteoderms, the homology of characters such as ornamentation pattern and presence of certain processes cannot be determined.

A previous work (Parker, 2007) incorporated many scorings from past studies (Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 1999) some of which were determined to be erroneous (Schoch, 2007; Desojo and Ezcurra, 2011; Desojo et al., 2012). For this study the matrix was scored from scratch and the scorings completed from carefully studying ~~actual~~ material~~s~~ for most taxa, and using photos and the literature for any not studied first-hand (*Stagonolepis olenkae*, *Aetosaurus ferratus*, SMNS 19003, *Stenomyti huangae*, *Redondasuchus rineharti, Gorgetosuchus pekinensis*, *Polesinesuchus aurelioi*). ~~Errors in scoring based on misinterpretation of character states and materials probably exist, but much effort has gone into~~

detecting and fixing typographic errors, which can have a major effect on the final tree topologies (Harris et al., 2003). Taxon scoring completeness is shown in Table 1 for each ~~taxon, compiled by counting the number of characters scored to determine the percentage of completion.~~ Inapplicable characters were counted as scored. Completeness scores range from 98% (80 of 82) for *Desmatosuchus smalli*, which is known from several skulls and skeletons; to 22% for *Apachesuchus heckerti* (18 of 82), which is known only from five paramedian osteoderms. The average completeness score was 60%. The ~~biggest factor for~~ incompleteness is ~~the~~ lack of skull material which affected all taxa that scored lower than 50%. Because aetosaurians are generally identified by armor characters, there are no taxa that consist solely of cranial material in contrast with many other groups (e.g.~~,~~ synapsids, dinosaurs).

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published ~~under that Code from the electronic edition alone~~. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:841F81C7-A4AE-4146-94FE-DFE0A6725634. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

Institutional abbreviations – **AMNH**, American Museum of Natural History, New York, USA; **ANSP**, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA;

CPE2, Coleção Municipal, São Pedro do Sul, Brazil; **DMNH**, Perot Museum of Natural History, Dallas, Texas, USA; **DMNH**, Denver Museum of Nature and Science, Denver, Colorado, USA; **FMNH**, Field Museum, Chicago, IL, USA; **FR**, Frick Collection, American Museum of Natural History, New York, USA; **MCCDP**, Mesalands Community College Dinosaur Museum, Tucumcari, New Mexico, USA; **MCSNB,** Museo Civico di Scienze Naturali Bergamo, Bergamo, Italy; **MCP**, Museo de Ciencias e Tecnología, Porto Alegre, Brazil**; MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MCZD**, Marischal College Zoology Department, University of Aberdeen, Aberdeen, Scotland, UK; **NCSM**, North Carolina State Museum, Raleigh, North Carolina, USA; **NHMUK**, The Natural History Museum, London, United Kingdom; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, USA; **PEFO**, Petrified Forest National Park, Petrified Forest, Arizona, USA; **PFV**, Petrified Forest National Park Vertebrate Locality, Petrified Forest, Arizona, USA; **PVL**, Paleontología de Vertebrados, Instituto ‘Miguel Lillo’, San Miguel de Tucumán, Argentina; **PVSJ,** División de Paleontolog~~i~~a de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina, **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **TMM**, Texas Memorial Museum, Austin, Texas, USA; **TTUP**, Museum of Texas Tech, Lubbock, Texas, USA; **UCMP**, University of California, Berkeley, California, USA; **ULBRA PVT**, Universidade Luterana do Brasil, Coleção de Paleovertebrados, Canoas, Rio Grande do Sul, Brazil; **UMMP**, University of Michigan, Ann Arbor, Michigan, USA; **USNM**, National Museum of Natural History, Smithsonia~~m~~ Institution, Washington, D.C., USA; **VPL**, Vertebrate Paleontology Lab, University of Texas at Austin, Austin, Texas, USA; **YPM**, Yale University, Peabody Museum of Natural History, New Haven, Connecticut, USA; **VRPH**, Sierra College, Rocklin, California, USA; **ZPAL,** Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Warsaw; Poland.

TERMINAL TAXA

The phylogenetic analysis by Nesbitt (2011) is currently the most thorough study of archosauriform relationships. This study utilizes the format used in that study for the listing of terminal taxa and characters to make this work compatible.

Adamanasuchus eisenhardtae Lucas, Spielmann, and Hunt 2007

Holotype – PEFO 34638, partial skeleton including paramedian and lateral osteoderms, several vertebral centra, and a partial femur (Lucas et al., 2007a).

Referred Material – PEFO 35093, osteoderm fragments, nasal fragment; PEFO 36806, osteoderm fragments.

Remarks -- Lucas et al. (2007a) refer a lateral osteoderm (UCMP 126867) to *Adamanasuchus eisenhardtae* without explanation other than noting a 2007 personal communication from A. Heckert. They neither figure nor describe the specimen, but list its provenance as the *Placerias* Quarry near St. Johns, Arizona and attribute it as another Adamanian record of *Adamanasuchus eisenhardtae*. Examination of UCMP 126867 confirms the identification of the element as an aetosaurian lateral plate; however, the specimen was collected from PFV 075 (Karen's Point) in Petrified Forest National Park and not from the *Placerias* Quarry. PFV 075 is in the Martha's Butte beds of the Sonsela Member, which are Revueltian in age (Parker and Martz, 2011), thus this would represent a range extension of this taxon up into the Sonsela Member and into the

Revueltian biozone. This specimen differs from the holotype of *Adamanasuchus eisenhardtae* in possessing an extremely reduced dorsal flange and a dorsal eminence that forms a broadly triangular "spine" that projects dorsally. The outer surface of the lateral flange and the dorsal eminence bear an elongate ridge, which is located very close to the plate margin. Curiously the osteoderm lacks an anterior bar so it cannot be determined if this margin is the anterior or posterior edge. In *Adamanasuchus eisenhardtae*, the lateral osteoderms are more symmetrical with nearly equal lateral and dorsal flanges, and the eminence does not form a projected spine (PEFO 34638). Because of these anatomical differences and the discrepancy in the stratigraphic and locality data, the referral of this specimen to *Adamanasuchus eisenhardtae* is not supported.

PEFO 35093 includes osteoderm fragments that possess the unique surface ornamentation of a faint background, radial pattern, incised by deep randomly developed pits characteristic of *Adamanasuchus eisenhardtae*. An associated fragment of a nasal most likely belongs to the same specimen as it has an identical preservation and no other aetosaur specimens were recovered from the immediate area. Unfortunately the nasal fragment is too incomplete to provide more information. PEFO 36806 is another specimen and consists solely of osteoderm fragments. Both PEFO 35093 and PEFO 36806 were recovered from the upper part of the Blue Mesa Member at about the same stratigraphic horizon as the holotype specimen of *Adamanasuchus eisenhardtae*.

Age – Late Triassic, early to middle Norian, Adamanian (Ramezani et al., 2011; Parker and Martz, 2011).

Occurrence – upper Blue Mesa Member, Chinle Formation, Petrified Forest National Park, Arizona, U.S.A. (Lucas et al., 2007a; Parker and Martz, 2011).

Remarks – Lucas et al. (2007a) named *Adamanasuchus eisenhardtae* for a partial skeleton collected from the Blue Mesa Member (Chinle Formation) in Petrified Forest National Park in 1996 (Hunt, 1998; Parker, 2006). Parker (2006) incorrectly assigned this specimen to *Typothorax antiquum* based on the interpretations made by Hunt (1998) regarding this specimen. In 2010 park staff revisited the type locality and finished the excavation; several paramedian and lateral osteoderms had been covered and left by the original workers and these materials were not included in the original description. The diagnosis provided by Lucas et al. (2007a) does not adequately differentiate *Adamanasuchus eisenhardtae* from other known aetosaurians, in particular from *Calyptosuchus wellesi*; however, key characters found in *Adamanasuchus eisenhardtae* to the exclusion of *Calyptosuchus wellesi* is the strongly sigmoidal lateral edge, that results is a ventrolateral corner of the osteoderm that appears to have been sheared-off (J. Martz, pers. com. 2013), and a triangular patch in the posteromedial corner of the paramedian plate surface that is smooth and devoid of ornamentation. The first character state also occurs in paratypothoracins and the second is found in *Scutarx deltatylus*, except that in the latter taxon the triangular area is strongly raised.

Key References – Lucas et al. (2007a).

Aetobarbakinoides brasiliensis **Desojo, Ezcurra, and Kischlat 2012.**

Holotype – CPE2 168, partial postcranial skeleton (Desojo et al., 2012). A cast of this specimen is in the Petrified Forest National Park (PEFO) collections.

Referred Material – none.

Age – Late Triassic, late Carnian – earliest Norian, *Hyperodapedon* Assemblage Zone (Langer et al., 2007; Martinez et al., 2011).

Occurrence – Sequence 2, Santa Maria Supersequence, Rio Grande Do Sul, Brazil (Desojo et al., 2012).

Remarks – The holotype (CPE2 168) of *Aetobarbakinoides brasiliensis* is a fragmentary postcranial skeleton of a small aetosaurian that was originally referred to *Stagonolepis robertsoni* (=*Aetosauroides* in their hypothesis) by Lucas and Heckert (2001). The lack of open neurocentral sutures in the cervical and dorsal vertebrae suggests that CPE2 168 represents a skeletally mature individual (Irmis, 2007). Despite the fragmentary preservation of the holotype, Desojo and Ezcurra (2011) were able to distinguish this material from that of other South American aetosaurs, based on the presence of discrete vertebral laminae in the dorsal series, a character lacking in taxa such as *Aetosauroides scagliai* and *Neoaetosauroides engaeus*. Furthermore, *Aetobarbakinoides* is the only South American aetosaurian specimen with dorsal vertebrae that bear accessory articular structures (i.e. hyposphene), a feature recognized previously only in desmatosuchines (Parker, 2008b). Determining the phylogenetic position of this taxon is difficult because it is represented almost exclusively by endoskeletal (non-osteoderm) material. A few osteoderms are present, but the surface ornamentation is poorly preserved. Lateral osteoderms, which have been key to phylogenetic placement, are not preserved. Furthermore, the preserved paramedian osteoderms lack their lateral edges, which, if preserved, would have provided information about the medial edges of the lateral osteoderms allowing for the scoring of some characters. Desojo et al. (2012) recovered *Aetobarbakinoides brasiliensis* as the sister taxon of the clade Desmatosuchinae + Typothoracinae; however, Heckert et al. (2015) considered it to be a ‘wildcard’ (unstable) taxon in their analysis and pruned it *a posteriori* from their published tree. It performed as a wildcard taxon in this analysis as well, which is discussed in more detail below.

Key References – Desojo et al. (2012).

Aetosauroides scagliai **Casamiquela 1960**

Holotype – PVL 2073, postcranial skeleton including the majority of the carapace, vertebral column, and sacrum in articulation (Casamiquela, 1961).

Referred Material – see Desojo and Ezcurra (2011).

Age – Late Triassic, Carnian, *Hyperodapedon* Assemblage Zone (Rogers et al., 1993; Furin et al., 2006; Martinez et al., 2011).

Occurrence – Cancha de Bochas Member, Ischigualasto Formation, Argentina; Sequence 2, Santa Maria Supersequence, Rio Grande do Sul State, Brazil (Casamiquela, 1961; Desojo and Ezcurra, 2011).

Remarks – *Aetosauroides scagliai* was originally described by Casamiquela (1960, 1961) based on well-preserved cranial and postcranial material from the lower part of the Ischigualasto Formation of Argentina. Further material was assigned by Casamiquela (1967) who redescribed the specimens in light of the monograph on *Stagonolepis robertsoni* by Walker (1961). Strong similarities have been noted between *Aetosauroides* and *Stagonolepis* as well as *Aetosaurus* and based on element size *Aetosauroides* was considered to be somewhat morphologically transitional between the two European taxa (Casamiquela, 1967). In an unpublished masters thesis, Zacarias (1982) erected a second species of *Aetosauroides* ("*Aetosauroides* subsulcatus") for material from the Upper Triassic of Brazil. All of this material has been briefly redescribed, the majority of it assigned to *Stagonolepis robertsoni* (Lucas and Heckert, 2001; Heckert and

Lucas, 2002). Those authors argued that only superficial differences could be found between all of these specimens and that assignment of the South American material strengthened previously proposed biostratigraphic correlations between Brazil, Argentina, and the U.K., as well as to the southwestern United States. In contrast, Desojo and Ezcurra (2011) assigned the Brazilian material to *Aetosauroides scagliai* based on the presence of well-developed fossae on the lateral sides of the dorsal vertebrae and the exclusion of the maxilla from the external naris in the skull of *Aetosauroides scagliai*, a character first noted by Casimiquela (1967). A phylogenetic analysis recovered *Aetosauroides scagliai* as the sister taxon to all other aetosaurs (Stagonolepididae) (Desojo et al., 2012). A full redescription of the Argentinian material was presented in an unpublished dissertation (Parker, 2014), but this will not be published pending another redescription by Desojo and Ezcurra (J. Desojo, pers. communication, 2014).

The cranial material of *Aetosauroides scagliai* is significant because it exemplifies the plesiomorphic aetosaurian skull condition, optimizing characters such as the exclusion of the maxilla from the external naris, frontals that are wider than the parietals, nasals that taper anteriorly, a large triangular depression present anterior to the frontals, the lack of a 'slipper-shaped' mandible, the lack of a basal swelling in the teeth, and the mediolaterally compressed teeth with recurved tips (Parker, 2014). It demonstrates conclusively that the skull is significantly different from that of *Stagonolepis robertsoni*, *Stagonolepis olenkae*, *Neoaetosauroides engaeus*, and *Calyptosuchus wellesi* and that characters of the osteoderms used to unite these taxa (e.g., Heckert and Lucas 2002) are homoplasious (Desojo and Ezcurra, 2011; Parker 2008b).

Cerda and Desojo (2011) provide details of the osteoderm histology of *Aetosauroides scagliai*, although using referred specimens rather than the holotype. This adds to the increasing understanding of the bone histology of aetosaurians (e.g., Parker et al., 2008; Scheyer et al., 2013). It is possible that once histological features and their relationships with ontogenetic maturity at time of death and potential environmental effects are better known, that histological characters can be incorporated in phylogenetic analyses of the Aetosauria.

Key References – Casimiquela, 1960, 1961, 1967; Heckert and Lucas, 2002; Desojo and Ezcurra, 2011; Cerda and Desojo, 2011; Parker, 2014.

Aetosaurus ferratus **Fraas 1877**

Lectotype – SMNS 5770, specimen XVI (16) (Schoch, 2007).

Referred Material – SMNS 5770, at least 24 specimens recovered in the same block as the lectotype; SMNS 18554, articulated skeleton lacking the skull and pectoral girdle; SMNS 14882, articulated caudal segment; SMNS 12670, dorsal and ventral osteoderms; MCZ 22/92G, partial skull, limb bones and vertebrae, osteoderms; MCSNB 4864, dorsal osteoderms.

Age – Late Triassic, middle Norian to early Rhaetian, Revueltian (Deutsche Stratigraphische Kommission, 2005; Lucas, 2010).

Occurrence – Lower and Middle Stubensandstein, Löwenstein Formation, Germany; Calcare de Zorzino Formation, Italy; Ørsted Dal Member, Fleming Fjord Formation, eastern Greenland (Wild, 1989; Jenkins et al., 1994; Schoch, 2007).

Remarks – The genus *Aetosaurus* originally included two species, *Aetosaurus ferratus* and *Aetosaurus crassicauda*. *Aetosaurus crassicauda* is presently understood to represent a larger specimen of *Aetosaurus ferratus* (Schoch, 2007). Specimens of *Stegomus arcuatus* from eastern North American have been assigned to *Aetosaurus* (Lucas et al., 1998); however, the majority of this material consists of natural molds that do not preserve the surface ornamentation. These specimens are assignable to *Aetosaurus* only on the basis of "aetosaurine" (*sensu* Parker, 2007) synapomorphies such as a sigmoidal lateral margin of the paramedian osteoderms with a pronounced anterolateral projection, as well as their small size. Small osteoderms (e.g., NMMNH P-17165) from the Bull Canyon Formation of New Mexico referred to *Stegomus* (*Aetosaurus*) *arcuatus* by Heckert and Lucas (1998) possess an anterior bar, radial pattern, offset dorsal eminence, and an anterolateral projection, which are "aetosaurine" characters and not diagnostic of a less inclusive taxon Several authors consider the lack of dorsal ornamentation, including a dorsal eminence (boss) in the osteoderms of *Stegomus* (*Aetosaurus*) *arcuatus* to be diagnostic of the taxon (e.g., Heckert and Lucas, 2000; Heckert et al., 2001; Spielmann and Lucas, 2012); however, the lack of ornamentation is because the type and key referred specimens consist solely of natural molds of the ventral surfaces of the osteoderms which are typically smooth and unornamented in aetosaurs.

Purported specimens of *Aetosaurus ferratus* from the Chinle Formation of Colorado (Small, 1998) are now considered to represent a distinct taxon, *Stenomyti huangae* (Small and Martz, 2013). *Aetosaurus* has also been recognized from Greenland and Italy. The Greenland material consists of a partial skull, postcranial skeleton and osteoderms (MCZ 22/92G; Jenkins et al., 1994). This skull possesses the following characteristics of *Aetosaurus ferratus*; an anteroposteriorly short jugal, a round supratemporal fenestra; and an antorbital fossa that covers the majority of the lacrimal (Schoch, 2007). The Italian material (MCSNB 4864) consists of a short series of articulated dorsal paramedian and lateral osteoderms that possess an identical surface ornamentation to *Aetosaurus ferratus* (Wild, 1989). This specimen is significant as it was recovered from marine sediments of Norian age and represents a potential tie point to the marine biostratigraphic record for the Late Triassic (Lucas, 1998a, Irmis et al., 2010).

In summary, *Aetosaurus ferratus* is presently known from Greenland, Germany, and Italy, and purported North American occurrences cannot be substantiated (Schoch, 2007; Small and Martz, 2013). For this study *Aetosaurus ferratus* is scored only from the German lectotype and referred material.

Key References – Wild, 1989; Jenkins et al., 1994; Schoch, 2007.

Apachesuchus heckerti **Spielmann and Lucas 2012**

Holotype – NNMNH P-31100, left dorsal paramedian osteoderm.

Referred material – NMMNH P-63427, left cervical paramedian osteoderm; NMMNH P-63426, right caudal paramedian osteoderm. Both of these specimens were originally included in NMMNH P-31100 (Heckert et al., 2001; Spielmann and Lucas, 2012:fig. 70e), but have been renumbered. Spielmann and Lucas (2012) also report that much more complete material of this taxon, including postcrania, is currently under study by Axel Hungerbühler at the Mesalands Dinosaur Museum in Tucumcari, New Mexico. This new material is also from the Redonda Formation of New Mexico; however, the new material referable to *Apachesuchus heckerti* only consists of a few more paramedian osteoderms, whereas the rest of the material is actually referable to *Redondasuchus rineharti* (J. Martz, pers. comm., 2013).

Age – Late Triassic, late Norian-Rhaetian, Apachean (Spielmann and Lucas, 2012).

Occurrence – Quay Member, Redonda Formation, Dockum Group, New Mexico, U.S.A (Spielmann and Lucas, 2012).

Remarks – The holotype and paratype (referred) osteoderms were recovered in a microvertebrate assemblage found within a very large phytosaur skull and were originally assigned to *Neoaetosauroides* sp. because of the lack of surface ornamentation of the paramedian osteoderms (Heckert et al., 2001). However, *Neoaetosauroides* does have a surface orientation of radial grooves and ridges and therefore NMMNH material cannot be assigned to that taxon. The lack of surface ornamentation in the type material of *Apachesuchus heckert*i appears to be a real feature and is considered an autapomorphy of the taxon (Spielmann and Lucas, 2012; J. Martz, pers. comm., 2013). *Apachesuchus heckerti* is considered to possess a low width/length ratios (> 0.3) of the paramedian osteoderms; which was obtained by comparing the length of the lateral edge to the total plate length (Heckert et al., 2001; Spielmann and Lucas, 2012). However, the lateral edge of NMMNH P-31100 is greatly expanded anteroposteriorly than the rest of the osteoderm strongly skewing this ratio. The length at the center of the osteoderm is 32 mm, compared to an overall width of 104 mm. This provides a width/length ratio of 3.25, compared to the ratio of 2.5 provided by Spielmann and Lucas (2012). It is important to standardized areas of measurements for determining ratios of aetosaur osteoderms as simply using maximum length can skew results in plates with abnormal shapes. This is also true for osteoderms with elongate anterolateral processes of the anterior bars (e.g., *Scutarx deltatylus*). In these cases osteoderm lengths should be taken from the main osteoderm body and not from the anterior bar. Furthermore, an unnumbered referred anterior dorsal paramedian osteoderm in the Mesalands Community College Dinosaur Museum (MCCDM) collection (field number 20080618RET002RRB) has a width of 110 mm and a median length of 28 mm for a W/L ratio of 3.92. This is comparable to typothoracin aetosaurs such as *Typothorax coccinarum* (Long and Murry, 1995; Heckert et al., 2010).

Key References – Heckert et al., (2001); Spielmann and Lucas (2012).

Calyptosuchus wellesi **Long and Ballew 1985**

Holotype – UMMP 13950, articulated dorsal carapace from the posterior dorsal and caudal regions, associated with a portion of the vertebral column and the sacrum (Case, 1932; Long and Murry, 1995).

Referred Material – UMMP 7470, two dorsal paramedian osteoderms, three dorsal vertebrae, mostly complete, articulated sacrum; UCMP 27225, paramedian, lateral, and ventral osteoderms, partial right dentary. Numerous specimens from the *Placerias* Quarry from the UCMP and the MNA collections, as well as specimens from Petrified Forest National Park also can be referred to *Calyptosuchus wellesi* (Long and Murry, 1995; Parker, 2014).

Age – Late Triassic, early-middle Norian, early Adamanian (Ramezani et al., 2011, 2014; Parker and Martz, 2011).

Occurrence – upper Blue Mesa Member, Chinle Formation, Arizona, U.S.A.; Tecovas Formation, Dockum Group, Texas, U.S.A (Long and Murry, 1995; Parker and Martz, 2011).

Remarks – Case (1932) described a posterior portion of a carapace and associated pelvis and vertebral column of what he believed to be a phytosaur from the Upper Triassic of Texas. Although he discussed possible taxonomic affinities he was thoroughly perplexed by the material and thus did not assign the specimen to an existing taxon or coin a new taxonomic name. Mainly this is because of the common association of aetosaurian osteoderms with phytosaur remains (e.g., *Nicrosaurus kapffi*, Case, 1929) and because the osteoderms of UMMP 13950 possessed a radial surface ornamentation more similar to the osteoderm material then assigned to

"*Phytosaurus*" *kapffi* (now the holotype of the aetosaurian *Paratypothorax andressorum* Long and Ballew, 1985). This is unlike the surface ornamentation found in the other aetosaurian Case was familiar with *Desmatosuchus spurensis* (Case, 1922). Indeed, Case (1932) tentatively suggested that UMMP 13950 may belong to the genus *Phytosaurus*. Gregory (1953a) recognized that the specimen was probably more closely related to *Typothorax* than to phytosaurs and hence most likely a pseudosuchian (aetosaur), but still considered the purported close similarity of the rectangular osteoderms with those assigned to some phytosaurs to be problematic for taxonomic resolution of the material.

This problem was finally resolved by Long and Ballew (1985) who correctly determined that all of the material with broad, rectangular osteoderms was referable to aetosaurians. Those authors also listed UMMP 13950 as the holotype of a new genus, *Calyptosuchus wellesi*. They did not redescribe Case's specimen, but instead discussed the new taxon in terms of referred material from the Triassic of Arizona. The most recent description of the taxon is by Long and Murry (1995) who mainly described referred material from the *Placerias* Quarry of Arizona. Elsewhere I have questioned the referrals of material to *Calyptosuchus wellesi* by Long and Murry (1995) mainly because of the recognition that the cervical lateral osteoderms assigned to *Calyptosuchus wellesi* by Long and Ballew (1985) and Long and Murry (1995) actually belong to a paratypothoracin aetosaur demonstrating the presence of a third aetosaur taxon in the *Placerias* Quarry (Parker, 2005a, 2007).

Parker (2014) carefully sorted the *Placerias* Quarry material based on field numbers and use resulting associations as well as apomorphic comparisons to test these assignments. Referred elements of *Calyptosuchus wellesi* were redescribed and these referred specimens, as well as the holotype, are used to and score that taxon in this phylogenetic analysis. This anatomical work in association with detailed biostratigraphic work of the Chinle Formation (Parker and Martz, 2011) has also determined that *Calyptosuchus wellesi* is presently restricted to the upper part of the Blue Mesa Member and that specimens of *Calyptosuchus* noted from the Sonsela Member (e.g., Parker and Martz, 2011) belong to a new taxon, *Scutarx deltatylus*.

Key References – Case, 1932; Long and Ballew, 1985; Long and Murry, 1995; Parker, 2014.

Coahomasuchus kahleorum **Heckert and Lucas 1999**

Holotype – NMMNH P-18496, much of an articulated, but crushed skeleton (Heckert and Lucas, 1999).

Referred Material – TMM 31100-437, partial skull, paramedian, lateral, and ventral osteoderms, vertebrae, limb, and girdle material (Murry and Long, 1996; this study); NCSM 23168, much of a carapace (Heckert et al., 2015).

Age – Late Triassic, Carnian?, Otischalkian (Lucas, 2010).

Occurrence – Colorado City Formation, Dockum Group, west Texas, U.S.A.; Pekin Formation, Newark Supergroup, North Carolina, U.S.A (Heckert and Lucas, 1999; Heckert et al., 2015).

Remarks – The holotype of *Coahomasuchus kahleorum* is distinctive, but poorly preserved, consisting of a flattened carapace concealing the majority of the vertebrae, the posteroventral corner of the skull, the posterior portion of the mandible, and a poorly preserved braincase, as well as articulated limb and girdle material (Heckert and Lucas, 1999; Desojo and Heckert, 2004). Past phylogenetic analyses have recovered *Coahomasuchus kahleorum* as the sister taxon of *Typothorax coccinarum* and *Redondasuchus reseri* (Harris et al., 2003 correction of the Heckert and Lucas, 1999 dataset), as the sister taxon of an unresolved clade containing *Aetosauroides*, *Calyptosuchus*, *Aetosauroides*, and *Aetosaurus* (Parker, 2007), and in an unresolved position closer to the base of Stagonolepididae (Desojo et al., 2012). Moreover, the latter authors pruned *Coahomasuchus* from their final tree to achieve better resolution, thus the phylogenetic relationships of this taxon are far from resolved. However, a more recent analysis by Heckert et al. (2015), utilizing a modified version of the dataset in Parker (2007) and Desojo et al. (2012), recovered *Coahomasuchus* as a non-stagonolepidid aetosaur at the base of Aetosauria. In this analysis *Coahomasuchus kahleorum* is coded from the holotype as well as a newly referred specimen from the Dockum Group of Texas (TMM 31100-437) formally referred to as the 'carnivorous form' (Murry and Long, 1996), which was recovered from the same geographical area and stratum as the type specimen (Lucas et al., 1993). Fraser et al. (2006) documented the first occurrence of *Coahomasuchus* in the Pekin Formation of North Carolina providing a biostratigraphic correlation with the lower part of the Dockum Group of west Texas.

It was suggested that the holotype of *Coahomasuchus kahleorum* may represent a skeletally immature individual (Parker, 2003). However, histological sampling of the referred specimen TMM 31100-437, which is in the same size class, indicates that TMM 31100-437 is close to skeletal maturity (S. Werning, pers. comm., 2014). These findings will be presented elsewhere.

Key References – Heckert and Lucas (1999); Desojo and Heckert (2004).

***Desmatosuchus spurensis* Case 1920**

Holotype – UMMP 7476, skull, nearly complete carapace, articulated cervical and dorsal vertebral column, ilium (Case, 1922).

Referred Material – see Parker, 2008b.

Age – Late Triassic, early to middle Norian, Adamanian (Ramezani et al., 2011, 2014; Parker and Martz, 2011).

Occurrence – Tecovas Formation, Dockum Group, Texas, U.S.A., Los Esteros Member, Santa Rosa Formation, Dockum Group, New Mexico, U.S.A., upper Blue Mesa Member, Chinle Formation, Arizona, U.S.A (Long and Murry, 1995; Parker, 2008b).

Remarks – First described from much of a carapace, and associated vertebral column as well as a skull, *Desmatosuchus spurensis* is a well-known aetosaurian from the Upper Triassic of the southwestern United States. Despite this confusion exists regarding characters of the dorsal armor for referral of specimens. For example all of the specimens listed by Long and Ballew (1985) from Petrified Forest National Park actually pertain to paratypothoracins and the osteoderm of *Desmatosuchus haplocerus* figured by Lucas and Connealy (2008:26) for the Dawn of the Dinosaurs exhibit at the New Mexico Museum of Natural History and Science is actually referable to *Calyptosuchus wellesi*.

Gregory (1953a) synonymized *Desmatosuchus spurensis* with *Episcoposaurus haplocerus*, a form described by Cope (1892), and the taxon was known as *Desmatosuchus haplocerus* for several decades, until it was determined that *Episcoposaurus haplocerus* was actually a *nomen dubium* (Parker, 2008b; 2013) although this has not been accepted by all workers (e.g., Heckert et al., 2012). New material from the Chinle Formation of Arizona demonstrated that previous carapace reconstructions for *Desmatosuchus spurensis* were erroneous and the body was broader than previous believed (Parker, 2008b).

Limb and pectoral girdle for *Desmatosuchus spurensis* is not known from the two best preserved specimens (UMMP 7476, MNA V9300), but Long and Murry (1995) assigned isolated material from the *Placerias* Quarry to the taxon, which has been utilized for studies including bone histology (de Ricqlés et al., 2003). Unfortunately Long and Murry (1995) did not discuss the evidence for these referrals, which have been questioned (Parker, 2005a, 2008b); however, utilizing field numbers from the *Placerias* Quarry it may possible to refer some of this material to *Desmatosuchus spurensis*. For this analysis *Desmatosuchus spurensis* is coded from UMMP 7476 and MNA V9300.

Key References – Case, 1920, 1922; Long and Ballew, 1985; Long and Murry, 1995; Parker, 2008b.

Desmatosuchus smalli Parker 2005

Holotype – TTU P-9024, almost complete skull and right mandible, partial pelvis, femora, nearly complete cervical armor and numerous plates from the rest of the carapace (Parker, 2005b).

Referred Material – see Parker (2005b) and Martz et al. (2013).

Age – Late Triassic, mid-Norian, latest Adamanian and possibly earliest Revueltian (Ramezani et al., 2011; Martz et al., 2013).

Occurrence – Middle section of the Cooper Canyon Formation, Dockum Group, Texas, U.S.A. ; ?Martha's Butte beds, Sonsela Member, Chinle Formation, Arizona, U.S.A (Parker, 2005b; Martz et al., 2013).

Remarks – Small (1985, 2002) described new material of *Desmatosuchus* from the Cooper Canyon Formation of Texas. Although he noted differences in the cranial material of the new material from the holotype of *Desmatosuchus spurensis* (UMMP 7476), he did not feel they were of taxonomic significance. In a revision of the genus *Desmatosuchus*, significant differences in the lateral armor were noted between the Cooper Canyon specimens and the type of *Desmatosuchus spurensis* (Parker, 2003). Combined with the cranial differences noted by Small

(2002) the Cooper Canyon Formation material was assigned to a new species (Parker, 2005b). Further comments regarding this taxon including a novel reconstruction of the lateral cervical armor were provided by Martz et al., (2013). One of the problems in utilizing the non-osteoderm postcranial material of *Desmatosuchus smalli* is that some of it may actually pertain to an undescribed specimen of *Paratypothorax* from the quarry (Martz, 2008). A detailed apomorphy-based study of the aetosaurian material from the Post Quarry is needed along with field note reinvestigation to clarify some of the taxonomic assignments of the material (Martz, 2008).

Other than the Texas material, *Desmatosuchus smalli* is known from only one single referred lateral osteoderm from the Chinle Formation of Arizona (MNA V697), which had been assigned to *Desmatosuchus* by Long and Ballew (1985) as a cervical lateral osteoderm. MNA V697 actually represents a dorsal lateral osteoderm and is assigned to *Desmatosuchus smalli* based on the ventrally recurved spine tip, which is an autapomorphy of *Desmatosuchus smalli* and does not occur in *Desmatosuchus spurensis* (Parker, 2005b). Although MNA V697 is listed as originating from a locality in the upper part of the Sonsela Member near Petrified Forest National Park (Long and Ballew, 1985), the locality data for this specimen are ambiguous. However, if correct this would represent the only Revueltian occurrence of *Desmatosuchus* (Parker and Martz, 2011).

The holotype of *Desmatosuchus* (=*Episcoposaurus*) *haplocerus* (ANSP 14688; Cope, 1892) consists chiefly of lateral and paramedian osteoderms of the cervical and anterior dorsal regions (Gregory, 1953a, Parker, 2013). Unfortunately the tips of the spines on all of the dorsal lateral osteoderms are broken away so the material cannot be differentiated between *Desmatosuchus spurensis* and *Desmatosuchus smalli*. Interestingly, the shape of the cervical lateral osteoderms as well as the ornamentation of the dorsal paramedian osteoderms are more reminiscent of *Desmatosuchus smalli* rather than *Desmatosuchus spurensis*, but the data are not conclusive and therefore *Desmatosuchus haplocerus* is considered a *nomen dubium* (Parker, 2008b, 2013).

Key References – Small, 1985, 2002; Parker, 2005b; Martz et al., 2013.

Longosuchus meadei **(Sawin 1947)**

Lectotype – TMM 31185-84b, skull and much of a postcranial skeleton (Sawin, 1947). See Parker and Martz (2010) for detailed discussion of the status of the type materials.

Referred Material – TMM 31185-84a, partial skull and postcranial skeleton. See Long and Murry (1995) for a complete list.

Age – Late Triassic, ?Carnian, Otischalkian (Lucas, 2010).

Occurrence – Colorado City Formation, Dockum Group, Texas, U.S.A (Hunt and Lucas, 1990).

Remarks – The Works Progress Administration program in the 1930s made vast collections of vertebrate fossils from a series of quarries in strata of the Dockum Group in Howard County, Texas. This included several skeletons of an aetosaurian that Sawin (1947) described as a new species of *Typothorax*, *Typothorax meadei*. Several subsequent authors recognized the distinctiveness of this material (Long and Ballew, 1985; Small, 1989; Murry and Long, 1989) and the species was placed in a new genus*, Longosuchus*, by Hunt and Lucas (1990). Sawin’s original description is thorough but affected by a lack of good comparative material as well as a poor historical understanding of the taxonomic make-up of the Aetosauria. Thus he incorrectly reconstructed the incomplete lower jaw and pelvis, which confused aetosaur in-group relationships until these details were corrected by Walker (1961).

Most of the Otis Chalk material remains unprepared and numerous specimens, including partial skeletons, referable to *Longosuchus meadei* are in the Vertebrate Paleontology Lab (VPL) collections at the University of Texas (Austin) awaiting preparation.

An isolated fragment of a paramedian plate from the Salitral Shale (Chinle Formation) of New Mexico, assigned to *Longosuchus meadei* by Hunt and Lucas (1990), possesses a beveled posterior edge and a radial ornament pattern and is more likely referable to Paratypothoracini, in particular *Tecovasuchus* (Irmis, 2008). Lateral osteoderms from the Argana Group of Morocco assigned to *Longosuchus meadei* by Lucas (1998b) appear to also represent a paratypothoracin as they are strongly dorsoventrally compressed and slightly recurved (Parker and Martz, 2010). Unfortunately this cannot be tested as these specimens have been reported as lost (S. Nesbitt, pers. comm. 2013). Character state scorings for this study were made solely using the TMM material.

Key References – Sawin, 1947; Hunt and Lucas, 1990; Long and Murry, 1995; Parker and Martz, 2010.

***Lucasuchus hunti* Long and Murry 1995**

Holotype – TMM 31100-257, posterior dorsal paramedian osteoderm (Long and Murry, 1995).

Referred Material – see Parker and Martz (2010) and Long and Murry (1995).

Age – Late Triassic, Carnian?, Otischalkian (Lucas, 2010).

Occurrence – Colorado City Formation, Dockum Group, Texas, U.S.A.; Pekin Formation, Newark Supergroup, North Carolina, U.S.A (Long and Murry, 1995; Parker and Martz, 2010).

Remarks – Long and Murry (1995) recognized the presence of two distinct large aetosaurian morphotypes in material from the Otis Chalk quarries in Howard County, Texas, the first being *Longosuchus meadei* and a second for which they coined a new taxon, *Lucasuchus hunti*. Sawin (1947) had also recognized the presence of this second aetosaurian, which he erroneously assigned to *Typothorax coccinarum*. Hunt and Lucas (1990) overlooked Sawin's (1947) separation of the material when they reassigned all of the material to *Longosuchus meadei*. Separated out again by Long and Murry (1995), the presence of two distinct taxa was disputed by some workers (e.g., Heckert and Lucas, 1999, 2000) until Parker and Martz (2010) presented the differences in greater detail (Heckert et al., 2015).

The holotype of *Lucasuchus hunti* is a single paramedian plate, but Long and Murry (1995) assigned numerous postcranial elements to the taxon. However, lack of preparation of much of this material, questions regarding associated with apomorphic osteoderms, as well as apparent similarities with *Longosuchus meadei* makes many of these referrals questionable. Nonetheless there is still much unprepared material at the VPL that is almost certainly represents *Lucasuchus hunti*. A recently prepared partial skull (TMM 31100-531) from Howard County, Texas differs in some ways from the lectotype skull of *Longosuchus meadei* and could represent *Lucasuchus hunti* (Martz and Parker, unpublished data).

Osteoderms previously referred to *Desmatosuchus* and *Longosuchus* from the Pekin Formation of North Carolina actually pertain to *Lucasuchus* providing an important biostratigraphic correlation (Parker and Martz, 2010; Heckert et al., 2015).

Key References – Long and Murry, 1995; Parker and Martz, 2010; Heckert et al., 2015.

***Gorgetosuchus pekinensis* Heckert, Schneider, Fraser, and Webb 2015**

Holotype – NCSM 21723, a large portion of the cervical and anterior dorsal carapace.

Referred Material – none.

Age – Late Triassic, Carnian?, Otischalkian (Huber et al., 1993).

Occurrence – Upper portion of the Pekin Formation, Newark Supergroup, North Carolina, U.S.A. (Heckert et al., 2015).

Remarks – The holotype of *Gorgetosuchus pekinensis* (NCSM 21723) consists solely of the anterior portion of the dorsal carapace of a desmatosuchine aetosaur. Similar in overall anatomy to *Longosuchus meadei* and *Lucasuchus hunti*, *Gorgetosuchus pekinensis* differs from these two taxa, and all other desmatosuchines, mainly in the possession of cervical paramedian osteoderms that are wider than long.

Key References – Schneider et al., 2011; Heckert et al., 2015.

***Neoaetosauroides engaeus* Bonaparte 1969**

Holotype – PVL 3525, skull and postcranial skeleton (Bonaparte, 1969).

Referred Material – see Desojo and Báez (2007).

Age – Late Triassic, middle Norian, early Revueltian (Santi Malnis et al., 2011; Martinez et al., 2013).

Occurrence – Upper part of the Las Colorados Formation, Argentina (Desojo and Báez, 2005). Lucas (1998a) considered the Los Colorados Formation equivalent to his Apachean 'Land Vertebrate Faunachron' and therefore Rhaetian or at least latest Norian based on the presence of sauropodomorph dinosaurs and crocodyliform pseudosuchians. However, recent reexamination of strata in the Ischigualasto Basin, including a detailed paleomagnetic study, suggests instead that the vertebrate bearing portion of the Los Colorados may in fact be equivalent to the upper portion of the Sonsela Member of the Chinle Formation and thus Revueltian in age (Santi Malnis et al., 2011; Martinez et al., 2013).

Remarks – The holotype of *Neoaetosauroides engaeus* was diagnosed by Bonaparte (1969) and first described in detail by Bonaparte (1972). Poorly understood for the purpose of prior phylogenetic analyses the holotype and several referred skulls were recently redescribed by Desojo and Báez (2005, 2007). Heckert and Lucas (2000) considered the paramedian osteoderms almost completely devoid of ornamentation and this lack of ornamentation to be an autapomorphy of the taxon. However, personal examination of the type specimens shows that *Neoaetosauroides engaeus* possesses a clear radial ornamentation of the dorsal osteoderms (also see Desojo and Báez, 2005). Indeed, the ornamentation is indistinguishable from that of the Ischigualasto taxon *Aetosauroides scagliai*. Portions of the holotype carapace are devoid of ornamentation, but this is clearly the result of overpreparation of the material. Nonetheless, three small osteoderms from the Redonda Formation (Dockum Group) of New Mexico were assigned to *Neoaetosauroides* based upon a lack of distinct ornamentation (Heckert et al., 2001). These osteoderms subsequently became the holotype of a new taxon *Apachesuchus heckerti* (Spielmann and Lucas, 2012). Character state scorings for *Neoaetosauroides engaeus* are from the type and referred materials.

Key References – Bonaparte, 1969, 1972; Desojo and Báez, 2005, 2007.

***Paratypothorax andressorum* Long and Ballew 1985**

Holotype – SMNS unnumbered, left dorsal paramedian osteoderm (labeled L18 on red sticker) (Long and Ballew, 1985).

Paratypes – SMNS unnumbered, partial disarticulated carapace that includes the holotype osteoderm.

Referred Material – NHMUK R38070, posterior dorsal vertebra (Meyer, 1865:pl. XXVII, figs. 1-3); NHMUK R38083, left dorsal paramedian osteoderm; NHMUK R38085, partial right dorsal paramedian osteoderm (Meyer, 1865:pl. XXVIII, figs. 4-6); NHMUK R38086, partial right paramedian osteoderm; NHMUK R38087, pathologic left mid-caudal paramedian osteoderm (Meyer, 1865:pl. XXVIII, figs. 7-9; NHMUK R38090, right dorsal paramedian osteoderm, partial left dorsal paramedian osteoderm, three partial right paramedian osteoderms, partial left lateral osteoderm, left lateral osteoderm, two partial paramedian osteoderms; SMNS 3285, partial paramedian osteoderm; SMNS 2958, three pathologic paramedian osteoderms (Lucas, 2000); SMNS 4345 left dorsal lateral osteoderm; SMNS 4386, right dorsal lateral osteoderm (Meyer, 1861: pl. XLIII, fig. 1). ; SMNS 5721 right paramedian osteoderm (Meyer, 1865: Pl. XXVIII, figs. 1-3); YPM 3694, right dorsal lateral osteoderm (Gregory, 1953b).

Age – Late Triassic, Norian, Revueltian (Deutsche Stratigraphische Kommission, 2005; Lucas, 2010).

Occurrence – Lower Stubensandstein, Löwenstein Formation, Baden-Württemberg, Germany (Long and Ballew, 1985).

Remarks – The SMNS collections possess numerous osteoderms including much of what appears to be a carapace of a single individual that have had a confusing taxonomic history. The osteoderms were collected with and considered to belong to the phytosaur *Nicrosaurus* (=*Belodon* = *Phytosaurus*) until the mid-1980s (Long and Ballew, 1985). This belief caused significant confusion regarding the taxonomy of phytosaur and aetosaur material (Case, 1932; Gregory, 1962; Gregory and Westphal, 1969). The issue was finally ~~sorted out~~ when Long and Ballew (1985) recognized that all of the broad rectangular osteoderms belonged to aetosaurs and coined the name *Paratypothorax addressed* for the German osteoderms originally assigned to *Nicrosaurus*. The species epithet was correctly amended to *Paratypothorax andressorum* by Lucas and Heckert (1996). Long and Ballew (1985) also noted material from southwestern North America that is referable to *Paratypothorax* although they were unsure that it represented the same species as the European material. This has led to two views regarding the assignment of the North American material; 1) that it is referable to *Paratypothorax andressorum* (Hunt and Lucas, 1992; Heckert and Lucas, 2000; Lucas et al., 2006b), or that it may represent a new taxon (Long and Ballew, 1985; Long and Murry, 1995). This is not yet resolved and I treat them here as two separate taxa.

The German material has never actually been fully described and the present concept of *Paratypothorax* (*sensu* Long and Murry, 1995) is actually based on the referred North American material. There is also some confusion regarding the type specimens of *Paratypothorax andressorum*, with some workers treating a well preserved carapace (SMNS unnumbered) as the holotype or as a syntype series for the taxon (e.g., Hunt and Lucas, 1992, Lucas et al., 2006b) However, Long and Ballew (1985:57) clearly identify a single osteoderm as the holotype so the other osteoderms in this specimen can be no more than paratypes (Heckert and Lucas, 2000).

An impression of a partial dorsal paramedian osteoderm (MCZ field No. 23/92G) from Greenland was assigned to *Paratypothorax andressorum* (Jenkins et al., 1994). Although the specimen clearly possesses a raised anterior bar, radial pattern of pits and grooves, a dorsal eminence that contacts the posterior osteoderm margin, characteristic for paratypothoracins, the beveled posterior edge delineated by a distinct ridge is not a clear autapomorphy of *Paratypothorax andressorum* and thus this specimen should be assigned to Paratypothoracini (Martz and Small, 2006; Desojo et al., 2013). I have not examined the other three osteoderms mentioned by Jenkins et al. (1994) and assigned to *Paratypothorax andressorum*.

Key References – Long and Ballew, 1985.

***Paratypothorax* sp.**

Referred Material – PEFO 3004, associated osteoderms and vertebrae from the posterior dorsal and anterior caudal regions (Long and Murry, 1995); FMNH PR1610, partial paramedian osteoderm (same specimen as PEFO 3004); DMNH 9942; partial postcranial skeleton (Long and Murry, 1995); VRPH2, numerous paramedian and lateral osteoderms; see Martz et al. (2013) for additional specimens.

Age – Late Triassic, Adamanian-Revueltian, mid-Norian (Ramezani et al., 2011; Parker and Martz, 2011).

Occurrence – Chinle Formation, Arizona and New Mexico, U.S.A.; Dockum Group, Texas, U.S.A (Long and Murry, 1995; Parker and Martz, 2011; Martz et al., 2013).

Remarks – the presence of *Paratypothorax* material in North America was first recognized by Long and Ballew (1985) although they were unsure of its exact relationship with the German material they named *Paratypothorax andressorum*. Since that time numerous specimens referable to *Paratypothorax* sp. or Paratypothoracini have been collected from the Upper Triassic Chinle Formation and Dockum Group (see Long and Murry, 1995; Parker and Martz, 2011; Martz et al., 2013 for lists). This includes lateral osteoderms from the *Placerias* Quarry of

Arizona that were identified by Long and Ballew (1985) as cervical laterals of *Calyptosuchus wellesi* (Parker, 2005a). The best preserved specimen (PEFO 3004) is an associated set of posterior dorsal and anterior caudal osteoderms and vertebrae of a single individual from the Chinle Formation of Arizona. First mentioned by Long and Ballew (1985), but described by Hunt and Lucas (1992), the latter authors assigned PEFO 3004 to *Paratypothorax andressorum*. This assignment was followed by Heckert and Lucas (2000) and Lucas et al. (2006b). However, differences between the North American and European material were noted by Long and Murry (1995) based on a specimen from the Dockum Group of Texas (DMNH 9942). Therefore the North American material is treated separately for this study. *Paratypothorax* sp. is known almost solely from osteoderms and vertebrae (Hunt and Lucas, 1992; Long and Murry, 1995). However, DMNH 9942 contains some forelimb material (Long and Murry, 1995). Long and Murry (1995) also questionably referred an ilium from the Post Quarry of Texas to the taxon, but this assignment is ambiguous. Martz et al. (2013) figure a fibula (TTU P-09416) they assign to *Paratypothorax* sp. A dentary of *Paratypothorax* was mentioned by Small (1989); however, the specimen is now considered a lateral osteoderm (Martz et al., 2013). It is possible that cranial material referred by Small (2002) to *Desmatosuchus* actually represents *Paratypothorax* sp. (Martz et al., 2013), but this has not yet been fully demonstrated.

Key References – Hunt and Lucas, 1992; Small, 1989; Long and Ballew, 1985; Long and Murry, 1995; Martz et al., 2013.

Polesinesuchus aurelioi **Roberto-Da-Silva, Desojo, Cabriera et al. 2014**

Holotype—ULBRA PVT003, parietal and braincase fragments, much of a postcranial skeleton (Roberto-da-Silva et al., 2014).

Age – Late Triassic, late Carnian – earliest Norian, *Hyperodapedon* Assemblage Zone (Langer et al., 2007; Martinez et al., 2011).

Occurrence – Sequence 2, Santa Maria supersequence, Rio Grande Do Sul, Brazil (Desojo et al., 2012).

Remarks— *Polesinesuchus aurelioi* was erected for mainly the endoskeletal material of a skeletally immature aetosaurian from the Upper Triassic of Brazil (Roberto-da-Silva et al., 2014). The taxon was not diagnosed by any recognized autapomorphies, but rather from a unique combination of characters that differentiates it from all known South American aetosaurians. Overall the material is most similar to that of *Aetosauroides scagliai*, but lacks the deep lateral fossae found in the cervical and dorsal vertebrae of that taxon. The vertebrae of *Polesinesaurus aurelioi* are notable in that they appear to lack vertebral laminae, which may be an autapomorphy of the taxon. However, the laterally expansive prezygapophyses listed as a defining character of the taxon may actually represent prezygadiapophyseal laminae (*sensu* Wilson, 1999), as these laminae form a similar structure in the presacral vertebrae of *Scutarx deltatylus* (PEFO 31217). The skeletally immature status of the material is problematic because our present understanding of character variation and transformation through ontogeny is poor and these unique characteristics may simply be the result of the ontogenetic immaturity at time of death. Indeed, *Polosinesuchus aurelioi* appears to represent the well-preserved, but relatively unremarkable remains of a skeletal immature aetosaurian. Future histological studies of this taxon and others across will provide needed information on the timing of the appearance of key osteological landmarks in aetosaurian clades.

A phylogenetic analysis recovered *Polesinesuchus* as the sister taxon to *Aetobarbakinoides* in a clade that is sister taxon to Desmatosuchinae plus Typothoracinae, but this could be an artifact of missing data, especially from the paramedian and lateral osteoderms (Roberto-da-Silva et al., 2014).

Key Reference – Roberto-da-Silva et al., 2014.

Postosuchus kirkpatricki Chatterjee 1985

Holotype – TTU P-9000, almost complete skull and partial skeleton (Chatterjee, 1985).

Paratype – TTU P-9002, almost complete skull and partial skeleton (Chatterjee, 1985).

Age – Late Triassic, early to middle Norian, Adamanian (Martz et al., 2013).

Occurrence – Cooper Canyon Formation, Dockum Group, Texas, U.S.A (Martz et al., 2013).

Remarks – *Postosuchus kirkpatricki* is a well-known rauisuchid archosaurs represented by excellent material from the Post Quarry of Texas. The type materials were recently redescribed in detail by Weinbaum (2011, 2013).

Key References – Chatterjee, 1985; Weinbaum, 2011, 2013.

Redondasuchus rinehardti Spielmann, Hunt, Lucas, and Heckert 2006

Holotype – NMMNH P-43312, partial right dorsal paramedian osteoderm (Spielmann et al., 2006).

Referred Material – see Spielmann et al., 2006. With permission I also score unpublished material currently under study by Jeffrey Martz and Axel Hungerbühler at Mesalands Dinosaur Museum in Tucumcari, New Mexico.

Age – Late Triassic, late Norian to Rhaetian, Apachean (Spielmann and Lucas, 2012).

Occurrence – Redonda Formation, Dockum Group, New Mexico, U.S.A (Spielmann and Lucas, 2012).

Remarks – A fair amount of aetosaurian osteoderm material has been recovered from the Upper Triassic Redonda Formation of New Mexico, most of which appears to be from at least one typothoracine. *Redondasuchus reseri* was named by Hunt and Lucas (1991) for a small typothoracine aetosaurs that reportedly lacked lateral osteoderms, and instead used flexion of the dorsal paramedians to cover the flank of the animal (Heckert et al., 1996). However, the holotype osteoderm was interpreted backwards by those authors, and there is no evidence that *Redondasuchus reseri* differed from all other aetosaurs in lacking lateral osteoderms (Martz, 2002). Furthermore, Martz (2002) could not distinguish the osteoderms of *Redondasuchus reseri* from those of *Typothorax coccinarum* in any characteristic other than size. Spielmann et al. (2006) argued that *Redondasuchus reseri* was indeed distinct and named a second species, *Redondasuchus rineharti*, for isolated osteoderms and a proximal femur head from a larger aetosaurian. Those authors differentiated the new species from *Redondasuchus reseri* based on larger size and the presence of a dorsal eminence. This is problematic as no ontogenetic study has been made for *Redondasuchus* to refute the idea that *Redondasuchus reseri* is simply a skeletally immature specimen of another typothoracine. Moreover, in *Typothorax coccinarum*, the more anterior dorsal paramedian osteoderms lack dorsal eminences. Furthermore, strong flexion of paramedian osteoderms occurs in several aetosaur taxa including *Typothorax coccinarum* (PEFO 23388), *Paratypothorax* sp. (PEFO 3004), *Sierritasuchus macalpini* (UMMP V60817), and *Calyptosuchus wellesi* (UCMP 136744). Thus *Redondasuchus reseri* lacks clear autapomorphies or even a unique combination of characters and I do not include it in this study pending future reexamination. However, there are some fundamental differences between *Redondasuchus rineharti* and *Typothorax coccinarum* including the more closely packed and deep pits in *Redondasuchus rineharti*, as well as the oblong pits in the transverse trough posterior to the anterior bar and I include it in the present analysis, including scorings from new undescribed material from New Mexico (J. Martz, pers. comm. 2013).

Key References – Spielmann et al., 2006; Spielmann and Lucas, 2012.

Revueltosaurus callenderi Hunt 1989

Holotype – NMMNH P-4957, nearly complete premaxillary tooth.

Referred Material – PEFO 33787, partial skeleton and skull; PEFO 33788, partial skull; PEFO 34269, partial skeleton and skull; PEFO 34561, nearly complete skeleton and skull; PEFO 36875, nearly complete skeleton and skull; PEFO 36876, partial skeleton and skull (Parker and Martz, 2011; Nesbitt, 2011; Parker et al., 2007; in prep).

Age – Late Triassic, mid to late Norian, Revueltian (Ramezani et al., 2011; Parker and Martz, 2011).

Occurrence – Petrified Forest Member, Chinle Formation, Arizona, U.S.A.; Bull Canyon Formation, Dockum Group, New Mexico, U.S.A (Hunt, 1989; Parker et al., 2005).

Remarks – Originally known from only isolated teeth that were assigned to ornithischian dinosaurs (Hunt, 1989; Padian, 1990; Heckert, 2003), *Revueltosaurus callenderi* is currently one of the most completely documented pseudosuchians based on an as of yet undescribed series of skeletons recovered from the Chinle Formation of Petrified Forest National Park in Arizona (Parker et al., 2005, 2007). A current phylogenetic analysis of the Archosauriformes recovers *Revueltosaurus callenderi* as the sister taxon of Aetosauria (Nesbitt, 2011).

Key References – Heckert, 2003; Parker et al., 2005, 2007; Nesbitt, 2011.

Rioarribasuchus chamaensis (Zeigler, Heckert, and Lucas 2003)

Holotype – NMMNH P-32793, right anterior caudal paramedian osteoderm (Zeigler et al., 2003).

Referred Material – see Parker, 2007.

Age – Late Triassic, mid-late Norian, Revueltian (Irmis et al., 2011).

Occurrence – Petrified Forest Member, Chinle Formation, New Mexico, U.S.A.; Marthas Butte beds, Sonsela Member, Chinle Formation, Arizona, U.S.A (Zeigler et al., 2003; Parker and Martz, 2011).

Remarks – *Rioarribasuchus chamaensis* was first described as a new species of *Desmatosuchus* by Zeigler et al. (2003) based on isolated paramedian and lateral osteoderms from the Revueltian Snyder Quarry in New Mexico. Parker (2003) demonstrated with a phylogenetic analysis that "*Desmatosuchus*" *chamaensis* was closer to *Paratypothorax* rather than *Desmatosuchus*, a finding opposed by Heckert et al. (2003) who argued that the taxon was more like *Desmatosuchus* than *Paratypothorax*. Parker and Irmis (2005) and Parker (2006) argued that "*Desmatosuchus*" *chamaensis* should be assigned to a new genus, differing from studies such as Lucas et al. (2005) and Heckert et al. (2005a, b) who continued to assign the species to the genus *Desmatosuchus*. Subsequently two names were coined for the taxon almost simultaneously, *Heliocanthus* Parker 2007 and *Rioarribasuchus* Lucas, Hunt, and Spielmann 2006a; however, the paper by Lucas et al., 2006a was published earlier and thus the name *Rioarribasuchus* has priority. The status of the taxonomic name is considered controversial (e.g., Dalton, 2008), but was resolved by Irmis et al. (2007), who as first reviser, used the name *Rioarribasuchus chamaensis* and accordingly *Heliocanthus* is the junior objective synonym of *Rioarribasuchus*. The close relationship between *Rioarribasuchus* and *Paratypothorax* has been recovered by all current phylogenetic analyses of the Aetosauria (Parker, 2007; Desojo et al., 2012; Heckert et al., 2015). Indeed *Rioarribasuchus chamaensis* possesses no desmatosuchine apomorphies (Parker, 2007).

Parker (2007) also provided a novel reconstruction of *Rioarribasuchus chamaensis* in which the sacral and anterior caudal paramedian osteoderms possess dorsal eminences that have the form of an elongate, anterior medially directed, curved spine. The presence of these eminences is an autapomorphy of the taxon. The anterior paramedians and all of the lateral osteoderms are identical to *Paratypothorax*, and originally were thought to represent that taxon by the discoverers (Heckert and Zeigler, 2003). *Rioarribasuchus chamaensis* is currently known from the Snyder and Hayden quarries in the Chama Basin of New Mexico and from Petrified Forest National Park in Arizona. All three of these localities are in Revueltian strata of the Chinle Formation (Heckert et al., 2005b; Irmis et al., 2007; Parker and Martz, 2011).

Rioarribasuchus chamaensis is currently known mainly from osteoderms, although Heckert et al., (2003) referred two astragali (NMMNH P-33927, NMMNH P-33932) and a calcaneum (NMMNH P-33931) from the Snyder Quarry. Those authors did not list any apomorphies or provide any comparisons to other taxa for the astragali and thus this referral is ambiguous given the co-occurrence of *Typothorax coccinarum* in the quarry. However, they did note that the referred calcaneum is not as dorsoventrally compressed as the calcaneum of *Typothorax coccinarum* (presumably AMNH FR 2713). Unfortunately there are no recognized paratypothoracin distal tarsals to use for a comparison to help verify these assignments. An isolated anterior aetosaurian caudal vertebrae (GR 174) from the Hayden Quarry bears caudal ribs that originate close to the base of the centrum rather than at the base of the neural arch. This character only occurs in *Paratypothorax* sp. (PEFO 3004) and not in *Typothorax* (Martz, 2002) so I consider the Hayden Quarry vertebra to represent a paratypothoracin, most likely *Rioarribasuchus chamaensis*.

Key References – Zeigler et al., 2003; Heckert et al., 2003; Parker, 2007.

Scutarx deltatylus gen et sp. nov.

Holotype – PEFO 34616, partial skull, cervical paramedian and lateral osteoderms.

Zoobank LSID -- urn:lsid:zoobank.org:act:E06A8E11-5864-4717-AFA2-9021842B886D

Referred Material – PEFO 31217, much of a postcranial skeleton including vertebrae, ribs, pectoral and pelvic girdles, osteoderms; PEFO 34919, much of a postcranial skeleton including vertebrae, ribs, osteoderms, ilium; PEFO 34045, much of a postcranial skeleton including vertebrae, ribs, and osteoderms; TTU P-09420, two paramedian osteoderms; UCMP 36656, paramedian and lateral osteoderms. The last two specimens were previously referred to *Calyptosuchus wellesi* (Long and Murry, 1995; Martz et al., 2013).

Age – Late Triassic, middle Norian, late Adamanian (Ramezani et al., 2011; Parker and Martz, 2011; Martz et al., 2013).

Occurrence – lower part of the Sonsela Member, Chinle Formation, Arizona, U.S.A.; middle part of the Cooper Canyon Formation, Dockum Group, Texas, U.S.A (Parker and Martz, 2011).

Etymology -- *Scutarx* 'shield fortress,' from Latin *scutum* 'shield' + Latin *arx* 'fortress, castle;' *deltatylus* 'triangular protuberance,' from Greek delta + Greek tylos 'knob, knot, swelling, callous, protuberance.'

Diagnosis – Medium-sized aetosaurian diagnosed by the following autapomorphies; the cervical and dorsal trunk paramedian osteoderms bear a strongly raised, triangular tuberosity in the posteromedial corner of the dorsal surface of the osteoderm (Figure 3); the occipital condyle lacks a distinct neck because the condylar stalk is mediolaterally broad (Figure 4); the base of the cultriform process of the parabasisphenoid bears deep lateral fossae; the frontals and parietals are very thick dorsoventrally; and there is a distinct fossa or recess on the lateral surface of the ilium between the supraacetabular crest and the posterior portion of the iliac blade. *Scutarx deltatylus* can also be differentiated from other aetosaurs a unique combination of characters including moderately wide dorsal trunk paramedian osteoderms with a strongly raised anterior bar that possesses anteromedial and anterolateral processes (shared with all aetosaurians except Desmatosuchini); osteoderm surface ornamentation of radiating ridges and pits that emanate from a posterior margin contacting a dorsal eminence (shared with *Calyptosuchus wellesi*, *Stagonolepis robertsoni*, *Adamanasuchus eisenhardtae*, *Neoaetosauroides engaeus*, and *Aetosauroides scagliai*); lateral trunk osteoderms with an obtuse angle between the dorsal and lateral flanges (shared with non-desmatosuchines); a dorsoventrally short pubic apron with two proximally located ‘obturator’ fenestrae (shared with *Stagonolepis robertsoni*); and an extremely anteroposteriorly short parabasisphenoid, with basal tubera and basipterygoid processes almost in contact and a reduced cultriform process (Figure 4; shared with *Desmatosuchus*).

Remarks – Aetosaurian material referable to *Calyptosuchus* occurs through Adamanian-age deposits in Arizona, New Mexico, and Texas. In Arizona, specimens from the Sonsela Member previously referred to *Calyptosuchus wellesi* (e.g., Long and Murry, 1995; Parker and Irmis, 2005; Parker, 2005a, 2006; Parker and Martz, 2011; Martz et al., 2013) possess a distinctive raised triangular boss on the posteromedial corner of the dorsal surface of the paramedian osteoderms (Figure 3). Detailed comparison demonstrates that this character is not present in the holotype of *Calyptosuchus wellesi* (UMMP 13950) or in referred material of that taxon from the *Placerias* Quarry. Thus this feature is autapomorphic of a new taxon, *Scutarx deltatylus,* which is named and diagnosed here, but will be fully described elsewhere. In this analysis, *Scutarx deltatylus* is coded from four new, partial skeletons from Petrified Forest National Park in Arizona. Newly recognized osteoderms of *Calyptosuchus* (TTU P-09420) from the Post Quarry of Texas also possess the diagnostic triangular boss and thus are actually referable to *Scutarx deltatylus* and not *Calyptosuchus wellesi* (differing from the interpretation by Martz et al., 2013). This occurrence supports correlation of the Post Quarry (middle Cooper Canyon Formation) to the lower part of the Sonsela Member of Arizona as suggested by Martz et al. (2013). Thus is may be possible to subdivide the Adamanian biozone utilizing *Calyptosuchus* and *Scutarx*.

Key References – Parker, 2014; Parker and Irmis, 2005; Martz et al., 2013.

***Sierritasuchus macalpini* Parker, Stocker, and Irmis 2008**

Holotype – UMMP V60817, partial postcranial skeleton consisting of vertebrae and osteoderms (Parker et al., 2008).

Referred Material – TTU P-10731, left lateral osteoderm.

Age – Late Triassic, early to mid-Norian, Adamanian (Ramezani et al., 2011; Lucas, 2010).

Occurrence – Tecovas Formation, Dockum Group, Texas, U.S.A (Long and Murry, 1995; Parker et al., 2008).

Remarks – The holotype (UMMP V60817) of *Sierritasuchus macalpini* was collected in 1939 from the Tecovas Formation of Texas by the late Archie J. MacAlpin (University of Notre Dame), who at the time was a student of Ermine C. Case of the University of Michigan. The specimen, which consists of vertebrae and osteoderms from the cervical and dorsal regions, was originally referred to *Desmatosuchus haplocerus* by Long and Murry (1995). Parker (2002) questioned this referral and considered the possibility that UMMP V60817 represented a skeletally immature specimen of *Longosuchus meadei* even though it was from a higher stratigraphic position.

Redescribed by Parker et al. (2008), this was the first aetosaurian specimen to have osteoderms histologically sampled to help determine the ontogenetic stage of the specimen. Histological analysis suggested that although it is not a full grown adult, the specimen has no indicators of skeletal immaturity either (Parker et al., 2008). Within Desmatosuchinae *Sierritasuchus macalpini* shares more characters with *Longosuchus meadei* than *Desmatosuchus spurensis*, but differs from the former in possessing dorsoventrally flattened, non- faceted, recurved spines on the lateral osteoderms. Parker et al. (2008) listed an additional difference, the lack of radial pattern on the dorsal paramedian osteoderms, but subsequent examination of the type materials of *Longosuchus meadei* demonstrate a random not radial pattern (Parker and Martz, 2010). *Longosuchus meadei* was scored as having a radial pattern in existing phylogenetic analyses (Heckert et al., 1996; Heckert and Lucas, 1999), and this scoring was repeated in subsequent analyses (Parker, 2007; Parker et al., 2008). Determining the exact position of *Sierritasuchus macalpini* within Desmatosuchinae has been problematic (Parker, 2007; Parker et al., 2008); but Desojo et al. (2012) recovered *Sierritasuchus macalpini* as the earliest branching member of the Desmatosuchinae.

Key References – Parker et al., 2008; Desojo et al., 2012.

Unnamed taxon SMSN 19003

Age – Late Triassic, Norian, Revueltian (Deutsche Stratigraphische Kommission, 2005; Lucas, 2010).

Occurrence – Lower and middle Stubensandstein, Löwenstein Formation, Germany (Desojo et al., 2013).

Remarks – SMNS 19003 represents an almost complete, articulated skeleton of a paratypothoracin aetosaur from the Upper Triassic of Germany. The specimen includes a beautifully preserved skull, which is the only unambiguous, non-braincase skull material known for a paratypothoracin. Desojo et al. (2013) refer the specimen as *Paratypothorax andressorum*, but the material has yet to be described and is currently under study by Rainer Schoch and Julia Desojo. However, some details of the skull were presented by Sulej (2010). One notable characteristic of the skull is that the apex of the premaxilla lacks the transverse expansion found in aetosaurs such as *Desmatosuchus* and *Stagonolepis*. *Typothorax coccinarum* (PEFO 38001/YPM 58121) also lacks this expansion, suggesting that this may be an apomorphy for Typothoracinae.

Key References – Sulej, 2010; Desojo et al., 2013.

Stagonolepis robertsoni Agassiz 1844

Holotype – EM 27 R, impression of a segment of the ventral carapace (Agassiz, 1844).

Referred Material – see Walker (1961) for a full list; particularly important is MCZD 2, an articulated partial skeleton including much of the skull with a well preserved braincase and articulated nuchal and cervical paramedian osteoderms.

Age – Late Triassic, ?Carnian (Lucas, 2010).

Occurrence – Lossiemouth Sandstone Formation, Scotland, U.K (Walker, 1961).

Remarks – Originally described by Agassiz (1844) as a fish from what was thought to be the Old Red Sandstone in Scotland, Charles Lyell first raised suspicions that *Stagonolepis* might instead be a reptile more closely related to *Mystriosuchu*s (Huxley, 1859). Reexamination the material showed it to be a parasuchian reptile and provided the first solid evidence that the Lossiemouth Sandstone Formation was Triassic in age (Huxley, 1859, 1875, 1877). Unfortunately much of the collected material consists of natural molds, which has made study of the specimens difficult and only possible through the making of casts (Huxley, 1859, 1877). *Stagonolepis robertsoni* was fully described by Walker (1961) who developed a new technique of creating flexible PVC casts to recover additional details from the deeper portions of the molds than was available to Huxley. Walker (1961) also had the benefit of new specimens, most importantly an actually articulated body fossil (MCZD 2), which represents a nearly complete skull and the anterior cervical armor (Walker, 1961; Gower and Walker, 2002). This specimen allowed for detailed reconstruction of the skull and braincase and demonstrated clearly that *Stagonolepis robertsoni* was an aetosaurian rather than a phytosaur as previously believed (e.g., Camp, 1930).

Although Walker's (1961) reconstruction of *Stagonolepis robertsoni* relied significantly on observations made from *Aetosaurus ferratus*, examination of the MCZD specimen and the NHMUK casts show that Walker's work is extremely reliable for comparisons; however, character scorings for this analysis are taken from the fossils and casts, not from the published reconstruction. And, of course, this is based on the assumption that only a single taxon is present in the Scottish quarries. Walker did note the presence of two different size categories in the specimens, but determined any anatomical differences between the two to represent sexual dimorphism. There is currently no evidence to refute this hypothesis, the most notable difference is in the coverage of ornamentation on the dorsal paramedian osteoderms where in the smaller individuals the posterior portions of the dorsal surfaces are devoid of any ornamentation. Unfortunately all of the quarries where all of the *Stagonolepis robertsoni* material originates have been closed and grown over, and it is unlikely that more material of *Stagonolepis robertsoni* will be found in the immediate future.

What is clear from examination of the Scottish material is that *Stagonolepis robertsoni* is anatomically distinct from *Calyptosuchus* from North America, and *Aetosauroides scagliai* from South America (Parker and Martz, 2011; Desojo and Ezcurra, 2011; differing from Lucas and Heckert, 2001 and Heckert and Lucas, 2002a). Although all share a basic radial patterning and a medially offset dorsal eminence, there are key differences in the osteoderms and especially in the cranial material of these taxa. Therefore all three are treated as separate terminal taxa in this analysis.

Key References – Huxley, 1877; Walker, 1961; Gower and Walker, 2002.

Stagonolepis olenkae **Sulej 2010**

Holotype –ZPAL AbIII/466/17, skull roof (Sulej, 2010).

Referred Material – see Sulej (2010).

Age – Late Triassic, late Carnian (Dzik and Sulej, 2007).

Occurrence – Drawno beds, Krasiejów, Opole Silesia, Poland (Sulej, 2010).

Remarks – *Stagonolepis olenkae* was described by Sulej (2010) for remarkably well preserved aetosaur material from the Krasiejów quarry in Poland (Dzik, 2001; Dzik and Sulej, 2007). The original description of the holotype (Sulej, 2010) is based mainly on the skull material; unfortunately much of the descriptive text is identical to that of Walker (1961) so it is not clear if the Polish material is accurately described. Sulej (2010) provides some obscure references to postcranial material (e.g., mentioning of a tibia in the diagnosis), but other than some of this material being mentioned and partly figured by Dzik (2001), Lucas et al. (2007b) have provided the only descriptions and photographs of this material, but assigned it to *Stagonolepis robertsoni* based mainly on the ornamentation of the dorsal paramedian osteoderms. The most recent discussion of this material suggests that characters used to differentiate *Stagonolepis olenkae* from *Stagonolepis robertsoni* are polymorphic and *S. olenkae* is simply a variant *of S. robertsoni* (Antczak, 2015).

Key References – Sulej, 2010; Lucas et al., 2007b; Antczak, 2015.

***Stenomyti huangae* Small and Martz 2013**

Holotype – DMNH 60708, skull with lower jaws, partial postcranial skeleton including well-preserved ventral armor (Small and Martz, 2013).

Referred Material – DMNH 61392, partial skull with lower jaws, osteoderms, ribs, and vertebrae; DMNH 34565, maxilla, scapula, pubis, ribs and osteoderms.

Age – Late Triassic, middle – late Norian, Revueltian (Ramezani et al., 2011; Small and Martz, 2013).

Occurrence – red siltstone member, Chinle Formation, Eagle County, Colorado (Small and Martz, 2013).

Remarks – *Stenomyti huangae* is a well-documented small~~-sized~~ aetosaurian that, when originally discovered, was presented as the first good evidence for the presence of *Aetosaurus* in western North America (Small, 1998). Subsequent preparation and study revealed that it was anatomically distinct (Small and Martz, 2013). *Stenomyti huangae* possesses a unique ventral armor arrangement, which instead of rows of articulated square osteoderms, consists of an arrangement of oval and irregularly shaped osteoderms that do not contact each other. The removal of these specimens from the genus *Aetosaurus* eliminates a proposed biochronological correlation between Europe and eastern North America, with western North America (Lucas et al., 1998).

Key References – Small, 1998; Small and Martz, 2013.

Tecovasuchus chatterjeei **Martz and Small 2006**

Holotype – TTU P-00545, paramedian and lateral osteoderms of the dorsal region, braincase, partial vertebra (Martz and Small, 2006).

Referred Material – UMMP 9600, right dorsal paramedian osteoderm; TTU P-09222, left dorsal paramedian osteoderm; TTU P-07244, dorsal paramedian osteoderm; NMMNH P-25641, left (?) dorsal lateral osteoderm; TMM 31173-54, partial left paramedian osteoderm; PEFO 37871, partial paramedian osteoderm; MNA V3202, partial right paramedian osteoderm, three right dorsal lateral osteoderms, one ?left dorsal lateral osteoderm fragment (Parker, 2005a); MNA V3000, left dorsal lateral osteoderm; MNA V2898, left dorsal lateral osteoderm (Heckert et al., 2007).

Age – Late Triassic, early to middle Norian, Adamanian (Lucas, 2010).

Occurrence – Tecovas Formation, Dockum Group, Texas, U.S.A.; ?Bluewater Creek Member, Chinle Formation, New Mexico, U.S.A.; upper Blue Mesa Member, Chinle Formation, Arizona, U.S.A (Parker, 2005a; Martz and Small, 2006; Heckert et al., 2007).

Remarks – The holotype (TTU P-00545) was collected in the 1950s by Wann Langston Jr. from the Tecovas Formation near Potter County, Texas. A referred specimen (UMMP 9600) was collected near the same area in 1925 by William Buettner of the University of Michigan. TTU P-00545 was assigned to *Typothorax coccinarum* by Small (1985:8) and TTU P-00545, TTU P-09222, and UMMP 9600 were assigned to *Paratypothorax* sp. by Long and Murry (1995). Lucas et al. (1995) recognized the distinctness of the UMMP osteoderm, but hesitated to erect a new taxonomic name based on a single osteoderm and were apparently unaware of the Texas Tech specimen. The TTU material was later described under the name *Tecovasuchus chatterjeei* (Martz and Small, 2006).

Parker (2005a) and Heckert et al. (2007) referred material from the lower part of the Chinle Formation, including MNA V3202, which had previously used as support for the presence of cervical spines in *Calyptosuchus wellesi* (Long and Ballew, 1985; Long and Murry, 1995). However, the lateral osteoderms of MNA V3202 possess apomorphies of Paratypothoracini most notably the greatly reduced triangular dorsal flange. The preserved paramedian osteoderm in MNA V3202 appears to have a high width/length ratio and the posterior edge is distinctly beveled, which is an autapomorphy of *Tecovasuchus chatterjeei* (Parker, 2005a; Martz and Small, 2006). PEFO 37871 is a portion of a paramedian osteoderm that also preserves the beveled posterior edge and therefore represents another occurrence from the lower part of the Chinle Formation, in this case the upper Blue Mesa Member. *Tecovasuchus chatterjeei* has been postulated as an index taxon for the early Adamanian (Heckert et al., 2007).

These authors also assigned additional material from the NMMNH collections (Heckert et al., 2007:fig. 3) to *Tecovasuchus*; however, no apomorphies of that taxon are apparent in the published figures or listed in the text so I do not include those specimens here.

Key References – Lucas et al., 1995; Parker, 2005a; Martz and Small, 2006; Heckert et al., 2007.

Typothorax coccinarum **Cope 1875**

Lectotype – USNM 2585, five paramedian osteoderm fragments.

Referred Material – Numerous specimens, see Long and Murry, 1995; Hunt, 2001; Martz, 2002; and Parker and Martz, 2011 for lists. Notable referred specimens include AMNH FR 2709, paramedian osteoderms, left femur; AMNH FR 2710, right femur (probably same specimen as AMNH FR 2709); AMNH FR 2713, lateral osteoderms, right femur, left calcaneum, caudal vertebra (lectotype of *Episcoposaurus horridus*); NMMNH P- 56299, articulated carapace missing the skull; NMMNH P-12964, nearly complete skeleton with skull (mostly destroyed); TTU P-09214, osteoderms, vertebrae, braincase, dentary; UCMP 34227, numerous dorsal paramedian osteoderms; UCMP 34255, articulated tail, limb and girdle material; PEFO 38001/YPM 58121, associated skeleton with complete skull; partial skeleton with skull (still in preparation).

Age – Late Triassic, middle to late Norian, latest Adamanian and Revueltian (Ramezani et al., 2011; Irmis et al., 2011).

Occurrence – Sonsela and Petrified Forest members, Chinle Formation, Arizona, U.S.A.; middle part of the Cooper Canyon Formation, Dockum Group, Texas, U.S.A.; Bull Canyon Formation, Dockum Group, New Mexico, U. S. A. (Long and Ballew, 1985; Heckert et al., 2010; Parker and Martz, 2011; Martz et al., 2013).

Remarks – Fossils of *Typothorax coccinarum* are extremely common in Revueltian rocks across the southwestern United States, but despite the large amount of available material most specimens have only been superficially or not described. An exception is a nearly complete skeleton (NMMNH P-56299) described by Heckert et al. (2010), which provides key information on the lateral osteoderms and especially the ventral armor. Some of the best figured materials are from the Canjilon Quarry (Martz, 2002), which forms the basis of much of the description by Long and Murry (1995) as well as our understanding of the taxon.

To date the best cranial material was a complete skull (NMMNH P-12964) from the Bull Canyon Formation (Dockum Group) of New Mexico. This skull was very preliminarily described by Hunt et al. (1993) and later figured, but not described by Heckert et al. (2010). Unfortunately this specimen was badly damaged during molding and is currently only visible in a cast (NMMNH C-4638) that is on exhibit at the New Mexico Museum of Natural History and Science (Heckert et al., 2010:628). Fieldwork by Yale University in the Petrified Forest Member (Chinle Formation) of Petrified Forest National Park in the summer of 2008 resulted in the discovery of two skeletons of *Typothorax coccinarum* both which include well-preserved skulls. One of these skulls (PEFO 38001/YPM 58121) was used to code *Typothorax* for this study, but unfortunately the braincase is not exposed in that specimen. The second skull is still in preparation (M. Fox, pers. comm, 2014).

The type material of *Typothorax coccinarum* consists of only a few fragments of paramedian osteoderms and most descriptions and referrals have been made using better preserved material such as AMNH FR 2709, AMNH FR 2710, or UCMP 34227. The type material is not diagnostic above the level of Typothoracinae and accordingly *Typothorax coccinarum* is most likely a *nomen dubium* (Parker, 2013). Note that, following discussion by Parker (2006), Parker and Martz (2011), and Martz et al. (2013) *Typothorax antiquum* Lucas, Heckert, and Hunt, 2003 is not considered to be a valid taxon in this study, but rather a less skeletally mature specimen of *Typothorax coccinarum*. The occurrence (NMMNH P-25745) of the Revueltian index taxon *Machaeroprosopus* (=*Pseudopalatus*) at the type locality for *Typothorax antiquum* also necessitates a detailed review of the stratigraphic position of this material, which is purportedly Adamanian in age (Lucas et al., 2003; Hunt et al., 2005).

Key References – Cope, 1875, 1877, 1887; Long and Ballew, 1985; Long and Murry, 1995; Martz, 2002; Heckert et al., 2010; Parker, 2013.

PHYLOGENETIC ANALYSIS

The character matrix of 28 taxa and 83 characters (Appendices A and B) was assembled and edited in Morphobank (O'Leary and Kaufman 2012) as matrix number 2617 of project number 1009, and exported as a NEXUS file (Appendix A). Submatrices (partitions) were edited using NEXUS Data Editor for Windows version 5.0 (Page, 2001). All matrices were analyzed in PAUP* (Version 4.0b10 for 32-bit Microsoft Windows, Swofford, 2003). *Postosuchus kirkpatricki* was constrained as the outgroup for the analysis. *Revueltosaurus callenderi* was utilized as a second outgroup, but unconstrained.

PAUP* determined three characters to be parsimony uninformative (39, 42, 72), which were excluded *a priori* to eliminate inflation of tree C.I. values (Kitching et al., 1998). The final matrix consists of 52 binary and 28 multi-state characters ten of which were treated as ordered if they were judged to form a morphocline (Slowinski, 1993)..

Branches were set to collapse and form polytomies if the maximum branch length was zero. This is the default setting for PAUP* and preferable to collapsing minimum branch lengths of zero for this small dataset as the latter method can be too strict for small datasets, eliminating possible topologies (Swofford and Begle, 1993; Coddington and Scharff, 1994). Nonetheless, a test run with the ‘minbrlens’ setting was conducted, but obtained the same results as ‘maxbrlens’, as there is good support for all recovered branches. The matrix was analyzed using the Branch and Bound (‘bandb’) search option and the resultant trees were rooted with the outgroup *Postosuchus kirkpatricki* (‘outroot=para’).

A Permutation Tail Probability (PTP) test (Faith, 1991; Faith and Cranston, 1991) was conducted to test whether the data contain a signal ~~that is more significant than random.~~ The result of P=0.01 is demonstrative that the constructed dataset for this study (28 taxa, 83 characters) is significantly more structured than a random dataset (Faith and Cranston, 1991; Hillis and Huelsenbeck, 1992).

Results

The initial run of 27 in-group taxa and 83 characters (80 parsimony informative), with the settings given above, yielded 30 most parsimonious trees (MPTs) with a length of 203 steps; a reported Consistency Index (C.I.) of 0.5567, Homoplasy Index (H.I.) of 0.4433, a Retention Index (R.I.) of 0.7345, and a Rescaled Consistency Index (R.C.) of 0.4089. The strict consensus of these trees is provided in Figure 5a and features a large polytomy ~~of~~ at the base of the tree. An Adams consensus (Adams, 1972) of the 30 MPTs (Figure 5b) recovers *Aetobarbakinoides brasiliensis* at the base of this large polytomy, and examination of the 30 MPTs demonstrates that this taxon occurs in 10 possible positions throughout the strict consensus tree including as the sister taxon to *Revueltosaurus callenderi,* the sister taxon to all aetosaurs, the sister taxon to the Desmatosuchinae, and the sister taxon to the Typothoracinae. A 50% Majority Rule consensus tree (Figure 5c) places *Aetobarbakinoides* in a polytomy with *Stagonolepis olenkae* and Desmatosuchinae in 70% of the recovered trees.

Coahomasuchus kahleorum is recovered in three positions in the strict consensus, as the sister taxon to *Aetosaurus ferratus*, the sister taxon to Typothoracinae, and as the sister taxon to *Aetosaurus ferratus* + Typothoracinae.

A reduced consensus tree (Figure 5d) was generated by pruning *Aetobarbakinoides brasilensis*. Thus, this final matrix has 27 taxa and 83 characters (80 are parsimony informative). The reduced consensus tree has a length of 201 steps, a C.I. of 0.5622, H.I. of 0.4378, a R.I. of 0.7373, and a R.C. of 0.4145.

The reduced consensus (Figures 5d, 6) features a nearly resolved topology with the exception of a clade with the unresolved polytomy that includes *Coahomasuchus kahleorum*, *Aetosaurus ferratus*, and Typothoracinae. Bremer support values were calculated for each node utilizing PAUP* by running repeated heuristic searches keeping trees one step longer in each iteration and noting which nodes collapse in strict consensus trees until no nodes remain. No nodes had a support value higher than four and many clades collapsed after a single additional step (Figure 6).

Bootstrap values were calculated using 600 replicates. Because of computational constraints I was unable to calculate bootstrap values using a higher number of replicates. Although using more replicates provides a better representation of confidence values, replicate numbers as low as 100, will provide a "rough but useful estimate" (Efron et al., 1996: 13432). Bootstrap values for this analysis are provided for all nodes in Figure 6. Bootstrap values higher than 70%, the minimum meaningful value according to Hillis and Bull (1993), are noted in black, values less than 70% are provided in red, with values lower than 50% interpreted as having very low confidence. Synapomorphy lists for all nodes and definitions of clade names are provided in Appendix C.

Aetosauroides scagliai was recovered at the base of the tree as a non-stagonolepidid aetosaurian, similar to the most recent analyses (Desojo et al., 2012; Heckert et al., 2015; Roberto-da-Silva et al., 2014). Stagonolepididae (Heckert and Lucas, 2000) comprises two major clades, Aetosaurinae (Heckert and Lucas, 2000) and Stagonolepidoidea (clade nov.; Appendix C). The former includes Paratypothoracini (Parker, 2007) as the sister taxon to a clade consisting of *Typothorax coccinarum* and *Redondasuchus rineharti*. Paratypothoracini includes *Rioarribasuchus* (=*Heliocanthus*) *chamanensis*, SMNS 19003 (*Paratypothorax* sp. of Sulej, 2010 and Desojo et al., 2013), *Tecovasuchus chatterjeei*, *Paratypothorax andressorum*, and *Paratypothorax* sp. (North American *Paratypothorax* specimens). This clade is well supported by six unambiguous synapomorphies (listed below), as well as a high decay index (+4) and bootstrap value (95%).

The sister taxon to that clade ((*Typothorax* + *Redondasuchus*) + Paratypothoracini)) is the recently described *Apachesuchus heckerti* Spielmann and Lucas 2012, which is known from only a handful of osteoderms, and is situated here based mainly on the presence of the synapomorphy that supports the clade, width/length ratio of widest paramedian osteoderms 3.5 or higher (character 64-2).

In this analysis Typothoracinae, as defined by Parker (2007), would be equivalent to Aetosaurinae, so Typothoracinae is redefined here with an additional specifier (*Aetosaurus ferratus*, see Appendix C). Under this new definition Typothoracinae presently consists of *Apachesuchus heckerti*, Paratypothoracini, and *Typothorax coccinarum* + *Redondasuchus rineharti*. This clade is well supported by bootstrap values and decay indices (Figure 6).

As previously mentioned *Aetosaurus ferratus* and *Coahomasuchus kahleorum* form a polytomy with Typothoracinae (Figure 6). This close relationship is novel, but not entirely unprecedented as these taxa were recovered as adjacent terminal taxa by Heckert et al. (2015) and Roberto-da-Silva et al., (2014). Nonetheless, because of the polytomy support for this clade is not robust and these taxa may form other relationships in future analyses. *Stenomyti huangae* (Small and Martz, 2013) is recovered at the base of Aetosaurinae, but this position is also very weakly supported and at present there can be little confidence in this position.

Stagonolepidoidea consists of two clades, Stagonolepidinae (Heckert and Lucas, 2000) and Desmatosuchinae (Heckert and Lucas, 2000). Stagonolepidinae consists of *Stagonolepis robertsoni* (by definition) and the newly described *Polesinesuchus aurelioi* (Roberto-da-Silva et al., 2014), however, this relationship is not very well supported with a decay index of +1 and a bootstrap value of 27% (Figure 6).

At the base of Desmatosuchinae lie *Stagonolepis olenkae* Sulej 2010 and *Neoaetosauroides engaeus* (Figure 6). *Neoaetosauroides* was previously recovered outside of Desmatosuchinae by Parker (2007) and Desojo et al., (2012), but within by Heckert and Lucas

(1999, 2000). Regardless these positions are not well supported with both branches having decay indices of +1 and bootstrap values under 10%.

Nested deeper in Desmatosuchinae is a clade consisting of *Calyptosuchus wellesi*, which is the sister taxon to *Adamanasuchus eisenhardtae* + *Scutarx deltatylus* (Figure 6). These clades are fairly well supported with decay indices of plus one and bootstrap values in the high 60th percentile nearly reaching the confidence threshold of 70% proposed by Hillis and Bull (1993). This is a novel position for these taxa as *Adamanasuchus eisenhardtae* and *Calyptosuchus wellesi* had been recovered outside of Desmatosuchinae in previous studies (e.g., Parker, 2007; Desojo et al., 2012). The presence of these five taxa within Desmatosuchinae is poorly supported with nodes having decay indices of only +1 and bootstrap values of less than 50% (Figure 6). Thus, this part of the tree may also prove to be highly labile in future analyses.

The subsequent nested clade within Desmatosuchinae; however, is highly supported by 13 unambiguous synapomorphies, a decay index of +5, and a bootstrap value of 94%. I name this clade Desmatosuchini and define it in Appendix C. In this study Desmatosuchini is well-resolved and includes *Gorgetosuchus pekinensis*, *Longosuchus meadei*, *Sierritasuchus macalpini*, *Lucasuchus hunti*, and *Desmatosuchus*. This new clade has the same constituent taxa as Desmatosuchinae *sensu* Parker (2007).

DISCUSSION

Comparisons to previous analyses

Constituency and Status of Major Clades of Aetosauria

Four major clades have been defined within Aetosauria: Stagonolepididae, Aetosaurinae, Stagonolepininae (emended to Stagonolepidinae by Sereno, 2005), and Desmatosuchinae (Heckert and Lucas, 1999, 2000). A fifth, Typothoracinae, was added by Parker (2007).

Historically the terms Stagonolepididae and Aetosauria have been used interchangeably for family-group names under the Linnaean taxonomic system (see discussion in Walker, 1961), but were first defined cladistically by Heckert and Lucas (2000), the former as stem-based and the latter as node based, although in that analysis they contained the same taxa. Parker (2007) also recovered these clades at a shared node, but cautioned that the definition provided by Heckert and Lucas (2000) was based on *Aetosaurus* occupying the base of the tree and left open the possibility for non-stagonolepidid aetosaurs, which would alter the historic usage of the name. Rescoring of character states in *Aetosauroides* moved it to the base of Aetosauria as a non-stagonolepidid aetosaur (Desojo et al., 2012), a position recovered in all subsequent analyses including the present study (Heckert et al., 2015; Roberto-da-Silva, et al, 2014).

In ~~their (Heckert and Lucas, 1999) original~~ defining analysis Aetosaurinae included only *Aetosaurus*; however, Parker (2007) and Parker et al. (2008) recovered Aetosaurinae as a greatly expanded clade that included all non-Desmatosuchines; however, this clade was generally unsupported and its constituents not accepted by all workers (e.g., Schoch, 2007). Moreover, subsequent analyses (Desojo et al., 2012; Heckert et al., 2015) do not recover Aetosaurinae as a more inclusive clade with *Aetosaurus ferratus* the only constituent by original definition. In these analyses the remnant of the "Aetosaurines" (*sensu* Parker, 2007) are poorly resolved along the spine of Stagonolepididae.

The present study recovers a different result (Figure 6) with *Aetosaurus ferratus*, *Coahomasuchus kahleorum*, and *Stenomyti huangae*, which was originally referred to the genus

Aetosaurus (Small and Martz, 2013), situated near the base of Aetosaurinae, which also includes the Typothoracinae. This still differs from Aetosaurinae as recovered by Parker (2007), which also included *Stagonolepis robertsoni*, *Aetosauroides scagliai*, *Neoaetosauroides engaeus*, and *Calyptosuchus wellesi*, all of which are now recovered as more closely related to *Desmatosuchus* (Figure 6). However, constraining the analysis to recover all of these taxa in a monophyletic Aetosaurinae (*sensu* Parker, 2007) now requires 11 additional steps.

As defined by Heckert and Lucas (2000) Stagonolepidinae consisted of *Stagonolepis robertsoni* and *Coahomasuchus kahleorum*. Parker (2007) recovered Stagonolepidinae at the same node as Aetosaurinae and chose to use the latter name for that clade. Subsequently the name Stagonolepidinae has fallen out of use in recent analyses although it would have pertained solely to *Stagonolepis robertsoni* in other recovered topologies (Desojo et al., 2012; Heckert et al., 2015). However, in the present study Stagonolepidinae is distinct from Aetosaurinae as originally conceived and consists of *Stagonolepis robertsoni* and *Polesinesuchus aurelioi* (Figure 6).

Desmatosuchinae was first recovered as a clade by Heckert and Lucas (1999, 2000) where it was comprised of *Desmatosuchus*, *Typothorax*, *Paratypothorax*, and *Longosuchus*; however, aspects of the published tree were affected by typographical and scoring errors, as well as reductive coding methods by Harris et al. (2003), who provided a revised version of the Heckert and Lucas (1999) matrix. The cladogram in Harris et al. (2003) based solely on the revised Heckert and Lucas (1999) matrix recovered Desmatosuchinae as consisting of *Desmatosuchus*, *Longosuchus*, *Lucasuchus*, and *Acaenasuchus*, all of which have remained constituent taxa in all subsequent analyses (Parker, 2007; Parker et al., 2008; Desojo et al., 2012, Heckert et al., 2015; this study), although this present study did not include *Acaenasuchus* as an Operational Taxonomic Unit (see explanation above).

The present study differs from all others in recovering several taxa within Desmatosuchinae for the first time, including *Stagonolepis olenkae*, *Neoaetosauroides engaeus*, *Adamanasuchus eisenhardtae*, *Scutarx deltatylus*, and *Calyptosuchus wellesi* (Figure 6).

Nevertheless, support for these included taxa is weak, and it is probable that in future analyses they may continue to migrate between the bases of Aetosaurinae and Stagonolepidoidea. A new robust clade, Desmatosuchini, is erected for the taxa originally within Desmatosuchinae (*sensu stricto*) as originally recovered by Harris et al. (2003) and Parker (2007).

Typothoracinae was first recovered and defined by Parker (2007) and is comprised of taxa more closely related to *Typothorax* and *Paratypothorax* than to *Aetosaurus*, *Stagonolepis*, or *Desmatosuchus*. This clade was well-supported by Parker (2007) and has been recovered in all subsequent analyses including the present analysis (Figure 6).

Desmatosuchinae and Aetosaurinae were recovered as sister taxa, with Typothoracinae nested within Aetosaurinae (Parker, 2007). Desojo et al. (2012) and Heckert et al. (2015) did not recover a similar topology after rescoring and adding taxa to the Parker (2007) matrix. Instead they presented trees with Desmatosuchinae and Typothoracinae as sister taxa. The present analysis recovers Typothoracinae within Aetosaurinae and a distinct Desmatosuchinae (Figure 6).

In sum, the results of five most recent phylogenetic analyses demonstrate that Typothoracinae and Desmatosuchini are robust clades within Aetosauria, well-supported and stable when taxa are added and scorings are changed. Recovery of an inclusive Aetosaurinae is not consistent across studies, with weak support values for non-desmatosuchine and typothoracine taxa causing the constituent taxa to be shuffled around the base of the tree in most studies. The significance of and a possible reason for this are addressed below.

The Monophyly of **Stagonolepis**

It has been recognized that aetosaurian material, especially osteoderms, recovered from southwestern North America (Chinle Formation, Dockum Group) is very similar in overall anatomy to that of *Stagonolepis robertsoni*. In fact, the first person to directly compare these materials was convinced of their congeneric status (Charles Lewis Camp, unpublished notes, 1935). The North American material was eventually named *Calyptosuchus wellesi* by Long and Ballew (1985); however, soon afterwards that species was reassigned to the genus *Stagonolepis* (Murry and Long, 1989; Long and Murry, 1995).

This potential relationship was first discussed in a numerical phylogenetic framework by Heckert and Lucas (1999:62) who noted that *Calyptosuchus wellesi* and *Stagonolepis robertsoni* "score almost identically throughout the matrix", and therefore they removed *Calyptosuchus wellesi* prior to their final run. For the same reasons they removed *Aetosauroides scagliai*, considering it also to represent *Stagonolepis robertsoni* and several anatomical descriptions were published detailing these proposed synonymies (Lucas and Heckert, 2001; Heckert and Lucas, 2002). However, investigation of the original matrix by Harris et al., (2003) determined that because these three taxa were not scored identically, *Calyptosuchus wellesi* and *Aetosauroides scagliai* could not be removed without affecting the final analysis. A reanalysis did not recover a "*Stagonolepis*" clade with *Calyptosuchus wellesi* and *Stagonolepis robertsoni*, but did find a clade with *Stagonolepis robertsoni* and *Aetosauroides scagliai* (Harris et al., 2003: fig. 9).

The strict consensus tree published by Parker (2007: fig. 13) offered no resolution to this problem, recovering all three taxa in an unresolved polytomy with *Aetosaurus ferratus*. However, Desojo (2005) argued against the synonymy of *Aetosauroides* and *Stagonolepis* and in a recent redescription of *Aetosauroides scagliai* demonstrated key differences in the skull and postcranial skeleton that preclude an assignment of that material to *Stagonolepis robertsoni* (Desojo and Ezcurra, 2011). More recent phylogenetic analyses featuring a rescoring of *Aetosauroides scagliai* do not recover the three '*Stagonolepis*-like' species as a discrete clade (Desojo et al., 2012; Heckert et al., 2015). The present study rescores *Calyptosuchus wellesi* based on material from the *Placerias* Quarry (Parker, 2014) and also does not recover *Stagonolepis*, *Calyptosuchus*, and *Aetosauroides* as a discrete clade. Constraining the present analysis to recover them in an exclusive clade requires 10 additional steps. Thus, anatomical comparisons and several phylogenetic analyses strongly support the separation of these three taxa and the genera *Calyptosuchus* and *Aetosauroides* should no longer be considered junior synonyms of *Stagonolepis* (Parker, 2008a; Desojo and Ezcurra, 2011).

Numerous well-preserved cranial bones from Krasiejów Poland were described as a new species of *Stagonolepis*, *Stagonolepis olenkae* (Sulej, 2010). Postcranial bones and osteoderms were also recovered from the same quarry (Dzik, 2001; Dzik and Sulez, 2007) and were assigned to *Stagonolepis robertsoni* by Lucas et al., (2007b). In a traditional (i.e., non-cladistic) analysis *Stagonolepis olenkae* was considered to be an early member of an anagenetic '*Stagonolepis-Aetosaurus*' lineage (Sulej, 2010). Differences between *Stagonolepis olenkae* and *Stagonolepis robertsoni* appear to all be in the skull and include contrasting dimensions of various cranial bones, the presence of a massive ridge on the anterior end of the palatine in *S. olenkae*, the presence of a lateral ridge on the maxilla of *Stagonolepis robertsoni*, and most notably a reduced number of dentary teeth and the presence of large tubercles on the parietals of *Stagonolepis olenkae* (Sulej, 2010). These were considered to possibly represent individual variation by Antczak (2015), who suggested that the Krasiejów material is probably referable to *Stagonolepis robertsoni*. In the phylogenetic analysis presented here these two taxa are scored differently for five characters, four are cranial and the fifth is that the humeral head is more expanded in *Stagonolepis olenkae*. In the recovered tree *Stagonolepis robertsoni* + *Polesinesuchus aurelioi* is the sister taxon to *Stagonolepis olenkae* + Desmatosuchinae. A topological constraint to force the two purported species of *Stagonolepis* to form an exclusive clade requires only an additional two steps. Therefore, even though both purported species were not recovered as a clade, I do not suggest erecting a new generic name to receive *Stagonolepis olenkae*. Differences between the taxa are too few and potentially explained by the much larger size of *Stagonolepis olenkae*, although Sulej (2010) explicitly argued against this possibility. A full description of the postcranial material and osteoderms will hopefully provide further evidence for or against the potential generic synonymy of these two taxa although a preliminary analysis proposes synonymy (Antczak, 2015).

The Phylogenetic Position of Aetosaurus ferratus

The earliest exhaustive treatment of the Aetosauria (Walker, 1961) considered *Aetosaurus ferratus* as the 'basal' aetosaurian, a position supported by the first phylogenetic analyses of the Aetosauria (Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 1999). Indeed, an early study constrained *Aetosaurus ferratus* to this position by utilizing it as the sole outgroup for the entire analysis (Heckert et al., 1996). Nonetheless that study considered other aetosaurs to be more 'advanced' than *Aetosaurus* based on characters of the teeth, especially the presence of bulbous rather than recurved teeth and an edentulous anterior portion of the dentary. Those characters and scorings for *Aetosaurus* were taken directly from Parrish (1994), and used again by Heckert and Lucas (1999) to diagnose *Aetosaurus*. Parker (2007) followed Walker (1961:164) in considering the teeth of *Aetosaurus* bulbous, rather than mediolaterally flattened and recurved, with the anterior portion of the dentary edentulous. In the accompanying analysis *Aetosaurus ferratus* was recovered more deeply nested within Stagonolepididae (Parker, 2007), the first time it had not been recovered at the base of Aetosauria in a phylogenetic analysis (Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 1999). This alternate placement prompted detailed discussion by Schoch (2007) who acknowledged that the teeth were as Walker (1961) had described, but argued that the more nested placement of *Aetosaurus* was somewhat ambiguous as other character states found in *Aetosaurus ferratus* supported a position closer to the base of Aetosauria.

In subsequent analyses (Desojo et al., 2012; Heckert et al., 2015) *Aetosaurus* has been recovered closer to the base of Aetosauria in part mainly because of a change in character polarities based on the scoring of *Aetosauroides scagliai* as having a maxilla that is excluded from the margin of the external naris (Desojo and Ezcurra, 2011); a change that pulled both *Aetosauroides* and *Aetosaurus* towards the root of the tree. In the present analysis *Aetosaurus* is recovered in a polytomy with *Coahomasuchus* and Typothoracisinae, and two taxa are still fairly close to the base of Aetosauria (Figure 6), but constraining the clade of *Aetosaurus* plus *Coahomasuchus* to the base of Aetosauria requires an additional six steps.

Low Support Values in Data Partitions

Overall, the tree of Heckert et al. (2015) is the most similar of all past studies to the one presented here, suggesting that the incorrect scorings that affected the earliest analyses (Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 1999) still played a major role in the recovered topology of Parker (2007). Some of these errors were directly inherited from the previous studies (Parrish, 1994; Heckert et al., 1996), but others resulted from a general lack of good specimens and a necessary reliance on outdated literature to score characters as redescriptions of key taxa such as *Aetosaurus ferratus*, *Aetosauroides scagliai*, *Neoaetosauroides engaeus*, and *Desmatosuchus spurensis* had not yet been published (Desojo and Báez, 2005, 2007; Schoch, 2007; Parker, 2008b; Desojo and Ezcurra, 2011). Still, this early work should be recognized for pioneering phylogenetic studies of aetosaurians, especially the study of Heckert et al., (1996), which introduced many key characters still used in current analyses. However, this also demonstrates the importance of discovering and utilizing new specimens of existing taxa (e.g., MNA V9300, PEFO 38001/YPM 58121; NMMNH P-56299; TMM 31100-437), as well as crucial reinvestigations of original type materials (e.g., Desojo and Báez, 2005, 2007; Schoch, 2007), in phylogenetic work.

I find the results of the new study presented here to be generally disappointing because of the lack of support for the base of the tree, essentially all nodes outside of Typothoracinae and Desmatosuchini. This problem also plagued the previous study by Parker (2007) and was apparent in the way topologies shifted significantly in new studies when characters were rescored and new taxa added (Desojo et al., 2012; Heckert et al., 2015). The present work sought to increase character support by creating as many new characters as possible, particularly those from skeletal elements outside of the dorsal carapace. Inclusion of endoskeletal (non-armor) characters was suggested as a way to provide tree stability (Desojo et al., 2012; Heckert et al., 2015).

Parker (2007) scored 35 parsimony informative characters with 23 (66%) of these characters from the osteoderms. This new study has expanded the dataset to 80 parsimony informative characters, an increase of over 100%, with only 31 of these characters scoring osteoderm characters (39%). Thus, it was expected to see an increase in stability in the overall tree metrics utilizing a dataset with better skeletal region sampling, but unfortunately this was not realized in the final results.

One of the possible reasons for these low support values is that the non-osteoderm characters of aetosaurians appear to generally have higher levels of homoplasy. For example, the 35 parsimony informative cranial characters have an average Consistency Index value of 0.596. This value was computed by simply adding up the C.I. scores for each character and dividing the resulting number by the number of characters, thus this is a calculation of a 'raw' C.I. average and does not equate the final reported C.I. number for the MPTs as determined by PAUP*. Vertebral characters score much higher with an average C.I. value of 0.767. However, the paramedian osteoderm characters have an average value of 0.697, whereas the lateral osteoderms have an average value of 0.833 demonstrating the value of the osteoderm characters. Overall the non-osteoderm characters have an average C.I. value of 0.606, compared to an average value of 0.746 for the osteoderm characters. What this signifies is that the non-osteoderm characters included in the study are more apt to change across the tree than the osteoderm characters, which signifies a higher degree of homoplasy in non-osteoderm characters or that non-comparable maturity at time of death among specimens plays a greater role than expected.

Overall, sampling of non-osteoderm characters remains poor, with the majority of characters taken from the cranial region. Only four characters sample the appendicular skeleton, and the limbs and girdles represent a potential area for character expansion. Unfortunately, many aetosaur taxa do not have limb and girdle material referred to them, and, in some cases, these materials are present but covered by an articulated carapace and not accessible for study without non-invasive (e.g., CT) scanning. Where limb and girdle elements are known (e.g., femora, scapulae, ilia) many of the characters appear to be conserved across taxa. Still, with increasing sample sizes and better comparisons, more informative characters can probably be derived from this dataset in future analyses.

Dataset Partitioning

An interesting question brought up during the construction of this dataset is what if aetosaurians did not possess an extensive armor carapace? What if all of the characters and character states used in phylogenetic analyses of the Aetosauria were derived from the skull, axial, and appendicular portions of the skeleton as is the case for the majority of vertebrate animals? In sum, what would the phylogeny of aetosaurians look like without utilizing characters of the osteoderms?

Fundamental limitations of phylogenetic analyses lie in the various properties of the data set being utilized. These properties define the data set and thus are intrinsic to the final results as factors such as the number of taxa and characters included, amount of missing data, and degree of character weighting dictate the most parsimonious tree(s), but also the number of plausible topologies available to be chosen from. The literature is replete with studies addressing these various aspects of phylogenetic analysis, not simply because they are of some statistical interest, but because they are fundamental to the process itself. One particular aspect of data set analysis is the discussion of data partitioning, which entails the separation of a data set of phylogenetic characters into discrete parts based on types of characters (e.g.~~,~~ molecular sequences vs. morphological), or positional (e.g.~~,~~ skull vs. postcranium). In most published cases, the debate ~~on~~ data partitioning in phylogenetic analyses revolves around the advantages or disadvantages of combining ~~of~~ molecular sequence and morphological data into a single data set (e.g.~~,~~ Bull et al., 1993). Considerable discussion is available regarding partitioning of strictly morphological data into discrete character sets based mainly on anatomical subregions (Rowe 1988; Gauthier et al. 1988; Donoghue et al. 1989; Rae, 1999; Clarke and Middleton, 2008; Mounce, 2013), but none pertains to the special case of osteoderms versus endoskeletal features.

~~The purpose of this section is to differentiate morphological (anatomical) characters from the study presented earlier in this discussion into discrete partitions.~~ As discussed throughout this study, aetosaurs have an elaborate bony armor carapace covering the main skeleton and characteristics such as the surface ornamentation, size, osteoderm geometry, and articulation patterns of this armor are the main factor utilized for aetosaurian taxonomy, whereas characters from the rest of the skeleton have generally been under-developed (Desojo, 2005). Thus, aetosaurs provide an excellent example of a group where historically the taxonomy is based almost entirely on characters from a single non-cranial anatomical subregion. A major assumption of aetosaur workers is that not only is osteoderm anatomy taxonomically informative, but that it is also phylogenetically significant, providing an accurate signal of evolutionary relationships within the group (Parker, 2007). Dataset partitioning provides a test of which characters, in this case integumentary versus non-integumentary, are providing the main phylogenetic signal for this group and allows for in-depth examination of possible underlying factors regarding the poorly resolved phylogenetic relationships recovered in past studies (Harris et al., 2003).

Why partition?

Osteoderms represent a mineralized component of the dermis in tetrapods (Romer, 1956; Hill, 2005). As such they are hypothetically an autonomous (i.e., they are not found in all vertebrates) unit (module) of the skeletal and circulatory systems. This independence is further supported by the finding that onset of osteoderm development is delayed, by as much as a year, in comparison with the rest of the skeleton in *Alligator* with the result that they are absent in very young animals (Vickaryous and Hall, 2008). This independence also suggests that the osteoderms, with specific proposed functions (e.g., defense, heat transfer, species recognition; Seidel, 1979; Main et al., 2005), may be under different evolutionary selection pressures than other parts of the body such as the head, which is mainly focused on resource acquisition, or the limbs, which are mainly focused on locomotion and/or environmental manipulation. Although the presence of osteoderms can hypothetically influence some ~~factors~~ of the rest of the skeleton, such as the development of transversely expanded apices on the neural spines, a robust olecranon process of the ulna for bearing additional weight, and modified parietal bones of the skull for reception of the anterior portion of the armor characters, they can be considered a distinct module of the skeleton. This begs the question of how does the non-integumentary portion of the aetosaur skeleton compare to other taxonomic groups, but more importantly how does it compare within Aetosauria proper?

Methods

Morphobank (O'Leary and Kaufmann, 2012) was used to divide the main dataset into smaller partitions based on cranial characters, osteoderm characters, and the full set of non-osteoderm characters. The cranial dataset consists of characters 1-35, the osteoderm dataset consists of characters 52-83, and the full endoskeletal set consists of characters 1-51. All analyses for this study were run using PAUP* version 4.0.b10 (Swofford, 2003). All characters were weighted equally and the most parsimonious trees (MPTs) were subject to an exact solution search using the branch and bound implementation under the program default settings. Bootstrap support values for each dataset were calculated from 1000 replicates with only scores above 50% being recorded as informative, although only values above 70% probably represent well-supported clades (Hillis and Bull, 1993). Distribution of character states was analyzed in Mesquite 2.75 (Maddison and Maddison, 2011).

The reduced consensus tree provided earlier utilized the full data set for this entire project (26 in-group taxa and 83 characters) and establishes the baseline relationships for this study. For this portion of the study runs used the subsets outlined above. Because some taxa are only known from osteoderms (e.g., *Apachesuchus heckerti*) it was necessary to remove taxa where no characters could be scored for one of the partitions, as inclusion of taxa with no scored characters causes the algorithm to generate all possible trees, which increases exponentially given the total number of taxa with the end result of a completely unresolved consensus tree. Therefore all taxa lacking skull material were also removed from the matrices so that the final trees could be directly compared. Taxa were also removed if taxonomic equivalence could be demonstrated, utilizing the Safe Taxonomic Reduction method of Wilkinson (1995a) to reduce the number of MPTs and increase resolution. For the cranial set this included *Tecovasuchus chatterjeei*, which can only be scored for two characters, and for *Desmatosuchus spurensis*, which for this partition is identically coded to *Desmatosuchus smalli*. *Desmatosuchus smalli* was retained for the analysis as its overall scoring contains fewer missing data (98% complete). For the osteoderm-only dataset this included *Stagonolepis olenkae*, which is scored identical to *Stagonolepis robertsoni*, *Desmatosuchus spurensis* which is scored the same as *Desmatosuchus smalli*, and *Redondasuchus rineharti*, which is scored the same as *Typothorax coccinarum*. The final partition datasets initially contain 13 taxa. *Postosuchus kirkpatricki* and *Revueltosaurus callenderi* are utilized as the outgroup, and the in-group taxa consist of *Aetosaurus ferratus*, *Stagonolepis robertsoni*, *Scutarx deltatylus*, *Aetosauroides scagliai*, *Coahomasuchus kahleorum*, *Desmatosuchus smalli*, *Longosuchus meadei*, *Neoaetosauroides engaeus*, *Typothorax coccinarum*, SMNS 19003, and *Stenomyti huangae*.

A ‘Simultaneous Analysis’ dataset (all 83 characters; *sensu* Baker and DeSalle, 1997), although with the reduced number of taxa (13), was run to see the effects of reduced taxon sampling, which has been hypothesized to reduce phylogenetic accuracy (Hillis, 1998), and to establish a baseline topology for comparison with the partitioned datasets. Nonetheless, it should be recognized that partitioning datasets is an analytical tool and should not be expected to represent the final phylogenetic hypothesis. This simultaneous analysis matrix was subsequently portioned into three datasets, one including only cranial characters, another including only osteoderm characters, and a third including all non-osteoderm characters including the cranial set. All uninformative and constant characters were excluded, further reducing the sizes of the matrices (13 taxa, 35 characters from the cranial set; 13 taxa, 24 characters for the osteoderm only set, and 13 taxa, 46 characters for the non-osteoderm only set). Because the datasets were reduced, Permutation Tail Probability (PTP) tests were run in PAUP* to test the null hypothesis that the datasets are no better than random and thus phylogenetically uninformative (Faith and Cranston, 1991). The cranial and the armor only datasets had PTP scores of 0.01 and the endoskeletal dataset had a score of 0.02 which are less than the required PTP of 0.05 that is considered to be significant, thus falsifying the null hypothesis. These datasets were run under the branch and bound settings in PAUP* and the results of the partition sets were compared with each other, as well as to the full and reduced taxon datasets containing all 83 characters.

Results

Reduction of the number of taxa in the full working matrix from 28 to 13 taxa produced 14 parsimony-uninformative characters (including four constant characters) out of the original set of 83. The uninformative characters were excluded *a priori* from the final matrix of 69 characters and 12 in-group taxa. Ten characters were unordered. The initial run (branch and bound) resulted in three most parsimonious trees of 178 steps. The strict consensus of which (C.I. = 0.6067, H.I. = 0.3933, R.I. = 0.5270, R.C. = 0.3198), which is provided in Figure 7a. This tree is similar to the reduced strict consensus tree recovered in the complete analysis presented earlier except that the base of Aetosauria is unresolved, consisting of *Stenomyti*, *Stagonolepis*, Aetosaurinae and Desmatosuchinae. Nonetheless, taxa recovered in Aetosaurinae and Desmatosuchinae in the full analysis are recovered in those same clades in this reduced analysis. Thus the reduction of taxa as well as the loss of the 14 constant/uninformative does not significantly change relationships within the tree.

Overall clade support in the base of the reduced matrix tree is not good, with some clades collapsing with only a single additional step. However, Typothoracinae (*Typothorax* + SMSN 19003) collapses after six steps, and Desmatosuchini (*Desmatosuchus* + *Longosuchus*) is particularly well-supported, not collapsing until nine additional steps. Thus, there appears to be no negative effects to clade support as a result of reduced taxon sampling as the nodes are even better supported than in the tree recovered for the complete analysis. Thus, this reduced matrix tree provides a suitable baseline topology to compare to the other partition sets.

A branch and bound search of the reduced matrix utilizing the osteoderm only dataset (12 in-group taxa, 24 informative characters, eight ordered; outgroup constrained) results in a strict consensus tree (Figure 7b) from three MPTs of 58 steps each (C.I. = 0.8276, R.I. = 0.7727, R.C. = 0.6395). These metrics are high, suggesting that there is reduced homoplasy in this data partition (H.I. = 0.1724). Nonetheless, the recovered tree topology is mostly unresolved and poorly supported. Four clades are recovered; 1) *Desmatosuchus smalli* + *Longosuchus meadei*, which is the sister taxon to all of the other aetosaurians; 2) all of the non-desmatosuchine taxa; 3) *Stenomyti huangae* + *Neoaetosauroides engaeus*, and 4) *Typothorax coccinarum* + SMNS 19003 (Figure 7b). In this partitioned analysis *Stenomyti* + *Neoaetosauroides* is supported by two unambiguous synapomorphies, dorsal eminence of the dorsal paramedian osteoderms is strongly offset medially (66-2), and anterolateral projection of the anterior bar of the dorsal paramedian osteoderms is present and elongate (68-1). *Typothorax coccinarum* + SMNS 19003 are supported by six unambiguous synapomorphies: 1) lateral edge of the dorsal paramedian osteoderms in dorsal view are strongly sigmoidal with a strongly posteromedially oriented posterolateral corner (63-1); 2) width/length ratio of widest paramedian osteoderms (rows 9-11) in dorsal trunk series is greater than 3.5 (64-2); 3) dorsal eminence of cervical lateral osteoderms is a moderate length, dorsoventrally flattened, slightly recurved spine (74-1); 4) mid-dorsal lateral osteoderms with a strongly acute angle of flexion between the dorsal and lateral flanges (79-2); 5) lateral flange of pelvic and anterior caudal lateral osteoderms is roughly triangular in lateral vie with a semicircular ventrolateral border and a hook-like eminence (81-1); and 6) carapace is broad and discoidal in dorsal view (82-2).

Desmatosuchus plus *Longosuchus* (Desmatosuchini) is the best supported clade with 14 unambiguous synapomorphies: 1) cervical paramedian osteoderms are longer than wide (57-1);

2) ratio of cervical vertebrae/paramedian osteoderms significantly less than 1:1 (58-1); 3) adjacent paramedian and lateral cervical osteoderms are often fused (59-1); 4) in the paramedian osteoderms dorsal to the cervical and anterior trunk vertebrae, lateral edge articulation with lateral osteoderms is dorsoventrally thickened, angled contact, with deeply incised interdigitation (='tongue and groove') (60-1); 5) dorsal eminence shape in the cervical paramedian osteoderms are a low pyramidal or rounded boss, or elongate keel (61-1); 6) in the dorsal trunk paramedian osteoderms the anterior edge of the lateral osteoderm overlaps the anterior edge of the paramedian osteoderm (62-1); 7) lacks the sharp anteromedial projection of the anterior bar (reversed in *Lucasuchus hunti*) (67-1); 8) the anterior bar of the trunk distal paramedian osteoderms lacks an anterolateral projection (68-2); 9) anterior bar of the dorsal trunk paramedian osteoderms lacks scalloping of the anterior margin on the medial side of the osteoderm (69-1); 10) dorsal eminence in the mid-trunk osteoderms is a conical spike (78-2); 11) approximately 90 degree angle between the dorsal and lateral flanges of the mid-trunk lateral osteoderms (79-1); 12) dorsal trunk lateral osteoderms strongly asymmetrical with the dorsal flange longest (80-1); 13) lateral flange of the pelvic and anterior caudal lateral osteoderms are rectangular and ventral to a well-developed spine (81-2); and 14) overall shape in of the dorsal carapace in dorsal view is moderately spinose (82-1).

Overall support is mixed with the clades *Neoaetosauroides* + *Stenomyti*, and *Typothorax* + SMNS 19003 having Decay Indices of +1 and +2 respectively, but *Desmatosuchus* plus *Longosuchus* is very strongly supported with a Decay Index of +9. Furthermore, *Typothorax* + SMNS 19003 has a bootstrap value of 86% for 1000 replicates, and *Desmatosuchus* plus *Longosuchus* occurs in 100% of the replicates (Figure 7b).

A branch and bound run of the endoskeletal (non-osteoderm) dataset (12 in-group taxa, 46 informative characters, four ordered) results in two MPTs of 115 steps (C.I. = 0.5217, H.I. = 0.4783, R.I. = 0.4762, R.C. = 0.2484), the strict consensus of which is shown as Figure 7c. The tree is nearly completely resolved and the topology more closely resembles the total evidence tree rather than the cranial only tree. *Aetosauroides* is recovered at the base of the tree, and the clade (*Neoaetosauroides* + (*Scutarx* + (*Desmatosuchus* + *Longosuchus*))) is recovered. A significant difference, however, is that SMNS 19003 forms a novel clade with *Aetosaurus* in this partition tree rather than with *Typothorax*. Therefore the clade Typothoracinae is not supported by this character set. Support for this topology is weak with only clade (Aetosauria) with a bootstrap value higher than 50%. *Aetosaurus* + SMNS 19003 has a Decay Index of +1, a bootstrap value of 48%, and is supported by three unambiguous synapomorphies: 1) ventrolateral margin of the nasal forms part of the dorsal border of the antorbital fossa (10-1); 2) postorbital contacts quadratojugal (15-1); and 3)) supratemporal fenestra is greatly reduced in size compared to the orbit (22-2).

A subset of the non-osteoderm dataset, consisting of only cranial characters, was also run using the branch and bound search criteria. This run (12 in-group taxa, 35 informative characters, four ordered) resulted in thirteen MPTs of 82 steps (C.I. = 0.5488, H.I. = 0.4512, R.I. = 0.5542, R. C. = 0.3041) shown as Figure 7d. This tree is most similar to the non-osteoderm dataset tree, but less resolved. The base of the tree is a large polytomy with *Aetosaurus*, *Aetosauroides, Typothorax*, *Coahomasuchus*, SMSN 19003, and *Stenomyti*. *Longosuchus* and *Desmatosuchus* form a clade (Desmatosuchini) with *Scutarx*, *Neoaetosauroides*, and *Stagonolepis robertsoni* as successive sister taxa. Support is no better than in the endoskeletal (non-osteoderm) tree, with all clades a Decay Indices of +1 and a bootstrap values less than 50% (Figure 7d). As with the endocranial set Typothoracinae is not recovered. However, neither is the clade *Aetosaurus* + SMNS 19003, which was recovered in the endocranial set.

Dataset Incongruence

A partition homogeneity test was conducted in PAUP* for the 'simultaneous analysis' matrix (excluding uninformative characters following the recommendations of Lee, 2001) divided into three partitions (osteoderm, postcranial, and cranial) using the CHARSET command in PAUP*. The test resulted in a p-value score of 0.03 suggesting that some character conflict exists between the partitioned datasets. Incongruence Length Difference (ILD) tests (Farris et al., 1995) were run for each partition set, comparing each to the other two sets. The test without the cranial set had a p-value score of 0.70, that without the endoskeletal (non-osteoderm) set had a score of 0.08, and the test excluding the osteoderm set had a p-value of 0.35. These results all show significant incongruence over the 0.05 threshold. These numbers also suggest that although the cranial and osteoderm sets are the most compatible, with low conflict, the osteoderm and postcranial sets and the cranial and postcranial sets have high levels of conflict. Size differences between the partitions (i.e. number of characters) do not influence the ILD test, thus datasets with higher amounts of characters do not ‘overwhelm’ partitions with lower numbers of characters (Farris et al., 1995; Baker et al., 1998). Therefore these numbers are the result of dataset incongruence.

Bull et al., (1993) argued that dataset partitions with high levels of character conflict should not be combined for analyses (the prior agreement approach), whereas others (e.g., Kluge, 1989; Barrett et al., 1991) argue that data should be combined in all cases (the total evidence approach). Still others argued that these debates have been mostly theoretical and it is important to examine the actual data to understand the consequences of these approaches (Baker and DeSalle, 1997). The Partition Homogeneity Test (and ILD) measures levels of disagreement between partitions, but does not identify specific nodes where this conflict occurs (Lambkin et al., 2002). Baker and DeSalle (1997) developed a new measure, Partitioned Bremer Support (PBS) to determine the amount of support individual data partitions contribute to the branch support of the full matrix. Partition datasets that conflict with other datasets at the same node will contribute negatively to the overall branch support. Therefore isolating Bremer Support values for nodes by partition allows for the determination of localized areas of disagreement. The higher the negative PBS number, the greater the support that partition provides for an alternative node that is not present in the combined data tree (Lambkin, 2004; Brower, 2006). Moreover, strong variance in PBS scores for nodes, demonstrates conflict between partitions for node resolution (Lambkin, 2004). Neutral (0) scores indicate that there is within-dataset incongruence and that the particular partition is ambivalent about the node, reducing overall support (Lambkin et al., 2002).

The program TreeRot.v3 (Sorenson and Franzosa, 2007) was employed to calculate PBS values for the partitioned dataset. This method works back and forth between the TreeRot.v3 program and PAUP*. First the ‘simultaneous analysis’ matrix is run in PAUP* using the same parameters as the earlier run (12 in-group taxa, 69 informative characters, ten characters ordered, branch and bound search) with the three partitions set-up using the CHARSET command. PAUP* was also used to calculate Bremer Support (BS) values for the entire dataset. The resulting tree file is then entered into TreeRot to generate a PAUP* command file, which includes the Partitioned Bremer Support (PBS) values. Minimum, maximum and averaged values are given for each partition at each node. Baker and DeSalle (1997) recommended utilizing the averaged value, but Lambkin et al., (2002) argued that averaging masks some of the conflict found at each node. For this study I did use the averaged values, however, because it is the averaged values for each partition that sum to match the Bremer Support value listed for each node. The values for this analysis are provided for branches in Figure 7a. There are three numbers listed, the first is from the cranial character set, the second from the postcranial (vertebrae, girdles, limbs) character set, and the third from the osteoderm character set. Note that the three PBS values equal the total BS value for that branch and as mentioned earlier negative numbers denote negative support (homoplasy) and neutral numbers indicate node ambivalence for that dataset. Also note that these character set (CHARSET) divisions are for the purpose of determining the PBS and do not pertain directly to the partition dataset trees presented in Figures 7b-d.

The cranial character set supports eight nodes, showing no conflict with the other character sets, although support is low for four of these nodes (below +0.5). The postcranial character set supports only a single node (*Coahomasuchus* + Typothoracinae), but is mostly neutral except for two nodes where it shows moderate conflict with the other datasets, especially in one node, *Desmatosuchus* + *Longosuchus* (=Desmatosuchini), which has a PBS of -1.50. The osteoderm character set shows positive, but low, for seven out of eight nodes, including good support (+5.53) for Desmatosuchinae. The osteoderm character set shows conflict for Desmatosuchini (-1.17). In sum, character dataset conflict occurs in two nodes, Aetosauria and Desmatosuchini, with all conflict occurring with the postcranial and osteoderm datasets (Figure 7a) meaning that these partitions better support alternative phylogenies.

Discussion

Dataset partitioning and partition homogeneity tests (PHT) strongly suggest that the main character suites (i.e. cranial, postcranial, osteoderm) possess some conflicting phylogenetic signals. The PHT suggests that the postcranial dataset conflicts the most with the other datasets, and Partitioned Bremer Support analyses identify the nodes where this conflict exists.

It had been suggested by previous studies that adding more non-osteoderm character data would stabilize weakly supported and labile relationships outside of the Typothoracinae and Desmatosuchini (Desojo, 2005; Desojo et al., 2012; Heckert et al., 2015; Roberto-da-Silva et al., 2014), but doubling the size of the matrix and increasing the number of endoskeletal characters to be dominant did not create more support, these inner tree relationships still remain weakly supported, and there is little confidence in the recovered clades. It is presently unclear how stable these nodes will be. Lack of support and accuracy could be caused by the need for more taxon sampling or by large amounts of missing data (Wiens, 1998b; Heath et al., 2008), but it is also possible that it is caused by incongruence between and within character suites (Lambkin et al., 2002). Moreover, missing or inapplicable data has been argued to cause ambiguous character optimizations at nodes (Ezcurra et al., 2014).

Using the total evidence approach of Kluge (1989) and adding more solid character data may overcome dataset noise (Barrett et al., 1991), and this should be tested in future analyses. Furthermore, the present matrix contains little data from the appendicular skeleton, where the characters appear to be well-conserved, or what differences are apparent cannot be viewed outside of the realm of ontogenetic or sexual variation, but this should be a source of future characters where possible. Increased taxonomic sampling from future discoveries, including the potential discovery of other suchian taxa with lateral armor to serve as improved outgroup taxa, will undoubtedly help improve dataset resolution.

Bull et al., (1993) argued that combining heterogeneous datasets can result in ~~an~~ erroneous parsimony estimates and that it is better to keep these data separate to avoid getting a single wrong answer. Data that fail statistical tests for heterogeneity should not be combined and used in analyses that assume the data to be homogeneous, because character datasets that appear to be independent may in fact be the result of two distinct histories of character change (Bull et al., 1993). However, according to those authors Hillis (1987) argued that because some character sets may be useful in resolving certain areas of the tree, all data should be combined. If incongruent datasets are combined, any underlying positive signal will be amplified and can often cancel out dataset noise (Lee, 2009).

In the tree recovered in the main part of this study (Figure 6) it is encouraging that the topology ‘makes sense’, that is that there is nothing in the topology that would be a major surprise to an aetosaur worker, suggesting that an underlying positive signal is present. For example, *Scutarx deltatylus* and *Calyptosuchus wellesi*, are recovered in the same clade, which is expected as several specimens of *Scutarx* had initially been assigned to *Calyptosuchus* (e.g., Parker and Irmis, 2005; Parker and Martz, 2011; Martz et al., 2013). *Stenomyti huangae* and *Aetosaurus ferratus* are recovered close together just outside of Typothoracinae (Figure 6) and therefore presents a proposed relationship with little statistical support, yet when originally discovered the material of *Stenomyti* was originally assigned to *Aetosaurus* (Small, 1998) and utilizing only anatomical comparisons it would be expected for the two to be recovered close together, again suggesting an underlying positive signal. In contrast, the tree presented by Parker (2007) introduced two strong clades (Typothoracinae, Desmatosuchinae), but generally the overall recovered topology did not ‘make sense’ in regards that, 1) no terminal taxa stemmed from the base of the tree (i.e. there is no ‘basal’ species-group taxon), and 2) outside of the two

~~strong~~ clades, all of the other taxa were an unresolved ‘hodge-podge’ unsupported by synapomorphies other than a few armor characters.

Nonetheless, caution is warranted when equating ‘sense’ with accuracy. For example, at one time it was thought that taxa with a radial ornamentation on the paramedian osteoderms, and similar lateral osteoderm anatomy formed a widely inclusive clade (Aetosaurinae, Parker, 2007), or a genus-group taxon (*Stagonolepis sensu* Heckert and Lucas, 2000) and the tree presented by Parker (2007) supported th~~o~~se hypotheses to some extent. However, these hypotheses quickly ~~fell apart~~ when new cranial data were added ~~showing~~ that these osteoderm characters are potentially homoplastic (Parker, 2008b; Desojo et al., 2012). Indeed, in the partition analyses presented here those clades are not recovered in the endoskeletal analyses (Figures 3c, d) and therefore are based almost entirely on osteoderm characters. Moreover, the full analysis shows that the main character combining these taxa~~,~~ radial ornamentation of the paramedian osteoderms~~,~~ is simply a plesiomorphic character of non-desmatosuchins. Thus, these data strongly suggest that even in a tree with much ‘noise’ (conflicting character data, weak clade support) that a well-supported phylogenetic signal is coming through that is only amplified over the ‘noise’ when all of the data are combined (Baker and DeSalle, 1997).

Prospectus

Many of the discussions of dataset partitioning and character congruence and the strategies devised to deal with problems are from studies where morphological and molecular data are being combined (e.g., Bull et al., 1993; Huelsenbeck et al., 1996; Cunningham, 1997; DeSalle and Brower, 1997; Wiens, 1998a, but see Mounce, 2013). However, there is no reason not to suspect that the same phenomena may occur in studies using purely morphological data. Different anatomical modules may possess different histories and thus present conflicting character data that can mask true phylogenetic relationships or support false ones. I would encourage workers conducting phylogenetic analyses of morphological datasets to explore the possibilities of incongruent subsets in their data.

Furthermore, ontogenetic change in aetosaurians is still poorly understood and it is important that specimens scored are at the same relative ontogenetic stage to rule out the possibility of differences caused by developmental history. Determination of maturity indicators can identify synonymous taxa (originally scored separately) and provide a baseline for morphological equivalence of taxa (or specimens) used in phylogenetic studies (Brochu, 1996). Presently the most often used indicator for pseudosuchians, including aetosaurians) is the progression of neurocentral suture ~~close~~ in the vertebral column (Brochu, 1996). In aetosaurians this progression begins in the caudal series and ends with the axis/atlas (Irmis, 2007). Unfortunately, many aetosaurian specimens lack relatively complete series (e.g., *Tecovasuchus chatterjeei*, TTU P-545) or completely lack preserved vertebrae (e.g., *Paratypothorax andressorum*, SMNS unnumbered). In others, the vertebral column is covered by the articulated carapace (*Coahomasuchus kahleorum*, NMMNH P-18496). Fortunately, other methods such as CT scanning and histological sectioning are available, but to date only a handful of specimens have been sampled and only two of these are holotypes (e.g., Parker et al., 2008; Cerda and Desojo, 2011). Aetosaur workers are encouraged to carefully determine and document maturity indicators for as many specimens as possible with a future goal of incorporating this information into phylogenetic analyses.

As with any scientific study, this is a work in progress. Unfortunately, it is presently unclear whether phylogenetic relationships resulting from a matrix with an abundance of osteoderm characters (e.g., Parker, 2007) are any more correct (accurate) than those formed by a matrix with an abundance of endoskeletal (non-osteoderm) characters (this study), although I have given my reasons above for preferring the latter. This study has attempted to carefully reexamine all characters used in past analyses and to construct unambiguous characters and states. Characters were scored as carefully as possible, but certainly errors exist. The Partitioned Bremer Support analysis shows where character support for individual nodes is weak or conflicting for suites of characters and therefore can be used to examine node stability when new data are added (Gatesy et al., 2003; Wahlberg and Nylin, 2003; Lambkin, 2004). Thus, future analyses should look to increase the number of informative characters, fill in blanks caused by missing data and correct erroneous scorings to improve accuracy and clade support. However, they should avoid adding large numbers of poorly supported characters (i.e. heavy on missing data) just for the sake of increasing characters numbers and instead focus on creating characters that can be fully or nearly fully coded to avoid decreasing overall accuracy (Wiens, 1998b).

REFERENCES

Much of this manuscript was originally submitted for the partial requirements for the Doctor of Philosophy Degree in Geology from the University of Texas at Austin. Constructive comments on this earlier version were provided by Sterling Nesbitt, Hans Dieter-Sues, Christopher Bell, Timothy Rowe, and Julia Clarke. Access to specimens under their care was provided by T. Scott Williams and Matt Smith (PEFO); Pat Holroyd, Mark Goodwin, and Kevin Padian (UCMP); David and Janet Gillette (MNA); Julia Desojo (MACN); Jaime Powell (PVL); Ricardo Martinez (PVSJ); Sandra Chapman, Lorna Steel, and David Gower (NHMUK); Lindsay Zanno and Vince Schneider (NCSM); Sankar Chatterjee and Bill Mueller (TTUP); Matthew Carrano (USNM); Tony Fiorillo and Ron Tykoski (DMNH); Alex Downs (GR); Charles Dailey and Dick Hilton (Sierra College); Tim Rowe, Lyndon Murray, Matt Brown, and Chris Sagebiel (UT VPL). Permission to include and discuss certain unpublished specimens was provided by Jeffrey Martz, Axel Hungerbühler, Rainer Schoch, Julia Desojo, and Tomajz Sulej. Photographs of specimens were provided by Sterling Nesbitt, Julia Desojo, Jeff Wilson, Jeff Martz, Randy Irmis, and Richard Butler. Ben Creisler graciously formulated the new taxonomic name for the Petrified Forest aetosaur. This is Petrified Forest National Park Paleontological Contribution 36.

REFERENCES

Adams, E. N. 1972. Consensus techniques and the comparison of taxonomic trees. Systematic Zoology 21:390-397.

Agassiz, L. 1844. Monographie des poisons fossiles du vieux grés rouge ou Système Dévonian (Old Red Sandstone) des Isles Britanniques ed de Russie. Jent et Gassman, Neuchâtel, 171 pp.

Antczak, M. 2015. Late Triassic aetosaur (Archosauria) from Krasiejów (SW Poland): new species or example of individual variation? Geological Journal. Published online in Wiley Online Library. DOI: 10.1002/gj.2691.

Baker, R. H., and R. DeSalle. 1997. Multiple sources of character information and the phylogeny of Hawaiian dropsophilids. Systematic Biology 46:654-673.

Baker, R. H., Yu, X., and R. DeSalle. 1998. Assessing the relative contribution of molecular and morphological characters in simultaneous analysis trees. Molecular Phylogenetics and Evolution 9:427-436.

Barrett, M, Donoghue, M. J., and E. Sober. 1991. Against consensus. Systematic Zoology 40:486-493.

Bonaparte, J. F. 1969. Dos nuevas “faunas” de reptiles Triásicos de Argentina; pp. 283-306 *in* Amos, A. J. (ed.), Gondwana Stratigraphy, IUGS Symposium, Buenos Aires, 1-15 October 1967. United Nations Educational Scientific and Cultural Organization, Paris.

Bonaparte, J. F. 1972 [imprint 1971]. Los tetrápodos del sector superior de la Formación Los Colorados, La Rioja, Argentina (Triásico Superior). I Parte. Opera Lilloana 22:1-183.

Brady, L. F. 1958. New occurrence of *Desmatosuchus* in Northern Arizona. Plateau 30:61-63.

Brochu, C. A., 1996. Closure of neurocentral sutures during crocodilian ontogeny: implications for maturity assessment in fossil archosaurs. Journal of Vertebrate Paleontology 16:49-62.

Brower, A. V. Z. 2006. The how and why of branch support and partioned branch support, with a new index to assess partition incongruence. Cladistics 22:378-386.

Bull, J. J., Huelsenbeck, J. P., Cunningham, C. W., Swofford, D. L., and P. J. Waddell. 1993. Partitioning and combining data in phylogenetic analysis. Systematic Biology 42:384-397.

Camp, C. L. 1930. A study of the phytosaurs with description of new material from Western North America. Memoirs of the University of California 10:1-174.

Casamiquela, R. M. 1960. Noticia preliminar sobre dos nuevos estagonolepoideos Argentinos. Ameghiniana 2:3-9.

Casamiquela, R. M. 1961. Dos nuevos estagonolepoideos Argentinos (de Ischigualasto, San Juan). Revista de la Asociación Geológica de Argentina 16:143-203.

Casamiquela, R. M. 1967. Materiales adicionales y reinterpretación de *Aetosauroides scagliai* (de Ischigualasto, San Juan). Revista del Museo de La Plata (nueva serie), Tomo 5, Sección Paleontología 33:173-196.

Casamiquela, R. M. 1980. Nota sobre restos de un reptile aetosauroideo (Thecodontia, Aetosauria) de Quimal, Cordillera de Domeyko, Antofagasta. Prueba de la existencia del Neotriásico continental en los Andes del Norte de Chile; pp. 135-142 *in* Anonymous (ed.), Actas del Segundo Congreso Argentino de Paleontología y Bioestratigrafía y Primer Congreso Latinoamericano de Paleontología, Buenos Aires, Argentina, 2-6 de Abril, 1978, Volume 1. Asociación Paleontológica Argentina, Buenos Aires.

Case, E. C. 1920. Preliminary description of a new suborder of phytosaurian reptiles with a description of a new species of *Phytosaurus*. Journal of Geology 28:524–535.

Case, E. C. 1922. New reptiles and stegocephalians from the Upper Triassic of western Texas. Carnegie Institution of Washington Publication 321:1-84.

Case, E. C. 1929. Description of the skull of a new form of phytosaur with notes on the characters of described North American phytosaurs. Memoirs of the University of Michigan Museums, Museum of Paleontology 2:1-56.

Case, E. C. 1932. A perfectly preserved segment of the armor of a phytosaur, with associated vertebrae. Contributions from the Museum of Paleontology, University of Michigan 4:57-80.

Cerda, I. A., and J. B. Desojo. 2011. Dermal armour histology of aetosaurs (Archosauria: Pseudosuchia), from the Upper Triassic of Argentina and Brazil. Lethaia 44:417-428.

Chatterjee, S. 1985. *Postosuchus,* a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. Philosophical Transactions of the Royal Society of London, Series B 309:395-460.

Clarke, J. A., and K. M. Middleton. 1998. Mosaicism, modules, and the evolution of birds: results from a Bayesian approach to the study of morphological evolution using discrete character data. Systematic Biology 57:185-201.

Coddington, J., and N. Scharff. 1994. Problems with zero-length branches. Cladistics 10:415-423.

Cope, E. D. 1875. Report on the geology of that part of northwestern New Mexico examined during the field season of 1874; pp. 981-1017 (61-97 of separate report LL) *in* Wheeler, G. M. (ed.) Annual report upon the geographical explorations west of the one hundredth meridian in California, Nevada, Nebraska, Utah, Arizona, Colorado, New Mexico, Wyoming and Montana. United States Government Printing Office, Washington, DC.

Cope, E. D. 1877. The extinct vertebrata obtained in New Mexico by parties of the expedition of 1874; pp.1-36B *in* Wheeler, G. M. (ed.), Report upon United States geographical surveys west of the one hundredth meridian, volume 4, paleontology. United States Government Printing Office, Washington, D. C.

Cope, E. D. 1887. A contribution to the history of the Vertebrata of the Trias of North America. Proceedings of the American Philosophical Society 24:209-228.

Cope, E. D. 1892. A contribution to the vertebrate paleontology of Texas. Proceedings of the American Philosophical Society 30:123-131.

Cunningham, C. W. 1997. Can three incongruence tests predict when data should be combined? Molecular Biology and Evolution 14:733-740.

Dalton, R. 2008. Fossil reptiles mired in controversy. Nature 451:510.

de Ricql~~é~~s, A. J., Padian, K., and J. R. Horner. 2003. On the bone histology of some Triassic pseudosuchian archosaurs and related taxa. Annales de Paléontologie 89:67-101.

DeSalle, R., and A. V. Z. Brower. 1997. Process partitions, congruence, and the independence of characters: inferring relationships among closely related Hawaiian *Drosophilla* from multiple gene regions. Systematic Biology 46:751-764.

Desojo, J. B. 2005. Los aetosaurios (Amniota, Diapsida) de América ~~D~~el Sur: sus relaciones y aportes a la biogeografía y bioestratigrafía del Triásico continental. Unpublished Ph.D dissertation, Universidad de Buenos Aires, Buenos Aires, 176 pp.

Desojo, J. B., and A. M. Báez. 2005. El esqueleto postcraneano de *Neoaetosauroides* (Archosauria: Aetosauria) del Triásico Superior del centro-oeste de Argentina. Ameghiniana 42:115-126.

Desojo, J. B., and A. M. Báez. 2007. Cranial morphology of the Late Triassic South American archosaur *Neoaetosauroides engaeus*: evidence for aetosaurian diversity. Palaeontology 50:267-276.

Desojo, J. B., and M. D. Ezcurra. 2011. A reappraisal of the taxonomic status of *Aetosauroides* (Archosauria, Aetosauria) specimens from the Late Triassic of South America and their proposed synonymy with *Stagonolepis*. Journal of Vertebrate Paleontology 31:596-609.

Desojo, J. B., and A. B. Heckert. 2004. New information on the braincase and mandible of *Coahomasuchus* (Archosauria: Aetosauria) from the Otischalkian (Carnian) of Texas. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 2004:605-616.

Desojo, J. B., and S. F. Vizcaíno. 2009. Jaw biomechanics in the South American aetosaur *Neoaetosauroides engaeus*. Paläontologische Zeitschrift 83:499–510.

Desojo, J. B., Ezcurra, M. D., and E. E. Kischlat. 2012. A new aetosaur genus (Archosauria: Pseudosuchia) from the early Late Triassic of southern Brazil. Zootaxa 3166:1-33.

Desojo, J. B., Heckert, A. B., Martz, J. W., Parker, W. G., Schoch, R. R., Small, B. J., and T. Sulej. 2013. Aetosauria: a clade of armoured pseudosuchians from the Upper Triassic continental beds; pp. 203-239 *in* Nesbitt, S.J., Desojo, J. B., and R. B. Irmis (eds.), Anatomy, Phylogeny, and Palaeobiology of Early Archosaurs and their Kin. Geological Society, London, Special Publications 379. The Geological Society Publishing House, Bath.

Deutsche Stratigraphische Kommission. 2005. Stratigraphie von Deutschland IV: Keuper. Courier Forschungs-Institut Senckenberg 253:1-296.

Donoghue, M. J., Doyle, Gauthier, J. A., Kluge, A. G., and T. Rowe. 1989. The importance of fossils in phylogeny reconstruction. Annual Review of Ecology and Systematics 20:431-460.

Dzik, J. 2001. A new *Paleorhinus* fauna in the early Late Triassic of Poland. Journal of Vertebrate Paleontology 21:625-627.

Dzik, J., and T. Sulej. 2007. A review of the early Late Triassic Krasiejów biota from Silesia, Poland. Palaeontologia Polonica 64:3–27.

Efron, B., Halloran, E., and S. Holmes. 1996. Bootstrap confidence levels for phylogenetic trees. Proceedings of the National Academy of Sciences of the U. S. A. 93:7085-7090.

Ezcurra, M. D., Scheyer, T. M., and R. J. Butler. 2014. The origin and early evolution of Sauria: reassessing the Permian saurian fossil record and the timing of crocodile-lizard divergence. PLoS ONE 9(2):e89165.

Faith, D. P. 1991. Cladistic permutation tests for monophyly and nonmonophyly. Systematic Biology 40:366-375.

Faith, D. P., and P. S. Cranston. 1991. Could a cladogram this short have arisen by chance alone? On permutation tests for cladistic structure. Cladistics 7:1-28.

Farris, J. S., Källersjö, M., Kluge, A. G., and C. Bult. 1995. Testing significance of incongruence. Cladistics 10:315-319.

Fraas, O. 1877. *Aetosaurus ferratus*, die gepanzerte Vogelechse aus dem Stubensandstein bei Stuttgart. Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg 33:1-21.

Fraser, N. C., Heckert, A. B., Lucas, S. G., and V. P. Schneider. 2006. The first record of *Coahomasuchus* (Archosauria: Stagonolepididae) from the Carnian of eastern North America. Journal of Vertebrate Paleontology 26 (supplement to number 3):63A.

Furin, S., Preto, N., Rigo, M., Roghi, G., Gianolla, P., Crowley, J. L., and S. A. Bowring. 2006. High-precision U-Pb zircon age from the Triassic of Italy: implications for the Triassic time scale and the Carnian origin of calcareous nannoplankton and dinosaurs. Geology 34:1009-1012.

Gatesy, J., Amato, G., Norell, M., DeSalle, R., and C. Hayashi. 2003. Combined support for wholesale taxic atavism in gavialine crocodylians. Systematic Biology 52:403-433.

Gauthier, J. A., Kluge, A. G., and T. Rowe. 1988. Amniote phylogeny and the importance of fossils. Cladistics 4:105-209.

Gower, D. J., and A. D. Walker. 2002. New data on the braincase of the aetosaurian archosaur (Reptilia: Diapsida) *Stagonolepis robertsoni* Agassiz; pp. 7-23 in Norman D. B. and D. J. Gower (eds.), Archosaurian Anatomy and Paleontology. Essays in Memory of Alick D. Walker. Zoological Journal of the Linnaean Society 136. The Linnaean Society of London, London.

Gregory, J. T. 1953a. *Typothorax* and *Desmatosuchus.* Postilla 16:1-27.

Gregory, J. T. 1953b. *Typothorax* scutes from Germany. Postilla 15:1-6.

Gregory, J. T. 1962. The genera of phyosaurs. American Journal of Science 260:652-690.

Gregory, J. T., and F. Westphal. 1969. Remarks on the phytosaur genera of the European Trias. Journal of Paleontology 43:1296-1298.

Harris, S. R., Gower, D. J., and M. Wilkinson. 2003. Intraorganismal homology, character construction, and the phylogeny of aetosaurian archosaurs (Reptilia, Diapsida). Systematic Biology 52:239-252.

Heath, T. A., Hedtke, S. M., and D. M. Hillis. 2008. Taxon sampling and the accuracy of phylogenetic analysis. Journal of Systematics and Evolution 46:239-257.

Heckert, A. B. 2003 [imprint 2002]. A revision of the Upper Triassic ornithischian dinosaur *Revueltosaurus*, with a description of a new species; pp. 253-268 *in* Heckert, A. B., and S. G. Lucas (eds.), Upper Triassic Stratigraphy and Paleontology. New Mexico Museum of Natural History and Science Bulletin 21. New Mexico Museum of Natural History and Science, Albuquerque.

Heckert, A. B., and S. G. Lucas. 1998. First occurrence of *Aetosaurus* (Reptilia: Archosauria) in the Upper Triassic Chinle Group (USA) and its biochronological significance. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1998:604-612.

Heckert, A. B., and S. G. Lucas. 1999. A new aetosaur (Reptilia: Archosauria) from the Upper Triassic of Texas and the phylogeny of aetosaurs. Journal of Vertebrate Paleontology 19:50-68.

Heckert, A. B., and S. G. Lucas. 2000. Taxonomy, phylogeny, biostratigraphy, biochronology, paleobiogeography, and evolution of the Late Triassic Aetosauria (Archosauria: Crurotarsi). Zentralblatt für Geologie und Paläontologie Teil I 1998 Heft 11–12:1539-1587.

Heckert, A. B., and S. G. Lucas. 2002. South American occurrences of the Adamanian (Late Triassic: latest Carnian) index taxon *Stagonolepis* (Archosauria: Aetosauria) and their biochronological significance. Journal of Paleontology 76:852-863.

Heckert, A. B., and K. E. Zeigler. 2003. The Late Triassic Snyder Quarry: A brief history of discovery and excavation; pp. 5-13 *in* Zeigler, K. E., Heckert, A. B., and S. G. Lucas (eds.), Paleontology and Geology of the Upper Triassic (Revueltian) Snyder Quarry, New Mexico. New Mexico Museum of Natural History and Science Bulletin 24. New Mexico Museum of Natural History and Science, Albuquerque.

Heckert, A. B., Hunt, A. P., and S. G. Lucas. 1996. Redescription of *Redondasuchus reseri*, a Late Triassic aetosaur (Reptilia: Archosauria) from New Mexico (U.S.A.), and the biochronology and phylogeny of aetosaurs. Geobios 29:619-632.

Heckert, A. B., Lucas, S. G., Hunt, A. P., and J. D. Harris. 2001. A giant phytosaur (Reptilia: Archosauria) skull from the Redonda Formation (Upper Triassic: Apachean) of east-central New Mexico; pp. 169-176 *in* Lucas, S. G., and D. S. Ulmer-Scholle (eds.), Geology of the Llano Estacado, 52nd Field Conference. New Mexico Geological Society Guidebook. New Mexico Geological Society, Socorro.

Heckert, A. B., Zeigler, K. E., and S. G. Lucas. 2003. Aetosaurs (Archosauria: Stagonolepididae) from the Upper Triassic (Revueltian) Snyder Quarry, New Mexico; pp. 115-126 *in* Zeigler, K. E., Heckert, A. B., and S. G. Lucas (eds.), Paleontology and Geology of the Upper Triassic (Revueltian) Snyder Quarry, New Mexico. New Mexico Museum of Natural History and Science Bulletin 24. New Mexico Museum of Natural History and Science, Albuquerque.

Heckert, A. B., Lucas, S. G., and A. P. Hunt. 2005a. Triassic vertebrate fossils in Arizona; pp. 16-44 *in* Heckert, A. B., and S. G. Lucas (eds.), Vertebrate Paleontology in Arizona. New Mexico Museum of Natural History and Science Bulletin 29. New Mexico Museum of Natural History and Science, Albuquerque.

Heckert, A. B., Lucas, S. G., Sullivan, R. M., Hunt, A. P., and J. A. Spielmann. 2005b. The vertebrate fauna of the Upper Triassic (Revueltian: early-mid Norian) Painted Desert Member (Petrified Forest Formation: Chinle Group) in the Chama Basin, northern New Mexico; pp. 302-318 *in* Lucas, S. G., Zeigler, K. E., Lueth, V. W., and D. E. Owen (eds.), Geology of the Chama Basin, 56th Field Conference. New Mexico Geological Society Guidebook. New Mexico Geological Society, Socorro.

Heckert, A. B., Spielmann, J. A., Lucas, S. G., and A. P. Hunt. 2007. Biostratigraphic utility of the Upper Triassic aetosaur *Tecovasuchus* (Archosauria: Stagonolepididae), an index taxon of St. Johnsian (Adamanian: Late Carnian) time; pp. 51-57 *in* Lucas, S. G., and J. A. Spielmann (eds.), The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41. New Mexico Museum of Natural History and Science, Albuquerque.

Heckert, A. B., Lucas, S. G., Rinehart, L. F., Celeskey, M. D., Spielmann, J. A., and A. P. Hunt. 2010. Articulated skeletons of the aetosaur *Typothorax coccinarum* Cope (Archosauria: Stagonolepididae) from the Upper Triassic Bull Canyon Formation (Revueltian: early-mid Norian), eastern New Mexico, USA. Journal of Vertebrate Paleontology 30:619-642.

Heckert, A. B., Lucas, S. G., and J. A. Spielmann. 2012. A new species of the enigmatic archosauromorph *Doswellia* from the Upper Triassic Bluewater Creek Formation, New Mexico, USA. Palaeontology 55:1333-1348.

Heckert, A. B., Schneider, V. P., Fraser, N. C., and R. A. Webb. 2015. A new aetosaur (Archosauria: Suchia) from the Upper Triassic Pekin Formation, Deep River Basin, North Carolina, U. S. A., and its implications for early aetosaur evolution. Journal of Vertebrate Paleontology 35:e881831.

Hill, R. V. 2005. Integration of morphological data sets for phylogenetic analysis of Amniota:

the importance of integumentary characters and increased taxonomic sampling. Systematic Biology 54:530-547.

Hillis, D. M., 1987. Molecular vs. morphological approaches to systematics. Annual Review of Ecology and Systematics 18:23-42.

Hillis, D. M. 1998. Taxonomic sampling, phylogenetic accuracy, and investigator bias. Systematic Biology 47:3-8.

Hillis, D. M., and J. P. Huelsenbeck. 1992. Signal, noise, and reliability in molecular phylogenetic analyses. Journal of Heredity 83:189-195.

Hillis, D. M., and J. J. Bull. 1993. An empirical test of bootstrapping as a method for accessing confidence in phylogenetic analysis. Systematic Biology 42:182-192.

Hillis, D. M., Huelsenbeck, J. P., and C. W. Cunningham. 1994. Application and accuracy of molecular phylogenies. Science 264:671-677.

Hoffstetter, R. 1955. Thecodontia; pp. 665-694 *in* Piviteau, J. (ed.), Traité de Paléontologie 5. Masson et Cie Éditeurs, Paris.

Huber, P., Lucas, S. G., and A. P. Hunt. 1993. Vertebrate biochronology of the Newark Supergroup Triassic, eastern North America; pp. 179-186 *in* Lucas, S. G., and M. Morales (eds.), The Nonmarine Triassic, Transactions of the International Symposium and Field Trip on the Nonmarine Triassic 17-24 October 1993 Albuquerque, New Mexico. New Mexico Museum of Natural History and Science Bulletin 3. New Mexico Museum of Natural History and Science, Albuquerque.

Huelsenbeck, J. P, Bull, J. J., and C. W. Cunningham., 1996. Combining data in phylogenetic analysis. Tree 11:152-157.

Huene, F. v. 1915. On reptiles of the New Mexican Trias in the Cope collection. American Museum of Natural History Bulletin 34:485-507.

Huene, F. v. 1936. The constitution of the Thecodontia. American Journal of Science 32:207-217.

Hunt, A. P. 1989. A new ?ornithischian dinosaur from the Bull Canyon Formation (Upper Triassic) of east-central New Mexico; pp. 355-358 *in* Lucas, S. G. and A. P. Hunt (eds.), Dawn of the Age of Dinosaurs in the American Southwest. New Mexico Museum of Natural History, Albuquerque.

Hunt, A. P. 1998. Preliminary results of the dawn of the dinosaurs project at Petrified Forest National Park, Arizona; pp. 135-137 *in* Santucci, V. L., and L. McClelland (eds.), National Park Service Paleontological Research. Geological Resources Division Technical Report NPS/NRGRD/GRDTR-98/01, October, 1998. Geological Resources Division, Lakewood.

Hunt, A. P. 2001. The vertebrate fauna, biostratigraphy and biochronology of the type Revueltian land-vertebrate faunachron, Bull Canyon Formation (Upper Triassic), east-central New Mexico; pp. 123-151 *in* Lucas, S. G., and D. S. Ulmer-Scholle (eds.), Geology of the Llano Estacado, 52nd Field Conference. New Mexico Geological Society Guidebook. New Mexico Geological Society, Socorro.

Hunt, A. P., and S. G. Lucas. 1990. Re-evaluation of '*Typothorax*' *meadei*, a Late Triassic aetosaur from the United States. Paläontologische Zeitschrift 64:317-328.

Hunt, A. P., and S. G. Lucas. 1991. A new aetosaur from the Redonda Formation (Late Triassic: middle Norian) of east-central New Mexico, U.S.A. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1991:728-736.

Hunt, A. P., and S. G. Lucas. 1992. The first occurrence of the aetosaur *Paratypothorax andressi* (Reptilia: Archosauria) in the western United States and its biochronological significance. Paläontologische Zeitschrift 66:147-157.

Hunt et al 1993. Typothorax.

Hunt, A. P., Lucas, S. G., and A. B. Heckert. 2005. Definition and correlation of the Lamyan: A new biochronological unit for the non-marine late Carnian (Late Triassic); pp. 357-366 *in* Lucas, S. G., Zeigler, K. E., Lueth, V. W., and D. E. Owen (eds.), Geology of the Chama Basin, 56th Field Conference. New Mexico Geological Society Guidebook. New Mexico Geological Society, Socorro.

Huxley, T. H. 1859. On the *Stagonolepis robertsoni* (Agassiz) of the Elgin Sandstone; and on the recently discovered footmarks in the Sandstones of Cummingstone. Proceedings of the Geological Society 15:440-460.

Huxley, T. H. 1875. On *Stagonolepis robertsoni*, and on the evolution of the crocodylia. Quarterly Journal of the Geological Society 31:423-438.

Huxley, T. H. 1877. The crocodilian remains found in the Elgin sandstones, with remarks on the ichnites of Cummingstone. Memoirs of the Geological Survey of the United Kingdom 3:1-58.

Irmis, R. B. 2007. Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. Journal of Vertebrate Paleontology 27:350-361.

Irmis, R. B. 2008. Perspectives on the origin and early diversification of dinosaurs. Unpublished Ph.D. dissertation, University of California, Berkeley, 421 pp.

Irmis, R. B., Nesbitt, S. J., Padian, K., Smith, N. D., Turner, A. H., Woody, D., and A. Downs. 2007. A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. Science 317:358-361.

Irmis, R. B., Martz, J. W., Parker, W. G., and S. J. Nesbitt. 2010. Re-evaluating the correlation between Late Triassic terrestrial vertebrate biostratigraphy and the GSSP-defined marine stages. Albertiana 38:40-52.

Irmis, R. B., Mundil, R., Martz, J. W., and W. G. Parker. 2011. High-resolution U–Pb ages from the Upper Triassic Chinle Formation (New Mexico, USA) support a diachronous rise of dinosaurs. Earth and Planetary Science Letters 309:258-267.

Jenkins, F. A. Jr., Shubin, N. H., Amaral, W. W., Gatesy, S. M., Schaff, C. R., Clemmensen, L. B., Downs, W. R., Davidson, A. R., Bonde, N., and F. Osbæck. 1994. Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland. Meddelelser om Grønland Geoscience 32:1-25.

Kitching, I. J., Forey, P. L., Humphries, C. J., and D. M. Williams. 1998. Cladistics: the Theory and Practice of Parsimony Analysis, 2nd edition. The Systematics Association Publication 11. Oxford University Press, Oxford.

Kluge, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Systematic Zoology 38:7-25.

Lambkin, C. L. 2004. Partitioned Bremer support localizes significant conflict in bee flies (Diptera: Bombyliidae: Anthracinae). Invertebrate Systematics 18:351-360.

Lambkin, C. L., Lee, M. S. Y., Winterton, S. L., and D. K. Yeates. 2002. Partitioned Bremer support and multiple trees. Cladistics 18:436-444.

Landry, S. O. 1958. The function of the entepicondylar foramen in mammals. American Midland Naturalist 60:100-112.

Langer, M. C., Ribeiro, A. M., Schultz, C. L., and J. Ferigolo. 2007. The continental tetrapod-bearing Triassic of South Brazil; pp. 201-218 *in* Lucas, S. G., and J. A. Spielmann (eds.), The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41. New Mexico Museum of Natural History and Science, Albuquerque.

Lee, M. S. Y. 2001. Uninformative characters and apparent conflict between molecules and morphology. Molecular Biology and Evolution 18:676-680.

Lee, M. S. Y. 2009. Hidden support from unpromising data sets strongly unites snakes with anguimorph 'lizards.' Journal of Evolutionary Biology 22:1308-1316,

Long, R. A., and K. L. Ballew. 1985. Aetosaur dermal armor from the late Triassic of southwestern North America, with special reference to material from the Chinle Formation of Petrified Forest National Park; pp. 45-68 *in* Colbert, E. H., and R. R. Johnson (eds.), The Petrified Forest Through the Ages, 75th Anniversary Symposium November 7, 1981. Museum of Northern Arizona Bulletin 54. Museum of Northern Arizona Press, Flagstaff.

Long, R. A., and P. A. Murry. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. New Mexico Museum of Natural History and Science Bulletin 4:1–254.

Lucas, S. G., 1998a. Global Triassic tetrapod biostratigraphy and biochronology. Palaeogeography, Palaeoclimatology, Palaeoecology 143:347-384.

Lucas, S. G. 1998b. The aetosaur *Longosuchus* from the Triassic of Morocco and its biochronological significance. Compte Rendus de l’Académie des Science ~~Paris~~. Sciences de la Terre et des Planètes 326:589–594.

Lucas, S. G. 2000. Pathological aetosaur armor from the Upper Triassic of Germany: Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie) 281:1-6.

Lucas, S. G. 2010. The Triassic timescale based on nonmarine tetrapod biostratigraphy and biochronology, pp. 447-500 *in* Lucas, S. G. (ed.) The Triassic Timescale. Geological Society, London, Special Publications 334. The Geological Society Publishing House, Bath.

Lucas, S. G., and A. B. Heckert. 1996. Vertebrate biochronology of the Late Triassic of Arizona; pp. 63-81 *in* Boaz, D., Dierking, P., Dornan, M., McGeorge, R., and B. J. Tegowski (eds.), Proceedings of the Fossils of Arizona Symposium Volume 4. Mesa Southwest Museum Bulletin and the City of Mesa, Mesa.

Lucas, S. G., and A. B. Heckert. 2001. The aetosaur *Stagonolepis* from the Upper Triassic of Brazil and its biochronological significance. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 2001:719–732.

Lucas, S. G., and S. Connealy. 2008. Triassic New Mexico: Dawn of the Dinosaurs. New Mexico Museum of Natural History and Science, Albuquerque, 48 pp.

Lucas, S. G., Hunt, A. P., and R. Kahle. 1993. Late Triassic vertebrates from the Dockum Formation near Otis Chalk, Howard County, Texas; pp. 237–244 *in* Love, D. W., Hawley, J. W., Kues, B. S., Adams, J. W., Austin, G. S., and J. M. Barker (eds.), Carlsbad Region, New Mexico and West Texas, 44th Field Conference. New Mexico Geological Society, Albuquerque.

Lucas, S. G., Heckert, A. B., and A. P. Hunt. 1995. Unusual aetosaur armor from the Upper Triassic of west Texas. Paläontologische Zeitschrift 69:467-473.

Lucas et al 1998. Aetosaurus.

Lucas, S. G., Heckert, A. B., and A. P. Hunt. 2003 [imprint 2002]. A new species of the aetosaur *Typothorax* (Archosauria: Stagonolepididae) from the Upper Triassic of east-central New Mexico; pp. 221-233 *in* Heckert, A. B., and S. G. Lucas (eds.), Upper Triassic Stratigraphy and Paleontology. New Mexico Museum of Natural History and Science Bulletin 21. New Mexico Museum of Natural History and Science, Albuquerque.

Lucas, S. G., Zeigler, K. E., Heckert, A. B., and A. P. Hunt. 2005. Review of Upper Triassic stratigraphy and biostratigraphy in the Chama Basin, northern New Mexico; pp. 170-181 *in* Lucas, S. G., Zeigler, K. E., Lueth, V. W., and D. E. Owen (eds.), Geology of the Chama Basin, 56th Field Conference. New Mexico Geological Society Guidebook. New Mexico Geological Society, Socorro.

Lucas, S. G., Hunt, A. P., and J. A. Spielmann. 2006a. *Rioarribasuchus*, a new name for an aetosaur from the Upper Triassic of north-central New Mexico; pp. 581-582 *in* Harris, J. D., Lucas, S. G., Spielmann, J. A., Lockley, M. G., Milner, A. R. C., and J. I. Kirkland (eds.), The Triassic-Jurassic Terrestrial Transition. New Mexico Museum of Natural History and Science Bulletin 37. New Mexico Museum of Natural History and Science, Albuquerque.

Lucas, S. G., Heckert, A. B., and L. F. Rinehart. 2006b. The Late Triassic aetosaur *Paratypothorax*; pp. 575-580 *in* Harris, J. D., Lucas, S. G., Spielmann, J. A., Lockley, M. G., Milner, A. R. C., and J. I. Kirkland (eds.), The Triassic-Jurassic Terrestrial

Transition. New Mexico Museum of Natural History and Science Bulletin 37. New Mexico Museum of Natural History and Science, Albuquerque.

Lucas, S. G., Hunt, A. P., and J. A. Spielmann. 2007a. A new aetosaur from the Upper Triassic (Adamanian: Carnian) of Arizona; pp. 241-247 *in* Lucas, S. G. and J. A. Spielmann (eds.), Triassic of the American West. New Mexico Museum of Natural History and Science Bulletin 40. New Mexico Museum of Natural History and Science, Albuquerque.

Lucas, S. G., Spielmann, J. A., and A. P. Hunt. 2007b. Biochronological significance of Late Triassic tetrapods from Krasiejów, Poland; pp. 248-258 *in* Lucas, S. G. and J. A. Spielmann (eds.), The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41. New Mexico Museum of Natural History and Science, Albuquerque.

Lydekker, R. 1887. The fossil Vertebrata of India. Records of the Geological Survey of India 20:51–80.

Maddison, W. P. and D. R. Maddison. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org.

Main, R. P., de Ricqlès, A., Horner, J. R., and K. Padian. 2005. The evolution and function of thyreophoran dinosaur scutes: implications for plate function in stegosaurs. Paleobiology 31:291-314.

Marsh, O. C. 1884. The classification and affinities of dinosaurian reptiles. Nature 31:68–69.

Martinez, R. N., Sereno, P. C., Alcober, O. A., Colombi, C. E., Renne, P. R., Montañez, I. P., and B. S. Currie. 2011. A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. Science 331:206–210.

Martinez, R. N., Apaldetti, C., Alcober, O. A., Columbi, C. E., Sereno, P. E., Fernandez, E., Santi Malnis, P., Correa, G. A., and D. Abelin. 2013 [imprint 2012]. Vertebrate succession in the Ischigualasto Formation; pp. 10-30 *in* Sereno, P. C. (ed.), Basal Sauropodomorphs and the Vertebrate Fossil Record of the Ischigualasto Formation (Late Triassic: Carnian-Norian) of Argentina. Society of Vertebrate Paleontology Memoir 12. Journal of Vertebrate Paleontology 32 (supplement to number 6), November 2012.

Martz, J. W. 2002. The morphology and ontogeny of *Typothorax coccinarum* (Archosauria, Stagonolepididae) from the Upper Triassic of the American Southwest. Unpublished M.S. thesis, Texas Tech University, Lubbock, TX, 279 pp.

Martz, J. W. 2008. Lithostratigraphy, chemostratigraphy, and vertebrate biostratigraphy of the Dockum Group (Upper Triassic), of southern Garza County, West Texas. Unpublished Ph.D. dissertation, Texas Tech University, Lubbock, Texas, 504 pp.

Martz, J. W., and B. J. Small. 2006. *Tecovasuchus chatterjeei*, a new aetosaur (Archosauria: Aetosauria) from the Tecovas Formation (Upper Triassic, Carnian) of Texas. Journal of Vertebrate Paleontology 26:308–320.

Martz, J. W., Mueller, B., Nesbitt, S. J., Stocker, M. R., Parker, W. G., Atanassov, M., Fraser, N., Weinbaum J., and J. R. Lehane. 2013. A taxonomic and biostratigraphic re-evaluation of the Post Quarry vertebrate assemblage from the Cooper Canyon Formation (Dockum Group, Upper Triassic) of southern Garza County, western Texas; pp. 339-364 *in* Parker, W., Bell, C., Brochu, C., Irmis, R., Jass, C, Stocker, M., and M. Benton (eds.), The Full Profession: A Celebration of the Life and Career of Wann Langston Jr., Quintessential Vertebrate Paleontologist. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 103.

Meyer, H. v.1865. Reptilien aus dem Stubensandstein des oberen Keupers. Palaeontographica 14:99-124.

Mounce, R. C. P. 2013. Comparative cladistics: fossils, morphological data partitions and lost branches in the fossil tree of life. Unpublished Ph.D. Dissertation, University of Bath, 161 pp.

Murry, P. A., and R. A. Long. 1989. Geology and paleontology of the Chinle Formation, Petrified Forest National Park and vicinity, Arizona and a discussion of vertebrate fossils of the southwestern Upper Triassic; pp. 29–64 *in* S. G. Lucas and A. P. Hunt (eds.), Dawn of the Age of Dinosaurs in the American Southwest. New Mexico Museum of Natural History, Albuquerque.

Murry, P. A., and R. A. Long. 1996. A diminutive carnivorous aetosaur from the Upper Triassic of Howard County, Texas. Journal of Vertebrate Paleontology 16 (supplement to number 3):55A.

Nesbitt, S. J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. Bulletin of the American Museum of Natural History 352:1–292.

O'Leary, M. A., and S. G. Kaufman. 2012. MorphoBank 3.0: Web application for morphological phylogenetics and taxonomy. http://www.morphobank.org.

Padian, K. 1990. The ornithischian form genus *Revueltosaurus* from the Petrified Forest of Arizona (Late Triassic, Norian; Chinle Formation). Journal of Vertebrate Paleontology 10:268-269.

Page, R. D. M. 2001. Nexus Data Editor for Windows (NDE), version 0.5.0. Program and documentation. Available online at: http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde.html. Published by the author, Glasgow, U.K.

Parker, W. G. 2002 [imprint 2001]. An enigmatic aetosaur specimen from the Upper Triassic Dockum Formation of Texas (Abstract); p. 17 *in* McCord, R. D., and D. Boaz (eds.), Western Association of Vertebrate Paleontologists with Mesa Southwest Museum and Southwest Paleontological Society Mesa, Arizona, First Meeting of the New Millennium. Mesa Southwest Museum Bulletin 8. Southwest Paleontological Society, Mesa Southwest Museum, and the City of Mesa, Mesa.

Parker, W. G. 2003. Description of a new specimen of *Desmatosuchus haplocerus* from the Late Triassic of northern Arizona. Unpublished M. S. Thesis, Northern Arizona University, Flagstaff, 315 pp.

Parker, W. G. 2005a. Faunal review of the Upper Triassic Chinle Formation of Arizona; pp. 34-54 *in* McCord, R. D. (ed.), Vertebrate Paleontology of Arizona. Mesa Southwest Museum Bulletin 11. Southwest Paleontological Society, Mesa Southwest Museum and the City of Mesa, Mesa.

Parker, W. G. 2005b. A new species of the Late Triassic aetosaur *Desmatosuchus* (Archosauria: Pseudosuchia). Compte Rendus Paleovol 4:327-340.

Parker, W. G. 2006. The stratigraphic distribution of major fossil localities in Petrified Forest National Park, Arizona; pp. 46-62 *in* Parker, W. G., Ash, S. R., and R. B. Irmis (eds.), A Century of Research at Petrified Forest National Park 1906-2006: Geology and Paleontology. Museum of Northern Arizona Bulletin 62. Petrified Forest Museum Association, Holbrook.

Parker, W. G. 2007. Reassessment of the aetosaur "*Desmatosuchus*" *chamaensis* with a reanalysis of the phylogeny of the Aetosauria (Archosauria: Pseudosuchia). Journal of Systematic Palaeontology 5:1–28.

Parker, W. G. 2008a. How many valid aetosaur species are there? Reviewing the alpha-taxonomy of the Aetosauria (Archosauria: Pseudosuchia) and its implications for Late Triassic global biostratigraphy. Journal of Vertebrate Paleontology 28 (supplement to number 3):125A.

Parker, W. G. 2008b. Description of new material of the aetosaur *Desmatosuchus spurensis* (Archosauria: Suchia) from the Chinle Formation of Arizona and a revision of the genus *Desmatosuchus*. PaleoBios new series 28:1–40.

Parker, W. G. 2013. Redescription and taxonomic status of specimens of *Episcoposaurus* and *Typothorax*, the earliest known aetosaurs (Archosauria: Suchia) from the Upper Triassic of western North America, and the problem of proxy 'holotypes;' pp. 313-338 *in* Parker, W., Bell, C., Brochu, C., Irmis, R., Jass, C, Stocker, M., and M. Benton (eds.), The Full Profession: A Celebration of the Life and Career of Wann Langston Jr., Quintessential Vertebrate Paleontologist. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 103.

Parker, W. G. 2014. Taxonomy and phylogeny of the Aetosauria (Archosauria: Pseudosuchia) including a new species from the Upper Triassic of Arizona. Unpublished Ph.D. dissertation. The University of Texas at Austin, 437 pp.

Parker, W. G., and R. B. Irmis. 2005. Advances in Late Triassic vertebrate paleontology based on material from Petrified Forest National Park, Arizona; pp. 45-58 *in* Heckert, A. B. and S. G. Lucas (eds.), Vertebrate Paleontology in Arizona. New Mexico Museum of Natural History and Science Bulletin 29. New Mexico Museum of Natural History and Science, Albuquerque.

Parker, W. G., and J. W. Martz. 2010. Using positional homology in aetosaur (Archosauria: Pseudosuchia) osteoderms to evaluate the taxonomic status of *Lucasuchus hunti*. Journal of Vertebrate Paleontology 30:1100–1104.

Parker, W. G., and J. W. Martz. 2011. The Late Triassic (Norian) Adamanian–Revueltian tetrapod faunal transition in the Chinle Formation of Petrified Forest National Park, Arizona; pp. 231-260 *in* Butler, R. J., Irmis, R. B., Langer, M. C., and A. B. Smith (eds.), Late Triassic Terrestrial Biotas and the Rise of Dinosaurs. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 101 (for 2010).

Parker, W. G., Stocker, M. R., and R. B. Irmis. 2008. A new desmatosuchine aetosaur (Archosauria: Suchia) from the Upper Triassic Tecovas Formation (Dockum Group) of Texas. Journal of Vertebrate Paleontology 28:692–701.

Parker, W. G., Irmis, R. B., Nesbitt, S. J., Martz, J. W., and L. S. Browne. 2005. The Late Triassic pseudosuchian *Revueltosaurus callenderi* and its implications for the diversity of early ornithischians dinosaurs. Proceedings of the Royal Society, Series B 272:963–969.

Parker, W. G., Brown, M. B., Nesbitt, S. J., Stocker, M. R., and R. B. Irmis. 2007. Revised osteology of *Revueltosaurus callenderi* (Archosauria: Pseudosuchia) based on new material from Petrified Forest National Park, Arizona. Journal of Vertebrate Paleontology 27 (supplement to number 3):127A.

Parrish, J. M. 1994. Cranial osteology of *Longosuchus meadei* and the phylogeny and distribution of the Aetosauria. Journal of Vertebrate Paleontology 14:196-209.

Rae, T. C. 1999. Mosaic evolution in the origin of the Hominoidea. Folia Primatologia 70:125-135.

Ramezani, J., Hoke, G. D., Fastovsky, D. E., Bowring, S. A., Therrien, F., Dworkin, S. I., Atchley, S. C., and L. C. Nordt. 2011. High-precision U–Pb zircon geochronology of the Late Triassic Chinle Formation, Petrified Forest National Park (Arizona, USA): temporal constraints on the early evolution of dinosaurs. Geological Society of America Bulletin 123:2142-2159.

Ramezani, J., Fastovsky, D. E., and S. A. Bowring. 2014. Revised chronostratigraphy of the lower Chinle Formation strata in Arizona and New Mexico (USA): high-precision U-Pb geochronological constraints on the Late Triassic evolution of dinosaurs. American Journal of Science 314:981-1008.

Roberto-Da-Silva, L., Desojo, J. B., Cabriera, S. F., Aires, A. S. S., Müller, S. T., Pacheco, C. P., and S. Dias-Da-Silva. 2014. A new aetosaur from the Upper Triassic of the Santa Maria Formation, southern Brazil. Zootaxa 3764:240-278.

Rogers, R. R., Swisher III, C. C., Sereno, P. C., Monetta, A. M., Forster, C. A., and R. N. Martinez. 1993. The Ischigualasto Tetrapod Assemblage (Late Triassic, Argentina) and ^{40}Ar/^{39}Ar dating of dinosaur origins. Science 260:794-797.

Romer, A. S. 1956. Osteology of the Reptiles. University of Chicago Press, Chicago. 772 pp.

Rowe, T. 1988. Definition, diagnosis, and the origin of Mammalia. Journal of Vertebrate Paleontology 8:241-264.

Santi Malnis, P., Kent, D. V., Colombi, C. E., and S. E. Geuna. 2011. Quebrada de la Sal magnetostratigraphic section, Los Colorados Formation, Upper Triassic Ischigualasto Villa Unión basin, Argentina; pp. B15, 1-7 *in* Sinito, A. M., Caballero Miranda, C. I., Soler Arrechadle, A. M., Sánchez Bettucci, L, and M. Aldana (eds), Proceedings of the Second Biennial Meeting of the Latin American Association of Paleomagnetism and

Geomagnetism, Tandil, Argentina, November 2011. Latinmag Letters Proceedings 1, Special Issue LL11-02SP. Instituto de Geofisica, Universidad Nacional Autónoma de México, Mexico City.

Sawin, H. J. 1947. The pseudosuchian reptile *Typothorax meadei*. Journal of Paleontology 21:201–238.

Scheyer, T. M., Desojo, J. B., and I. A. Cerda. 2013. Bone histology of phytosaur, aetosaur, and other archosauriform osteoderms (Eureptilia: Archosauromorpha). The Anatomical Record 297:240-260.

Schneider, V. P., Heckert, A. B., and N. C. Fraser. 2011. Diversity of aetosaurs (Archosauria: Stagonolepididae) in the Upper Triassic Pekin Formation (Deep River Basin), North Carolina. Society of Vertebrate Paleontology Abstracts of Papers Seventy-First Annual Meeting of the Society of Vertebrate Paleontology, Paris Las Vegas Hotel Las Vegas, Nevada, USA November 2-5, 2011, p. 188.

Schoch, R. R. 2007. Osteology of the small archosaur *Aetosaurus* from the Upper Triassic of Germany. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 246:1–35.

Seidel, M. R. 1979. The osteoderms of the American Alligator and their functional significance. Herpetologica 35:375-380.

Sereno, P. C. 1985. The logical basis of phylogenetic taxonomy. Systematic Biology 54:595-619.

Slowinski, J. 1993. ‘‘Unordered’’ versus ‘‘ordered’’ characters. Systematic Biology 42:155-165.

Small, B. J. 1985. The Triassic thecodontian reptile *Desmatosuchus*: osteology and relationships. Unpublished M.S. thesis, Texas Tech University, Lubbock, Texas, 83 pp.

Small, B. J. 1989. Aetosaurs from the Upper Triassic Dockum Formation, Post Quarry, West Texas; pp. 301-308 *in* Lucas, S. G., and A. P. Hunt (eds.), Dawn of the Age of Dinosaurs in the American Southwest, New Mexico Museum of Natural History, Albuquerque.

Small, B. J. 1998. The occurrence of *Aetosaurus* in the Chinle Formation (Late Triassic, USA) and its biostratigraphic significance. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1998:285-296.

Small, B. J. 2002. Cranial anatomy of *Desmatosuchus haplocerus* (Reptilia: Archosauria: Stagonolepididae). Zoological Journal of the Linnean Society 136:97-111.

Small, B. J., and J. W. Martz. 2013. A new basal aetosaur from the Upper Triassic Chinle Formation of the Eagle Basin, Colorado, USA; pp. 393-412 *in* Nesbitt, S. J., Desojo, J. B., and R. B. Irmis (eds.), Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. Geological Society, London, Special Publications 379. The Geological Society Publishing House, Bath.

Sorenson, M. D. and E. A. Franzosa. 2007. TreeRot, version 3. Boston University, Boston, MA.

Spielmann, J. A., and S. G. Lucas. 2012. Tetrapod fauna of the Upper Triassic Redonda Formation, east-central New Mexico: the characteristic assemblage of the Apachean land-vertebrate faunachron. New Mexico Museum of Natural History and Science Bulletin 55:1-119.

Spielmann, J. A., Hunt, A. P., Lucas, S. G., and A. B. Heckert. 2006. Revision of *Redondasuchus* (Archosauria: Aetosauria) from the Upper Triassic Redonda Formation, New Mexico, with a description of a new species; pp. 583-587 *in* Harris, J. D., Lucas, S. G., Spielmann, J. A., Lockley, M. G., Milner, A. R. C., and J. I. Kirkland (eds.), The Triassic-Jurassic

Terrestrial Transition. New Mexico Museum of Natural History and Science Bulletin 37. New Mexico Museum of Natural History and Science, Albuquerque.

Sulej, T. 2010. The skull of an early Late Triassic aetosaur and the evolution of the stagonolepidid archosaurian reptiles. Zoological Journal of the Linnean Society 158:860-881.

Swofford, D.L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates: Sunderland, Massachusetts.

Swofford, D. L., and D. P. Begle. 1993. User manual for PAUP*, Phylogenetic Analysis Using Parsimony, version 3.1. Illinois Natural History Survey, Champaign.

Vickaryous, M. K., and B. K. Hall. 2008. Development of the dermal skeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. Journal of Morphology 269:398-422,

Wahlberg, N., and S. Nylin. 2003. Morphology versus molecules: resolution of the positions of *Nymphalis*, *Polygonia*, and related genera (Lepidoptera: Nymphalidae). Cladistics 19:213-223.

Walker, A. D. 1961. Triassic Reptiles from the Elgin Area: *Stagonolepis*, *Dasygnathus*, and their allies. Philosophical Transactions of the Royal Society of London 244:103–204.

Weinbaum, J. C. 2011. The skull of *Postosuchus kirkpatricki* (Archosauria: Paracrocodyliformes) from the Upper Triassic of the United States. PaleoBios new series 30:18-44.

Weinbaum, J. C. 2013. Postcranial skeleton of *Postosuchus kirkpatricki* (Archosauria: Paracrocodylomorpha) from the Upper Triassic of the United States; pp. 525-553 *in* Nesbitt, S. J., Desojo, J. B. and R. B. Irmis, (eds.), Anatomy, Phylogeny and

Palaeobiology of Early Archosaurs and their Kin. Geological Society, London, Special Publications 379. The Geological Society Publishing House, Bath.

Wiens, J. J. 1998a. Combining datasets with different phylogenetic histories. Systematic Biology 47:568-581.

Wiens, J. J. 1998b. Does adding characters with missing data increase or decrease phylogenetic accuracy? Systematic Biology 47:625-640.

Wild, R. 1989. *Aetosaurus* (Reptilia: Thecodontia) from the Upper Triassic (Norian) of Cene near Bergamo, Italy, with a revision of the genus. Rivista del Museo Civico di Scienze Naturali 14:1–24.

Wilkinson, M. 1995a. Coping with abundant missing entries in phylogenetic inference using parsimony. Systematic Biology 44:501-514.

Wilkinson, M. 1995b. A comparison of two methods of character construction. Cladistics 11:297-308.

Wilson, J. A. 1999. Vertebral laminae in sauropods and other saurischian dinosaurs. Journal of Vertebrate Paleontology 19:639-653.

Zacarias, J. D. 1982. Una nova especie de tecodonte aetosaurio (*Aetosauroides subsulcatus*, sp. nov.) de Formaçáo Santa Maria, Triassico de Rio Grande du Sul, Basil. Unpublished M.S. thesis, Federal University of ~~the State of Rio Grande~~, Porto Alegre, Brazil, 69 pp.

Zeigler, K. E., Heckert, A. B., and S. G. Lucas. 2003 [imprint 2002]. A new species of *Desmatosuchus* (Archosauria: Aetosauria) from the Upper Triassic of the Chama Basin, north-central New Mexico; pp. 215-219 *in* Heckert, A. B. and S. G. Lucas (eds.), Upper

Triassic Stratigraphy and Paleontology. New Mexico Museum of Natural History and Science Bulletin 21. New Mexico Museum of Natural History and Science, Albuquerque.

APPENDIX A

PHYLOGENETIC MATRIX:

```
	MATRIX
	'Postosuchus kirkpatricki'
0000000000000000000000000000000000000000000000000-------------------00---------0
	'Revueltosaurus callenderi'
000000100110010110100001100000000120010001100101101100000000000000-0000011---------2
	'Adamanasuchus eisenhardtae'
???????????????????????????????????????????????????11101?????011010101?120?1-00000?
	'Aetosaurus ferratus'
011011100100021111010 2?101111100122?01000??000001?11110000000000101000011 2001-000002
	'Apachesuchus heckerti'
??????????????????????????????????????????????????1310?0?00?0020100?0????????????2?
	'Stagonolepis robertsoni'
1110111011101 10??0?100?00101211012200100001000001101110000000000001000011 2001-000002
	'Stagonolepis olenkae'
11101120101??20??1110000011111 10122???00001??0011??11100??00000001000011 2001-00000?
	'Calyptosuchus wellesi'
?????????????????????????0????????0000000100???0?0111010?000010101001 12001-000002
	'Scutarx deltatylus'
?????1????1????????101001???2??????0000000100???010111010?0000101010211 2001-000002
	'Aetosauroides scagliai'
?0100110010??2????1100?1010100???1000110001001000001110000000000001000011 2001-000002
	'Coahomasuchus kahleorum'
?????10???00??111?1??01000?0?0?12000100001 0?11????11100000000010100001 12001-000002
	'Desmatosuchus spurensis'
?1???121101110??0?1100101??????10??1020010000???100300001111110000121011 23100211210
	'Desmatosuchus smalli'
1122112110111001 0011??1012111101022002001000000111003000011111100001210112310021 1210
	'Rioarribasuchus chamaensis'
????????????????????????????????????????????1??????210000?000012020000412102112012?
	'Longosuchus meadei'
?1???121?0010????1?10111101111101221000000100101100101001111110001121011220012 11210
```

```
	'Lucasuchus hunti'
???????????????????????????????????????????????????11000111121000002103122000211?1?
	'NCSM 21723'
???????????????????????????????????????????????????20100010?210?011?10?122000?11?1?
	'Neoaetosauroides engaeus'
1110?12?0?1112???1?10100001121?1?22011000????01010?1100?00000000020100112001-000002
	'Typothorax coccinarum'
011?012000?0???2?10100?10?01010102211001101000110011210201000012010000112101-020122
	'Redondasuchus rineharti'
????????????????????????????????????120????????????121020?0000120100?01121?1-02012?
	'Paratypothorax andressorum'
????????????????????????????????????????1011???????210120?000012120000212102112012?
	'Paratypothorax sp.'
???????????????????????????????????????110111?0????210020?000012120000212102112012?
	'Tecovasuchus chatterjeei'
???????????????????????10???????????0?0????0???????110120???0012120000112102112012?
	'Sierritasuchus macalpini'
???????????????????????????????????0000010?0???????10100111111000012101122001211?1?
	'SMSN 19003'
01101110010002121?1112???1??01?0?11????????????????2101?000000120200?0112102112012?
	'Aetobarbakinoides brasiliensis'
???????????????????????????????????10?000000??01???11?0?0??000?001????1????????????
	'Stenomyti huangae'
0111111000000201000111???10121?1122????????????????1110?0000?000020100112001-000001
	'Polesinesuchus aurelioi'
???????????????????????0???????????00100??100000111111000?001000010?0011??????????2
	;
ENDBLOCK;
```

APPENDIX B

DESCRIPTION OF CHARACTERS

Many of these characters are taken from earlier phylogenetic studies by Parrish (1994), Heckert et al., (1996), and Heckert and Lucas (1999), although some have been modified to incorporate more recent understanding of aetosaurian anatomy. Thus, these are considered framework studies in addition to the phylogenetic work of Parker (2007), with each study building on the former as our knowledge of aetosaur anatomy and taxonomy has increased. Therefore, in this section rather than repeating all of the citations for every character, only the initial analysis where a character first appeared in its original form is listed.

Cranial Characters

1. Premaxilla, anterior portion in dorsal view: tapers anteromedially (0); laterally expanded (1). Modified from Parrish, 1994: character 3 (in part). Figures B1a, c, d, f.

In aetosaurians such as *Stagonolepis robertsoni* (Walker, 1961) and *Desmatosuchus smalli* (TTU P-9024) the anterior end of the premaxilla is mediolaterally wide and maintains a nearly constant width until the apex, which is an inclined and mediolaterally expanded, described as a “shovel” by previous workers (e.g., Parrish, 1994). This expanded apex was considered to be present in all aetosaurs for which a premaxilla was preserved, therefore in earlier phylogenetic analyses the character was an autapomorphy of Aetosauria and parsimony uninformative (Parrish, 1994; Heckert and Lucas, 1999a. Parker (2007) noted that an expanded apex was not present in *Aetosaurus* (SMNS 5770, S-16) and SMNS 19003. In these taxa the premaxillae gradually decrease in width anteriorly and bear flattened lateral margins (Small and Martz, 2013). The premaxillae of *Typothorax coccinarum* (PEFO 38001/YPM 58121), *Stenomyti huangae* (Small and Martz, 2013), and *Aetosauroides scagliai* (PVL 2073) also taper and lack the expanded apex.

2. Premaxilla, contact of posterior process with nasal: present, excludes maxilla from the margin of the external naris (0); absent, maxilla participates in the posterior margin of the external naris (1). Modified from Heckert and Lucas (1999a), character 13. Figures B1a, g.

Contact between the nasal and premaxilla, excluding the maxilla from participation in the margin of the external naris is an apomorphy of Archosauriformes (Nesbitt, 2011). However, with the exception of *Aetosauroides scagliai* (PVL 2073), this contact is not present in aetosaurians and the maxilla forms a portion of the posterior and posteroventral borders of the external naris. In the referred skull of *Aetosauroides scagliai* (PVL 2073) the posterior process of the premaxilla underlies the entire length of the external naris contacting the ventral process of the nasal and excluding the maxilla from the border of naris (Casimiquela, 1961; Desojo and Ezcurra, 2011). Conversely, Heckert and Lucas (2002) considered figures by Casimiquela (1961, 1967) to be inconclusive (see below) and that the maxilla bounded a portion of the naris as in *Stagonolepis robertsoni* (Walker, 1961). Examination of PVL 2059 and PVL 2052 found that the maxilla is definitely excluded. Heckert and Lucas (1999) introduced this character and because they were unsure of the condition in *Aetosauroides scagliai*, scored it as unknown. Parker (2007) excluded this character without explanation; however, it is reintroduced here.

3. Premaxilla, tooth arrangement: teeth present along ventral surface of entire element (0); teeth present, but restricted to posterior half of the element (1); teeth absent (i.e., premaxilla edentulous) (2). Modified from Heckert et al. (1996), character 21. Figures B1a, d, h.

Non-aetosaurian aetosauriforms such as *Revueltosaurus callenderi* have premaxillae with five alveoli present along the entire length of the element. At present, in all known aetosaurians with preserved premaxillae either the anterior portion (e.g., *Aetosaurus ferratus, Stagonolepis robertsoni*) or the entire element (*Desmatosuchus smalli*) lacks teeth. It was previously alleged that the premaxilla of *Typothorax coccinarum* is completely edentulous (e.g., Heckert et al., 1996) and was coded as such in all subsequent analyses (Heckert et al., 1999; Parker, 2007; Desojo et al., 2012); however, new specimens (e.g., PEFO 38001/YPM 58121) demonstrate that there are a minimum of four teeth present in the premaxilla of *Typothorax coccinarum*.

4. Premaxilla, tooth count (single ramus): 4 or more tooth positions (0); 3 tooth positions (1); edentulous (2). [Ordered] New character. Figures B1c, f.

In prior analyses all known aetosaurs either had edentulous premaxillae (e.g., *Desmatosuchus smalli*) or when teeth were present they numbered between 4 and 5 tooth positions (e.g., *Neoaetosauroides engaeus*, *Stagonolepis robertsoni*). However, the recently described *Stenomyti huangae* possesses only three premaxillary teeth (Small and Martz, 2013).

5. Premaxilla, dorsal surface of posterior process: smooth (0); with prominent dorsal tubercle that extends dorsally into the external naris (1). Small (2002). Figure B1a.

The presence of a tubercle on the dorsal surface of the premaxilla that projects into the naris of *Stagonolepis robertsoni* was briefly mentioned by Walker (1961); however, its possible phylogenetic significance was first recognized by Small (2002). In some taxa, such as *Stenomyti huangae*, the protuberance is weakly developed (Small and Martz, 2013); however it is still scored as present for this study.

6. External naris, anteroposterior length: less than the anteroposterior length of the antorbital fenestra (0); length is greater than or equal to that of the antorbital fenestra (1). Heckert and Lucas (1999), character 8. Figures B1g, h.

In *Postosuchus kirkpatricki* the anteroposterior length of the external naris is less than that of the antorbital fenestra (Weinbaum, 2011); however, it is longer in all known aetosaurians so presently this character is parsimony uninformative within Aetosauria as the extreme length found in aetosaurians is an autapomorphy of that group (Parker, 2007).

7. Maxilla, lateral surface, longitudinal ridge: present, rounded and bulbous (0); present, sharp (1); absent, lateral surface is smooth (2). Modified from Nesbitt (2011), character 26. Figures B1d; B2a.

Character state 2 refers to specimens with a smooth lateral surface of the maxilla ventral to the antorbital fenestra, as well as specimens that possess an antorbital fossa where the fossa rim is not raised above the surface of the maxilla (Nesbitt, 2011). Specimens with a fossa rim that is raised above the surface of the maxilla are scored as 1. A third character state where the raised ridge was bulbous (0) is only found in the outgroup taxon *Postosuchus kirkpatricki* (Nesbitt, 2011).

8. Maxilla, ventral portion of antorbital fossa in lateral view: dorsoventrally deep, more than 1/3

of the total element height (0); dorsoventrally shallow, less than 1/3 of the total element height, or absent (1). New character. Figures B1a; B2a.

Some aetosaurians (e.g., *Stagonolepis robertsoni*) possess a dorsoventrally deep antorbital fossa ventral to the antorbital fenestra; whereas in others (e.g., *Desmatosuchus spurensis*) the ventral portion of the fossa is extremely shallow.

9. Nasal, shape of anterior margin in dorsal view: tapering (0); maintains an equal width (1).New character. Figures B1b, e; B2b.

In some aetosaurians (e.g., *Stenomyti huangae*) the nasals reduce in transverse width anteriorly, tapering to a point dorsal to the premaxilla (Small and Martz, 2013). In others such as *Desmatosuchus smalli* (TTU P-9024), the nasals maintain a nearly constant width along the entire anterior portion, contacting the posterior margin of the premaxillae.

10. Nasal, lateral margin: does not form part of the dorsal border of the antorbital fossa (0); forms part of the dorsal border of the antorbital fossa (1). Nesbitt (2011), character 37. Figures B1a, g; B2a.

In taxa without an extensive antorbital fossa, the ascending process of the maxilla and the anterior portion of the lacrimal meet to exclude the nasal from bordering the antorbital fossa (Nesbitt, 2011).

11. Nasals, posterior portion of the midline suture area: triangular depression (formed at the midline) (0); flat or convex (1). New character. Figures B1b, e; B2b.

In *Stenomyti huangae* the lateral margins of the nasals are raised and this raised area widens anteriorly, causing a triangular depression to form on the posteromedial portion of the nasals (Small and Martz, 2011: fig. 11c). This triangular depression is also apparent in *Aetosaurus ferratus* (Schoch, 2007: fig. 8c), *Aetosauroides scagliai* (PVL 2059), and *Longosuchus meadei* (TMM 31185-97). In contrast, the nasals of *Stagonolepis olenkae* (AbIII/2000) lacks this depression, as do the nasals of *Desmatosuchus* (e.g., UMMP 7476).

12. Jugal, lateral view: ventral margin is nearly horizontal (0); ventral margin is strongly posteroventrally inclined (1). Modified from Nesbitt (2011), character 74, and Heckert and Lucas (1999), character 14. Figures B1a, d.

In lateral view the ventral margin of the jugal is oriented nearly horizontally in most archosauriforms (Nesbitt, 2011), including aetosaurians such as *Aetosaurus ferratus* (Schoch, 2007) and *Stenomyti huangae* (Small and Martz, 2013). In other aetosaurians such as *Desmatosuchus spurensis* (UMMP 7476) and *Longosuchus meadei* (TMM 31185- 97) the jugal is strongly inclined anterodorsally so that the quadrate condyle is situated ventrally to the maxillary tooth row. *Stagonolepis olenkae* has a nearly horizontal ventral margin of the jugal; however, the jugal and quadratojugal are unknown for that taxon and were reconstructed using bones from *Neoaetosauroides* and *Desmatosuchus* (Sulej, 2010:867, 869). Likewise the jugals are missing in the skull of *Aetosauroides scagliai* (PVL 2059) and *Scutarx deltatylus* (PEFO 34616). A referred specimen of *Aetosauroides scagliai* (PVL 2052) preserves the anterior portion of the jugal; however, not enough is preserved to determine if it was inclined or nearly horizontal.

13. Jugal, anterior process: excluded from the border of the antorbital fenestra by contact between the lacrimal and maxilla (0); contributes to the border of the antorbital fenestra. (1). New character. Figures B1a, d.

In *Stenomyti huangae* (Small and Martz, 2013) the posterior portions of the lacrimal and maxilla contact each other, excluding the anterior portion of the jugal from contributing to the border of the antorbital fossa. In *Desmatosuchus smalli* (Small, 2002) the posterior portions of the lacrimal and maxilla are separated from each other by the forward projection of the jugal into the margin of the antorbital fenestra.

14. Postfrontal, contact with parietal: absent (0); restricted by a posterolateral process of the frontal (1); extensive (2). [Ordered]. Desojo (2005), character 12. Figures B1b, e.

In some taxa (e.g., *Aetosaurus ferratus, Stenomyti huangae*), the postfrontal and parietal share an extensive border along the anterolateral margin of the parietal (Schoch, 2007; Small and Martz, 2013). In *Stagonolepis robertsoni*, this shared border is greatly restricted by a posterolateral process of the frontal that nearly contacts the anterodorsal corner of the dorsal process of the postorbital (Walker, 1961). In *Desmatosuchus smalli*, the postfrontal and parietal are separated from each other by a strong contact between the postorbital and the frontal (Small, 2002).

15. Postorbital: contact with quadratojugal - absent (0); present (1). Nesbitt (2011), character 64. Figures 6.1d, h.

In the majority of aetosaurians the postorbital and quadratojugal are separated from each other by an anterior process of the squamosal. However, in SMNS 19003 the squamosal process is reduced and there is extensive contact between the postorbital and quadratojugal. Schoch (2007) noted contact between the two bones in some specimens of *Aetosaurus ferratus*, and following Nesbitt (2011), *Aetosaurus ferratus* is coded as possessing character state 1.

16. Quadratojugal, anterior process: absent (0); forms ventral margin of lateral temporal fenestra (1); underlies jugal and is excluded from the lateral temporal fenestra (2). New character. Figure 6.1h.

In most aetosaurians, an anterior projection of the quadratojugal separates the dorsal portion of the posterior process of the jugal from the lateral temporal fenestra. However, in SMNS 19003, the posterior process of the jugal overlies the anterior process of the quadratojugal forming the entire fenestra border. *Neoaetosauroides* has a similar condition (state 1: Desojo and Báez, 2007); however, of the two referred skulls, one has had the lateral temporal fenestra artificially enlarged and the other is actually impressions of the bones in soft tissue, thus it is difficult to tell the actual condition and it is scored as unknown. In *Stagonolepis robertsoni* the anterior projection of the quadratojugal forms the ventral margin of the lateral temporal fenestra; however, this reconstruction is based on *Aetosauroides ferratus* (Walker, 1961: 127). The jugal and quadratojugal are unknown for *Stagonolepis olenkae* (Sulej, 2010).

17. Quadratojugal, anterior margin: lacks dorsal anteroprocess between the posterior process of the jugal and the lateral temporal fenestra (0); distinct anterior facing notch in the middle of the anterior margin for reception of posterior process of the jugal (1). New character. Figure B1a, h.

In *Revueltosaurus callenderi* (PEFO 34561) and some aetosaurians such as *Coahomasuchus kahleorum* (TMM 31100-437) the anterior margin of the quadratojugal bears a distinct anteriorly opening notch for reception of a posterior process of the jugal. Other aetosaurs such as *Stenomyti huangae* lack this notch and the posterior process of the jugal underlies the quadratojugal (Small and Martz, 2013).

18. Quadrate foramen, position: between the quadrate and the quadratojugal (0); completely within the quadrate (1). Modified from Nesbitt (2011), character 79. Figure B1a.

In *Stagonolepis robertsoni* the quadrate foramen is situated between the quadratojugal and the quadrate (Walker, 1961: 122). In *Coahomasuchus kahleorum* (TMM 31100-437) the foramen is entirely within the quadrate body.

19. Parietals/ frontals - transverse width at anteroposterior mid-points: parietal wider (0); frontal wider (1). New character. Figures B1b, e; B2b.

In *Aetosaurus ferratus* (Schoch, 2007) and *Stenomyti huangae* (Small and Martz, 2013) the transverse width of the parietals at their midpoint is greater than that of the frontals at their midpoint. In *Desmatosuchus smalli* (Small, 2002) and *Stagonolepis robertsoni* (Walker, 1961) the frontals are wider than the parietals at mid-point.

20. Supratemporal fenestra, position: only exposed in dorsal view (0); dorsolaterally or laterally oriented and visible in lateral view (1). Modified from Heckert and Lucas (1999), character 10. Figures B1a, h.

In *Revueltosaurus callenderi* (PEFO 34561) the supratemporal fenestra are exposed dorsally which is the typical archosauriform condition; however, in aetosaurians the squamosal and the postorbital-squamosal bar have shifted ventrally and the supratemporal fenestra is broadly exposed in lateral view. All aetosaur taxa that can be scored for this character have laterally exposed supratemporal fenestra so presently the character offers no in-group resolution (Parker, 2007). The supratemporal fenestra is completely exposed laterally in *Aetosauroides scagliai* (PVL 2073), a potential autapomorphy of that taxon.

21. Supratemporal fenestra, shape in lateral view: horizontal orientation of parietal forms a round or oval fenestra (0); strong posteroventral orientation of the posterior portion of the parietal forms a triangular fenestra (1). New character. Figures B1d, g.

The shape of the supratemporal fenestra is variable within Aetosauria and formed by the orientation of the parietal. *Desmatosuchus spurensis* (UMMP 7476) has a round fenestra, whereas it is triangular in SMNS 19003. In *Neoaetosauroides engaeus* (PVL 5698) the fenestra is strongly oval.

22. Supratemporal fenestra, anteroposterior diameter: larger than or nearly the same diameter as orbit (0); roughly half the size of the orbit (1); less than half the diameter of the orbit (2). [Ordered]. New character. Figures B1a, d, g.

The size of the supratemporal fenestra is variable in aetosaurs. It is nearly the size of the orbit in *Desmatosuchus spurensis* (UMMP 7476), roughly half the size of the orbit in *Neoaetosauroides engaeus* (PVL 5698), and much smaller than the orbit in SMNS 19003.

23. Post-temporal fenestra: present (0); absent (1). New character. Figures B1b, e.

In aetosaurs the posttemporal fenestra is a broad slit-like opening in the back of the skull between the ventral portion of the posteroventrally sloping flange (*sensu* Walker, 1961:114) of the parietal and the dorsal margin of the paroccipital process of the opisthotic. This fenestra is present in *Stagonolepis olenkae* (Sulej, 2010) and *Scutarx deltatylus* (PEFO 34616). Conversely, the fenestra is not present in *Desmatosuchus spurensis* (Case, 1922). This character is difficult to score in articulated specimens where the nuchal and anterior cervical paramedian osteoderms cover the back of the skull (e.g., *Aetosaurus ferratus*).

24. Basicranium, basal tubera: nearly or completely connected medially (0); clearly separate (1). Modified from Nesbitt (2011), character 104. Figures B3a-c.

In *Aetosauroides scagliai* (PVSJ 326) the basal tubera are distinctly separated by a broad anteroposterior trough between the occipital condyle neck and the basisphenoid recess. In *Scutarx deltatylus* (PEFO 34616) the basal tubera contact each other along the midline. In *Desmatosuchus spurensis* (UMMP 7476) are situated very closely together and are connected by a medial ridge. This latter condition is scored the same as a midline contact.

25. Basioccipital, distance between basal tubera and basipterygoid processes: widely separated anteroposteriorly (0); closely situated or nearly touching (1). Similar to Nesbitt (2011), character 103. Figures B3a-c.

In *Aetosauroides scagliai* (PVSJ 326) and *Stagonolepis robertsoni* (MCZD 2) the basal tubera and basipterygoid processes are widely separated anteroposteriorly the result of elongation of the parabasisphenoid. In *Desmatosuchus spurensis* (UMMP 7476) and *Scutarx deltatylus* (PEFO 34616), the basal tubera and basipterygoid processes are very closely situated anteroposteriorly, and this results in a foreshortened parabasisphenoid. This distance is the best way to quantify the differences in relative length of the parabasisphenoid between aetosaurians.

26. Dentary, dorsal and ventral posterior processes in lateral view: roughly equal lengths (0); upper process more elongate (1); lower process more elongate (2). New character. Figures B1a, d, h.

In most aetosaurians the posterior portion of the dentary splits into two posterior processes that are situated dorsal and ventral to the lateral mandibular fenestra. In lateral view these two processes are of roughly equal length in *Neoaetosauroides engaeus* (PVL 3525); however, in *Stagonolepis olenkae* (ZPAL AbIII/573) the dorsal process is much more elongate than the lower process. The reverse is found in *Desmatosuchus smalli*, where the ventral process in longer than the dorsal process (Small, 2002). The dentary of *Coahomasuchus kahleorum* (TMM 31100-437) also bears a median posterior (third) process as in *Revueltosaurus callenderi* (PEFO 34561), but for this character they are both scored as 0 as all of the processes are of equal length.

27. Dentary, tooth count: 9 or more (0); fewer than 9 (1). Parker (2007), character 9; modified from Heckert and Lucas (1999), character 16. Figures B1a, g.

Dentary tooth counts are variable across Aetosauria; however, the range of alveoli present seems to border on nine, with *Desmatosuchus smalli*, *Neoaetosauroides engaeus*, *Aetosaurus ferratus*, and *Longosuchus meadei* possessing between six and eight dentary tooth positions and *Aetosauroides scagliai* and *Stagonolepis robertsoni* having nine or ten. The original character of Heckert and Lucas (1999) used 10 positions as the division between character states, but Parker (2007) changed it to nine without discussion. The use of nine teeth is retained here as *Stagonolepis robertsoni* has nine or 10 teeth (Walker, 1961). Furthermore, *Stenomyti huangae* has a minimum of nine positions in an incomplete lower jaw (Small and Martz, 2013) so the choice of nine as the division simplifies these character state codings. There are seven to nine positions in *Stagonolepis olenkae* (Sulej, 2010), but the average value is used and scored as state 1. Parker (2007) followed Heckert and Lucas (1999) scored *Aetosaurus ferratus* as state 0; but despite that these teeth are poorly exposed in all known specimens, *A. ferratus* apparently has only seven or eight dentary tooth positions (Walker, 1961; Schoch, 2007). *Typothorax coccinarum* has more than nine dentary teeth based on PEFO 38001/YPM 58121. *Coahomasuchus kahleorum* can also be scored as 0 based on specimen TMM 31100-437.

28. Dentary, anterior half of dorsal margin: with teeth/alveoli (0); edentulous (1). Parrish (1994), character 9. Figures B1a, g, h.

In all aetosaurians with preserved dentaries, the anterior portions are edentulous, so this character is presently parsimony uninformative with respect to in-group relationships (Parker, 2007). However, *Revueltosaurus callenderi*, which is the sister taxon of Aetosauria (Nesbitt, 2011), bears alveoli for the entire length of the dentary so the possibility exists for an aetosaurian to possess the plesiomorphic character state. Earlier analyses (Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 1999) scored *Aetosaurus ferratus* as having teeth in the anterior portion of the dentary, but Walker (1961) noted that the anterior portion of the dentary was edentulous. This was also noted by Schoch (2007).

29. Mandibular ramus, ventral margin in lateral view: The ventral margin of the ramus is gradually convex (0); a 'chin' is present, formed by a ventral inflexion of the splenial, which is exposed ventral to the dentary (1); a 'chin' is present, formed by a ventral inflexion of the

dentary, which covers the splenial (2). New character. Descriptive terminology after Desojo and Ezcurra (2011). Figures B1a, d, g, h.

A 'classic' character of aetosaurians is the ventral inflexion of the mandibular ramus in some taxa forming a prominent 'chin', which is part of Walker's (1961) description of the element as 'slipper-shaped' (see discussion below). When present, this 'chin' is usually formed by the ventral inflexion of the splenial, extending below the concave ventral margin of the dentary. In this arrangement the ventral portion of the splenial is visible in lateral view. *Stenomyti huangae* possesses a different arrangement, where the ventral inflexion is actually on the dentary and the splenial is not visible in lateral view (Small and Martz, 2013). This may also be the case in *Neoaetosauroides engaeus* (Small and Martz, 2013). Examination of PVL 3525, a right mandibular ramus, shows that the anterior portion is mostly reconstructed in plaster, but there is a slight ventral inflexion of the dentary where the bone ends. A referred specimen of *Neoaetosauroides engaeus* (PULR 108) also shows that the ventral margin of the dentary bears the ventral inflexion (Desojo and Báez, 2007; Desojo and Vizcaíno, 2009).

30. Dentary, anterior end in lateral view: rounded (0); tapers to an acute point (1). Modified from Heckert and Lucas (1999a), character 15. Figures B1a, d, g-h.

Walker (1961) was the first to describe the acute termination of the anterior portion of the dentary as contributing to the 'slipper-shape' of the mandibular ramus. The presence or absence of this shape was used as a phylogenetic character by Heckert and Lucas (1999) and Parker (2007), although all aetosaurians with preserved dentaries were scored as possessing that character so it was parsimony uninformative. The condition 'slipper-shape' is separated into two distinct characters (also see Character 29). Desojo and Ezcurra (2011) noted that the dentary of

Aetosauroides scagliai was slender, lacking the ventral inflexion found *Stagonolepis robertsoni* (Walker, 1961), and therefore was not 'slipper-shaped.' Furthermore, although the anterior end of the dentary of *Aetosaurus scagliai* (PVL 2059) is distorted, it clearly was not acute and accordingly should be scored as bearing the 0 state (Desojo et al., 2012).

31. Surangular, dorsal margin: smooth (0); prominent rounded tuber (1). New character. Figure B4.

The surangular of *Stagonolepis olenkae* (ZPAL AbIII/578/34) bears a distinct rounded tuber on the dorsal surface dorsal to the lateral mandibular fenestra. A similar tuber is also present *in Stagonolepis robertsoni*, which Walker (1961) attributed to muscle or tendon attachment, most probably the *musculus adductor mandibulae externus* (Desojo and Vizcaíno, 2007). This tuber is absent in other specimens such as *Aetosaurus ferratus* (Schoch, 2007).

32. Articular, retroarticular process: height is greater than or equal to the length (0); longer than high (1). Desojo (2005), character 11. Figures B1a, B4.

In *Longosuchus meadei* (TMM 31185-84B) the retroarticular process of the articular is anteroposteriorly short and dorsoventrally tall. In contrast, the retroarticular process of *Desmatosuchus spurensis* (MNA V9300) is more elongate so that its anteroposterior length is greater than the dorsoventral height (Parker, 2008b).

33. Articular, dorsolateral surface: smooth (0); dorsally projecting tuber (1). New character. Figures B1a, d; B4.

The articular of *Stagonolepis olenkae* bears a pronounced dorsally projecting tuber (=articular projection) that is readily visible in lateral and medial views (Sulej, 2010:figs. 6, 7). It is also present in *Coahomasuchus kahleorum* (TMM 31100-437) and *Longosuchus meadei* (TMM 31185-98). This tuber is absent in *Desmatosuchus spurensis* (MNA V9300) where the dorsal surface of the articular is smooth. There is a mound in *Desmatosuchus smalli* (TTU P-9023) but not the sharp, well-developed tuber found in other taxa.

34. Tooth, maxillary, root and crown base shape in occlusal view: narrow, mediolaterally compressed (0); oval, but not strongly mediolaterally compressed (1); conical (2). [Ordered] Modified from Parrish (1994), character 8. Figure B5.

The teeth of *Postosuchus kirkpatricki* (e.g., TTU P-9000) are mediolaterally compressed in occlusal view. No aetosaurian possesses teeth that are as medially compressed. The teeth of SMNS 19003 are oval in occlusal view, but not mediolaterally compressed, whereas in other aetosaurians the teeth are conical or round in occlusal view (e.g., *Desmatosuchus smalli*, TTU P-9023).

35. Tooth, maxillary, crown shape in labial/lingular view: fully recurved, anterior edge is convex and posterior edge is straight or concave (0); bulbous and partly recurved, anterior edge is concave, posterior edge straight (1); bulbous with pointed or slightly recurved tips (2). Figures B5a-d.

Aetosaurian teeth are quite variable in their anatomy, even within an individual skull, and this variability is difficult to capture as discrete states for a phylogenetic character. The first study to try to capture this was Parrish (1994), who divided aetosaurian tooth form into two states, recurved or conical. Heckert and Lucas (1999) retained Parrish's original character and added a second character: teeth unreduced, mediolaterally compressed, or reduced in size, nearly conical. However, this essentially was a duplication of Parrish's character and indeed all taxa coded for these characters were coded similarly with the exception of *Aetosaurus ferratus*.

In each of these analyses *Aetosaurus ferratus* was coded as possessing recurved teeth (Parrish, 1994) and recurved conical teeth (Heckert and Lucas, 1999). The only other taxon coded for recurved, mediolaterally compressed teeth in the Heckert and Lucas (1999) analysis was the rauisuchid *Postosuchus kirkpatricki.* However, Walker (1961) had noted earlier that the teeth of *Aetosaurus ferratus* were actually conical, with a bulbous base of the crown, and that only the apices were recurved. Parker (2007) tried to capture this variation with three character states; 1) mediolaterally compressed and recurved; 2) bulbous and conical with recurved tips; and 3) bulbous and conical lacking recurved tips, but this actually describes two non-homologous characters.

Since that time Schoch (2007) published a full description of *Aetosaurus ferratus*, including the dentition. He noted that none of the teeth of *Aetosaurus ferratus* were recurved and that they were conical and more similar to the teeth of other aetosaurs, but they all had a well-curved anterior edge unlike other aetosaurians except for *Stenomyti huangae* and SMNS 19003. However, both *Aetosauroides scagliai* and the "carnivorous aetosaur" (=*Coahomasuchus kahleorum*) of Murry and Long (1996) have conical teeth that are fully recurved unlike the mediolaterally compressed, recurved teeth of *Postosuchus kirkpatricki*. Thus, these states are divided between two distinct characters, one (character 33) describing the tooth shape in occlusal view, and the other (character 34) describing crown shape in labio-lingular view.

Postcranial Characters

36. Cervical centra, ventral surface, at midline: keeled (0); smooth (1). Heckert and Lucas (1999), character 20. Figure B6b, c, f.

Many archosauriforms have prominent anteroposteriorly sharp flanges of bone (keels) on the ventral surface of the cervical centra (Nesbitt, 2011). However, some aetosaurs (e.g., *Desmatosuchus spurensis*) have smooth ventral surfaces (Parker, 2008b).

37. Cervical vertebrae, length: anteroposteriorly shorter (more than 50%) than dorsoventrally tall (0); anteroposteriorly shorter (less than 50%) than dorsoventrally tall (1). New character. Figures B6b, e.

Aetosaurians differ from many archosauriforms in possessing cervical centra that are much shorter anteroposteriorly, than they are tall. However, some aetosaurians have cervical centra that are even anteroposteriorly shorter such as *Typothorax coccinarum* (Long and Murry, 1995).

38. Cervical vertebrae, centrum, shape of articular face: transversely oval (0); circular (1); subrectangular (2). Desojo (2005), character 17. Figures B6a, d.

The shape of the anterior articular face of the cervical centrum is variable in aetosaurians, circular in *Aetobarbakinoides brasiliensis* (CPE2 168), *Sierritasuchus macalpini* (UMMP V60817), and *Stagonolepis robertsoni* (Walker, 1961); a shallow, wide oval in *Neoaetosauroides engaeus* (PVL 3525) and *Calyptosuchus wellesi* (UCMP 27225); and sub-rectangular in *Desmatosuchus spurensis* (MNA V9300; Desojo et al., 2012).

39. Cervical and trunk vertebrae, lateral surfaces of centra: concave or flat (0); concave with deep fossae (1). Desojo and Ezcurra, 2011. Figures B6e; B7d.

The cervical and trunk vertebrae of *Aetosauroides scagliai* bear prominent lateral fossae that cover much of the lateral surface of the centrum (Desojo and Ezcurra, 2011).

40. Trunk vertebrae, transverse processes: short, less than twice as wide as the centrum (0); elongate, more than twice as wide as the centrum (1). Heckert and Lucas (1999), character 18. Figures B7b, c, f.

The mid-trunk vertebrae of *Paratypothorax* sp. (TTU P-9169) and *Typothorax coccinarum* (e.g., TTU P-9214) have elongate transverse processes. The transverse process width is 2.5 times the centrum width in TTU P-9214 (Martz, 2002). These elongate transverse processes appear to coincide with the more discoidal carapace in *T. coccinarum* and *Paratypothorax*. Long and Murry (1995) considered the transverse processes of *Calyptosuchus wellesi* to be extremely long; however, they were examining the posterior dorsal vertebrae, which have ribs fused to the transverse processes and *Calyptosuchus wellesi* should be coded as having short transverse processes because the mid-dorsals less than twice the width of the centrum (Parker, 2007). In the specimen of *Calyptosuchus wellesi* with the longest transverse processes (UMMP 7470) the process is about 1.9 times the width of the centrum.

41. Mid-trunk vertebrae, neural spine height (from the base of the spine): greater than the height of the centrum (to the neurocentral suture) (0); equal to or less than the height of the centrum (1). Heckert and Lucas (1999), character 19. Figures B7b, c, f.

In *Desmatosuchus* (e.g., MNA V9300) and *Typothorax coccinarum* (e.g., TTU P-9124) the heights of the neural spines of the presacral vertebrae are less than the height of the centrum. In contrast, *Stagonolepis robertsoni* (Walker, 1961) and *Neoaetosauroides engaeus* (Desojo and Báez, 2005) have tall neural spines that are more than the height of the centrum. This character is restricted to the mid-trunk series because in *Scutarx deltatylus*, the anterior and mid-trunk vertebrae have neural spines that are shorter than the centrum. However, around the position of the 13th trunk vertebra the neural spine and centrum heights transition to be roughly equal and in the more posterior vertebrae the neural spine becomes taller than the centrum. This variation does not occur in other specimens with short neural spines such as *Desmatosuchus spurensis*, as the ratio remains constant through the entire vertebral column (Parker, 2008b).

42. Trunk vertebrae, zygadiapophyseal laminae, connecting the diapophysis to the zygapophyses: present (0); absent (1). Desojo (2005), character 19. Figures B7a, b, d.

The cervical and trunk vertebrae of some aetosaurians (e.g., *Desmatosuchus spurensis*, MNA V9300) bear distinct vertebral laminae (Parker, 2008b). Four sets are present in the cervical vertebrae of *Desmatosuchus spurensis*, following the terminology of Wilson (1999) they are the 1) the acdl, anterior centrodiapophyseal lamina, which originates on the diapophysis and terminates on the anterior margin of the neurocentral suture; 2) the pcdl, posterior centrodiapophyseal lamina, which originates on the diapophysis and terminates on the posterior margin of the neurocentral suture; 3) the podl, the postzygadiapophyseal lamina, which originates on the diapophysis and terminates on the postzygapophysis; and the 4) prezygadiapophyseal lamina, which originates on the diapophysis and terminates at the prezygapophyses. Furthermore, the trunk vertebrae of *Desmatosuchus spurensis* possess an additional two spinozygapophyseal laminae (*sensu* Wilson, 1999); 1) the spol, spinopostzygapophyseal lamina, which originates on the postzygapophysis and terminates on the posterior face of the neural spine; and 2) the sprl, the spinoprezygapophyseal lamina, which originates on the prezygapophysis and terminates on the anterior face of the neural spine. The presacral vertebrae of *Typothorax coccinarum* (TTU P-9214) and *Paratypothorax andressorum* (NHMUK 38070) possess all four laminae and the zygadiapophyseal laminae are extremely robust and confluent with the pre- and postzygapophyses.

A pair of laminae previously unrecognized in aetosaurs is present in the cervical vertebrae of *Scutarx deltatylus*. These laminae originate on the posteroventral surface of the postzygapophyses and form two sharp ridges that meet at the dorsomedial margin of the neural canal. These appear to be homologous to the intrapostzygapophyseal laminae (tpol) of Wilson (1999) found in saurischian dinosaurs.

Aetosaurian vertebrae generally tend to be poorly preserved, crushed and broken, or often are covered by the carapace and inaccessible. Furthermore, delicate portions of the bone such as accessory processes and laminae are often broken away making determination of their presence/absence difficult. Nonetheless, all known aetosaurians have presacral vertebrae with zygadiapophyseal laminae (except possibly *Polesinesuchus aurelioi*, Roberto-da-Silva et al., 2014) suggesting the presence may be an aetosaurian apomorphy. Future versions of this character may focus on the presence or absence of specific laminae (e.g., intrapostzygapophyseal laminae) once the presence or absence of general laminae have been demonstrated for most aetosaurians.

43. Trunk vertebrae, well-developed intervertebral articulations (hyposphene/hypantrum): present (0); absent (1). Figure B7f.

Desmatosuchus spurensis (e.g., MNA V9300) possesses a well-developed hyposphene and hypantrum in the trunk vertebrae (Parker, 2008b). Presently the only other known taxon with well-developed processes is *Aetobarbakinoides brasiliensis* (Desojo et al., 2012). TTU-P09416, a posterior presacral vertebra of *Paratypothorax* sp., has a very slight posterior projection at the base of the postzygapophyses (Figure B8b) that may represent an incipient hyposphene as it corresponds to a slight indentation in the ventral bar between the prezygapophyses, but this is not the same as the extremely well-developed processes in *Desmatosuchus* and *Aetobarbakinoides* and therefore is scored as 0. However if this feature is found to be present in more aetosaurian specimens, a new state could be added for this character.

44. Posterior trunk vertebrae (positions 14-16), ventral surface: smooth, rounded (0); lateral faces meet to form sharp edge or keel (1). New character. Figure B8a.

In the posterior trunk vertebrae of *Paratypothorax* sp., the lateral surfaces of the centrum meet to form a sharp ventral keel on the ventral surface of the centrum. This is best demonstrated by TTU P-09416, a posterior dorsal vertebra from the Post Quarry of Texas (Figure B8a). A ventral keel is present but weakly formed in NHMUK 38070, a posterior trunk vertebra of *Paratypothorax andressorum*.

45. Anterior caudal vertebrae (positions 1-12), origin point of caudal ribs: at the level of neural arch (0); near the base of the centrum (1). New character. Figure B7e, g.

In most aetosaurians the caudal ribs originate from the neural arch (e.g., *Desmatosuchus spurensis*, MNA V9300), but in *Paratypothorax* sp. (PEFO 3004) the caudal ribs originate low down on the centrum. An isolated caudal vertebra (GR 174) from the Hayden Quarry at Ghost

Ranch New Mexico possesses caudal ribs situated low on the centrum and is most likely referable to *Rioarribasuchus chamaensis*, which occurs in the quarry (Irmis et al., 2007).

46. Coracoid, posterolateral thickening below glenoid lip that divides coracoid into posterior and lateral faces ('subglenoid pillar'): present (0); absent (1). Desojo (2005), character 20. Figures B9a-b.

Walker (1961:145) described the subglenoid region of the coracoid of *Stagonolepis robertsoni* as bearing “a depressed area bounded in front by a stout pillar which makes a slight projection in the medial margin and thus divides the outer surface into two areas”. The first area contains the coracoid foramen and receives the insertion of *M. supracoracoideus*; whereas the second area is the insertion area for *M. coracobranchialis* (Desojo, 2005). A subglenoid pillar is also present in *Typothorax coccinarum* (Long and Murry, 1995) and absent in *Aetosauroides scagliai* and *Longosuchus meadei* (Desojo, 2005). A nearly complete scapulocoracoid of *Coahomasuchus kahleorum* (TMM 31100-437) lacks a prominent subglenoid pillar.

47. Humerus, distal end, lateral side of the ectepicondyle: proximodistally oriented groove present (0); proximodistally oriented foramen present (1). New character, but similar to Nesbitt (2011), character 234. Figures B9c-e.

The ectepicondylar foramen is present at the distal end of the humerus where it serves as a passage for the median (ulnar) nerve and the brachial artery (Landry, 1958). In stem- amniotes the opening is a foramen completely enclosed by bone in mature individuals (Romer, 1956). However; in some aetosaurs (e.g., *Aetosaurus ferratus*), the foramen is open laterally and thus a groove instead of a true foramen. A laterally open ectepicondylar groove is also found in

Revueltosaurus callenderi (PEFO 34561), suggesting that this is the plesiomorphic state for aetosaurians. Nesbitt (2011) notes that a groove is also present in phytosaurs and some paracrocodylomorphs.

48. Humerus, proximal head: expanded medially, but lacks significant lateral expansion (0); broadly expanded transversely, with significant lateral expansion (1). New character. Figures B9d-e.

The proximal head of the humerus of *Aetosauroides scagliai* (PVL 2073) is moderately expanded (about one-third the element length), with almost all of the expansion medially, and almost no lateral expansion. In contrast, the humeral head of *Desmatosuchus smalli* (TTU P-9024) is nearly one-half the element length. Not only is the head expanded medially, but there is also a significant lateral expansion.

49. Ilium, orientation of acetabulum: opens fully or mostly ventrally (0); opens fully or mostly laterally (1). Modified from Desojo (2005), character 23. Figures B10a, c.

As noted by Desojo (2005) the orientation of the acetabulum can be difficult to determine because of crushing of preserved pelves and even more difficult in taxa only known from isolated ilia. Nonetheless various specimens demonstrate that the acetabulum opens ventrally in *Aetosauroides scagliai* (PVL 2073). *Calyptosuchus wellesi* (UMMP 13950), *Scutarx deltatylus* (PEFO 31217), *Typothorax coccinarum* (PEFO 33967), and *Longosuchus meadei* (TMM 31100-236). The acetabulum opens mostly laterally in *Desmatosuchus spurensis* (MNA V9300) and in *Neoaetosauroides engaeus* (PVL 3525). The acetabulae of *Stagonolepis robertsoni* (Walker, 1961) and *Aetosaurus ferratus* (Schoch, 2007) to open ventrally (Desojo, 2005).

50. Pubis, proximal portion, number of 'obturator foramina': one (0); two (1). Modified from Heckert and Lucas (1999), character 25. Figure B10b.

Walker (1961) described two pubic foramina for *Stagonolepis robertsoni*, which differed from the condition in all other known aetosaurs. However, the pubis of *Scutarx deltatylus* (PEFO 31217) also has two foramina. This character was not considered by Parker (2007) who noted that two foramina were only known for a single taxon (*Stagonolepis robertsoni*) and thus the character was parsimony-uninformative; however, the discovery of that character state in a second taxon (*Scutarx deltatylus*) necessitates reinstatement of the character.

51. Pubis, symphysis length: long, more than one-half of the element length (0); short, less than one-half of the element length (1). New character. Figure B10c.

The pubis symphysis in *Aetosaurus ferratus* (Schoch, 2007) and *Typothorax coccinarum* (Long and Murry, 1995) is short, with the symphysis length less than half the length of the pubis. In contrast, the symphysis in *Desmatosuchus spurensis* (MNA V9300) is long, much more than half the element length (Parker, 2008b).

52. Osteoderms, dorsal carapace, transverse smooth strip along anterior edge of osteoderm (= anterior bar): absent (0); present but strongly raised (deliminated from remainder of osteoderm by a distinct trough) (1); present, but weakly raised (2); absent, depressed lamina present instead (3). Modified from Long and Ballew (1985): Table 1. Figure B11a, c-d, f-g, i.

Aetosaurians possess a smooth, narrow, transverse area along the anterior edge of osteoderms that represent the articular surface for slight overlap of the next anteriorly situated osteoderm. When this area is raised it is termed an “anterior bar” (Long and Ballew, 1985). According to those authors, a fully (strongly) raised anterior bar is delimited by a distinct trough along the posterior margin of the smooth area. In *Paratypothorax*, this distinct trough is lacking and the anterior bar is considered to be only weakly raised (Long and Ballew, 1985). In *Desmatosuchus*, the smooth articular surface is depressed below the level of the rest of the ornament surface. This is considered to be an anterior ‘lamina’ rather than an anterior bar (Long and Ballew, 1985).

53. Paramedian osteoderms (any), patterning of dorsal surface: random, no observable pattern (0); radiate (1); reticulate (2); smooth or flat (3). Modified from Long and Ballew (1985): Table 1. Figures B11f-g, j, l.

Long and Ballew (1985) first clearly defined the utility of the surface ornamentation of paramedian osteoderms for aetosaurian taxonomy, and Heckert et al. (1996) were th~~is~~ first to quantify this as a phylogenetic character. Heckert and Lucas (1999) divided this character into three based on discrete carapace regions (i.e., cervical, dorsal, lateral), but Harris et al.~~,~~ (2003) noted that there was no difference in the patterns of these areas and thus reductive coding of this character improperly weighted its~~’~~ significance in the analysis. Following this, Parker (2007) devised a composite coding, utilizing only a single character to capture this variation.

In past studies (Heckert et al., 1996; Heckert and Lucas, 1999; Parker, 2007) the ornament patterns in *Desmatosuchus* and *Typothorax* have both been considered to be ‘random’ as they lack a clear radial patterning. However, the ornamentation pattern is very different between these taxa with the ornamentation in *Typothorax* consisting mainly of uniformly placed small pits, surrounded by a nearly symmetrical latticework of raised areas, and that of

Desmatosuchus consisting of pits and grooves of various sizes, offset by raised ridges. The patterning in *Typothorax coccinarum* is described as reticulate or equally spaced, non-radiate pits (Desojo, 2005). Thus a new character state, reticulate, has been added to capture this variation and for scoring the nearly symmetrical pattern found in *Typothorax*.

54. Paramedian osteoderms, dorsal eminence (or center of ossification) position throughout the carapace does not contact the posterior margin of the osteoderm in most rows (0); contacts posterior margin of osteoderm in most osteoderm rows (1). Modified from Long and Ballew (1985), Table 1. Figures B11a-d, f-h, l.

In most aetosaurians the dorsal eminence contacts the posterior plate margin (e.g., *Calyptosuchus wellesi*); however, in *Desmatosuchus* (e.g., MNA V9300) the boss is just posterior to the center of the osteoderm. In *Paratypothorax*, the boss position varies from close to the center of the osteoderm as in *Desmatosuchus*, to just anterior of the posterior plate margin, to actually contacting the posterior plate margin. This variation is related to anteroposterior position within the carapace, with the bosses being smaller and more anteriorly situated in more anterior osteoderms. The boss migrates posteriorly backwards through the carapace reaching the posterior edge in the anterior caudal/posterior dorsal trunk paramedians. Nonetheless a boss that does not contact the posterior plate margin is more common in dorsal trunk paramedians of *Paratypothorax*, so they are scored as state 1.

The more forward situated eminence in *Paratypothorax* has caused confusion with some workers attempting to assign incomplete osteoderms to specific taxa. For example, all of the paramedian osteoderms from Petrified Forest National Park assigned to *Desmatosuchus* by Long and Ballew (1985) are actually incomplete osteoderms of *Paratypothorax* sp. The key difference is that the dorsal eminence is strongly offset medially in *Paratypothorax*, whereas the boss is centralized in *Desmatosuchus*. In the osteoderms assigned by Long and Ballew (1985) the lateral edges of the osteoderms are missing, making it appear that the bosses are located more centrally than they actually are.

55. Paramedian osteoderms, posterior margin: osteoderm maintains similar thickness throughout posterior to the anterior bar (0); posterior margin bears a transverse, posteroventrally sloping flange (bevel) (1). New character. Figure B11b, i, l.

Dorsal trunk paramedian osteoderms of *Tecovasuchus chatterjeei* (TTU P-00545) and *Paratypothorax andressorum* (SMNS uncatalogued – L10) have a distinct beveling of the posterior plate margin, which is extremely well-developed in *Tecovasuchus chatterjeei* (Martz and Small, 2006).

56. Paramedian osteoderms, transverse anteroposterior thickening (ventral keel or strut) absent, ventral surface is flat (0); weakly developed (1); strongly developed (2). Modified from Heckert et al. (1996), character 11. Figures B12a-c.

Dorsal trunk paramedian osteoderms with a ventral keel or strut bear a prominent mediolateral thickening of the ventral surface. The keel is strongly developed in *Typothorax coccinarum* (e.g., AMNH FR 2709) where it more than doubles the thickness of the osteoderm. Indeed, the first descriptions of *Typothorax coccinarum* interpreted this strut as a dorsal rib (e.g., Cope 1887; Huene 1915). There is a reduced strut in *Calyptosuchus wellesi* (UCMP 136744; Martz, 2002), and in *Adamanasuchus eisenhardtae* (PEFO 34638). In other taxa, such as

Desmatosuchus spurensis (MNA V9300), the ventral surface of the osteoderm is completely flat and there is no strut.

57. Paramedian osteoderms, dorsal to the cervical and anterior trunk vertebrae, relative dimensions: wider than long (0); longer than wide (1). Heckert et al. (1996), character 1. Figures B11a-b.

Aetosaurian cervical dorsal paramedian osteoderms are either rectangular (wider than long) or roughly square (longer than wide, with the anterolateral corner ‘cut off’). Osteoderms that are longer than wide are a synapomorphy of Desmatosuchinae (Parker et al., 2008); however, the newly described NCSM 21723, which possesses many desmatosuchine characters, has cervical paramedian osteoderms that are wider than long (Heckert et al., in press).

58. Paramedian osteoderms, dorsal to the cervical vertebrae (=cervical paramedian osteoderms), ratio of number of osteoderms to number of cervical vertebrae: approximately 1:1 (0); significantly less than 1:1 (1). New character.

Traditionally it was thought that aetosaurians with wider than long cervical paramedian osteoderms (character 56), possessed one osteoderm per cervical vertebra (generally nine), and that aetosaurians with longer than wide osteoderms only had about five or six osteoderms ~~per~~ for the nine vertebrae. However, *Typothorax coccinarum*, which possesses cervical ~~paramedians~~ that are wider than long, only had about five sets of osteoderms covering the entire cervical series (Heckert et al., 2010). This is similar to the counts in *Desmatosuchus* and *Longosuchus*, which have cervical paramedian osteoderms that are longer than wide and only five or six osteoderm sets over the cervical vertebrae.

59. Osteoderms dorsal to the cervical and anterior trunk vertebrae, articular surfaces: adjacent paramedian and lateral osteoderms are separate (0); adjacent paramedian and lateral osteoderms are often fully fused (1). New character. Figures B12c, d, g.

In *Desmatosuchus*, the dorsal and lateral cervical osteoderms are often complete~~d~~ fused (Parker, 2008b). This unrecognized fusion caused problems with the identification of some of these osteoderms in past studies (e.g., Brady, 1958:fig. 3; Long and Ballew, 1985: fig 6a). Fusion of the lateral and paramedian cervical osteoderms also occurs in *Longosuchus meadei* (Parker and Martz, 2010).

60. Paramedian osteoderms dorsal to the cervical and anterior trunk vertebrae, lateral edge articulation with lateral osteoderms: vertical 'flat' contact with some interdigitation (0); dorsoventrally thickened, angled contact, with deeply incised interdigitation (='tongue and groove') (1). Modified from Heckert and Lucas (1999a), character 46. Figure B11k.

The thickened and complex medial and lateral articular surfaces between osteoderms in *Desmatosuchus* was first described as ‘tongue and groove” by Long and Ballew (1985) and this has been followed by all subsequent workers. Long and Ballew (1985) described this articular surface as greatly thickened (dorsoventrally), strongly rugose and concave. This differs significantly from the thinner, vertical, and generally smoother articular surfaces found in other aetosaurs. This character is presently found only in both species of *Desmatosuchus*, *Longosuchus meadei*, *Lucasuchus hunti*, and *Sierritasuchus macalpini* and was considered a synapomorphy of Desmatosuchinae (Parker et al., 2008). The recently described *Gorgetosuchus pekinensis* was described as potentially being closely related to Desmatosuchinae; however, the original describers (Heckert et al., 2015) do not mention if the osteoderm articular surfaces have a ‘tongue and groove’ articular surface, so it is scored here as unknown.

61. Paramedian osteoderms dorsal to the cervical vertebrae, dorsal eminence shape: smooth, not raised above osteoderm surface (0); low, pyramidal or rounded boss or elongate keel (1); tall, cone-shaped in posterior view (2). New character. Figure B11a.

Longosuchus meadei (TMM 31185-97), *Desmatosuchus smalli* (TTU P-9024), and *Lucasuchus hunti* (e.g., TMM 31185-60) have cervical paramedian osteoderms which bear prominent raised dorsal eminences. In contrast, in *Aetosauroides scagliai* (PVL 2073) and *Stagonolepis robertsoni* (Walker, 1961) have dorsal eminences that are barely visible and in *Typothorax coccinarum* (e.g., NMMNH P-56299), dorsal eminences are not visible until well into the dorsal trunk paramedian series (Heckert et al., 2010).

62. Osteoderms dorsal to the trunk vertebrae, articulation of lateral and paramedian osteoderms: the anterior edge of paramedian osteoderm overlaps the anterior edge of lateral osteoderm (0); the anterior edge of lateral osteoderm overlaps the anterior edge of paramedian osteoderm (1). Parker and Martz (2010). Figures B11g-h.

Aetosaurians have two distinct articulation patterns between the anterior edges of the paramedian osteoderm and the corresponding lateral osteoderm. In *Longosuchus meadei* (TMM 81185-84B) the anterolateral corner of the paramedian osteoderm has a dorsally facing articular facet that in articulation is overlapped by the anteromedial corner of the lateral osteoderm. In *Scutarx deltatylus* (e.g., PEFO 34616) the anteromedial corner of the lateral osteoderm is rounded and has a dorsally facing facet that receives the anteromedial projection of the paramedian osteoderm.

63. Paramedian osteoderms dorsal to the trunk vertebrae, “shape of the lateral edge in dorsal view: roughly straight or sigmoidal (0); sigmoidal with strongly posteromedially oriented posterolateral ("cut-off") corner (1). New character. Figures B11d, f-g, i.

Stagonolepis robertsoni (Walker, 1961), *Desmatosuchus spurensis* (MNA V9300), and *Aetosaurus ferratus* (Schoch, 2007) possess dorsal trunk paramedian osteoderms with roughly straight to sigmoidal lateral edges in dorsal view. *Paratypothorax* sp. (PEFO 3004) and *Adamanasuchus eisenhardtae* (PEFO 34638) possess strongly sigmoidal lateral edges in dorsal view, with a posterolateral corner that appears to have been sheared off. The strongly posteromedially oriented edge corresponds with a prominent triangular posterolateral projection of the lateral plate that fills the space voided by the ‘cut-off corner’ of the paramedian in the dorsal carapace.

64. Paramedian osteoderms dorsal to the trunk vertebrae, width/length ratio of widest osteoderms (rows 9-11) in series: less than 3.0 (0); 3.01-3.5 (1); 3.5 or more (2). Modified from Parrish (1994), character 15. Figures B11d, f-g.

As originally constructed by Parrish (1994) this character had two states, width/length ratio greater than or equal to 4.0 and width/length ratio less than 4.0 (Heckert et al., 1996; Heckert and Lucas, 1999). Parker (2007) argued that only *Paratypothorax* possessed a width/length ratio greater than 4.0 so he reduced the division point to 3.5 to make the character more applicable. Heckert and Lucas (1999) coded *Typothorax coccinarum* as possessing a maximum width/length ratio of greater than 4.0; however, a paramedian osteoderm of *Typothorax* with that great of a ratio was not observed. The widest paramedian osteoderm from the UCMP Canjilion Quarry material has a ratio of about 3.88 and the Revuelto Creek *Typothorax* has a maximum of 3.5 (Heckert et al., 2010). Even the extremely large paramedian plate (PEFO 23388) discussed by Parker and Irmis (2005) falls short of having a 4.0 ratio. However, referred material of *Redondasuchus rineharti* at the MCCDM (field number 2011RRBWKB#9) has a ratio of around 4.5 (J. Martz, pers. comm., 2013).

Most aetosaurs fall within the 3.01-3.5 ratio range; however a few have maximum ratios of less than 3.0. These include *Longosuchus meadei*, *Desmatosuchus spurensis*, *Stagonolepis robertsoni*, and *Aetobarbakinoides brasiliensis*.

65. Paramedian osteoderms dorsal to the trunk vertebrae; posteromedial surface of osteoderm ornamentation: lacking distinct transverse ridge between dorsal eminence and medial margin of the osteoderm. (0); distinct sharp raised mediolateral ridge extends medially from dorsal eminence to medial osteoderm margin (1). New character. Figures B11b, i.

The dorsal trunk paramedian osteoderms of *Tecovasuchus chatterjeei* (TTU P-545) bear a distinct mediolateral ridge that originates at the dorsal eminence and extends medially to contact the posteromedial plate margin. This ridge delineates the posterior beveled area in *Tecovasuchus chatterjeei*. This ridge is also present in *Paratypothorax* sp. (TTU P-9169), and although faint is also present in *Paratypothorax andressorum* (SMNS uncatalogued, R12).

66. Paramedian osteoderms dorsal to the trunk vertebrae, position of dorsal eminence relative to the center of the osteoderm centralized (0); moderately offset medially (1); strongly offset medially (2). Parker (2007), character 29. Figures B11f-g, j.

In *Desmatosuchus spurensis* (UMMP 7476) the dorsal eminence is situated centrally on the mediolateral axis of the paramedian osteoderm. It is shifted medially in *Stagonolepis robertsoni* (Walker, 1961), and it is shifted even further medially, almost to the medial edge of the osteoderm, in *Paratypothorax andressorum* (Long and Ballew, 1985)

67. Paramedian osteoderms dorsal to the trunk vertebrae, anterior margin of the anteromedial corner of the anterior bar in dorsal view: anteriorly directed triangular projection (0); straight (1). New Character. Figures B11d, g.

In aetosaurians such as *Stenomyti huangae* (Small and Martz, 2013), *Stagonolepis robertsoni* (Walker, 1961), and *Paratypothorax andressorum* (SMNS uncatalogued, L16) the anteromedial corner of the anterior bar bears a sharp triangular anterior projection. This projection is lacking in other aetosaurs such as *Desmatosuchus spurensis* (MNA V9300) where the anteromedial corner of the anterior bar is mediolaterally straight.

68. Paramedian osteoderms dorsal to the trunk vertebrae, lateral margin of the anterolateral corner of the anterior bar: distinct triangular lateral projection that barely extends beyond the lateral osteoderm margin (projection may be rounded distally (0); distinct triangular lateral projection that extends well beyond the lateral osteoderm margin (1); corner embayed for reception of the anteromedial projection of the lateral osteoderm (2). New character. Figures B11d, i, l.

Many non-desmatosuchine aetosaurs possess dorsal trunk paramedian osteoderms with anterior bars that bear an anterolateral projection that extends beyond that lateral margin of the main plate body. The length and distal end shape of the process are variable. *Aetosauroides scagliai* (PVL 2073) possesses a projection that is mediolaterally short with a pointed distal end. *Scutarx deltatylus* (PEFO 34616) also possesses a pointed process that is significantly more elongate. *Paratypothorax* sp. (PEFO 3004) has the shorter process, which instead of being pointed, it is gently rounded in dorsal view. This condition is coded the same as the short, pointed process as this character is based on process length and not process end shape. These anterolateral projections fill in a void in the anteromedial corner of the adjacent lateral osteoderm, slightly overlapping that portion of the lateral osteoderm.

69. Paramedian osteoderms dorsal to the trunk vertebrae, anterior margin of anterior bar/lamina on the medial side of the osteoderm: anteriorly concave ('scalloped") (0); straight (1). New character. Figures B11d, g, j.

The anterior bar in many aetosaurians bear a ‘scalloped-out’ anterior margin on the medial side of the dorsal trunk paramedian osteoderm. In plates with this character the anterior edge of the anterior bar is concave in dorsal view with the bar thinning anteroposteriorly in the center of the medial portion of the bar. Often this scalloping is associated with a triangular anterior process of the anterior bar that is directly anterior to the dorsal eminence. This character state is very prominent in the dorsal trunk paramedians of *Stagonolepis robertsoni* (Walker, 1961) and *Scutarx deltatylus* (PEFO 34045). It is absent in *Desmatosuchus spurensis* (MNA V9300) and *Longosuchus meadei* (TMM 31185-97). In *Typothorax coccinarum* (e.g., UCMP

34227), the medial portion of the anterior bar thins drastically, but the anterior projection anterior to the dorsal eminence does not appear to be present.

70. Paramedian osteoderms dorsal to the trunk vertebrae, posteromedial corner: flat with ornamentation (0); flat triangular area devoid of ornamentation (1); prominent raised triangular tuberosity devoid of ornamentation (2). [Ordered]. New character. Figures B11l, B12e-f.

An apparent autapomorphy of *Scutarx deltatylus* (e.g., PEFO 34616) is the presence of a large triangular protuberance in the posteromedial corner of the dorsal trunk paramedian osteoderms. However, although *Adamanasuchus eisenhardtae* (PEFO 34638) lacks the tuberosity, a triangular area in the same position is devoid of ornamentation, and this is considered a variation of this character.

71. Paramedian osteoderms dorsal to the anterior caudal vertebrae, dorsal eminence shape: absent, no dorsal eminence (0); low and pyramidal or rounded and knob-like (1); moderate, bulbous spike (2); tall, cone-shaped (3); tall anteriorly curved elongate spine (4). Modified from Long and Ballew (1985): Table 1. Figures B11c-e, g, j.

All aetosaurians, with the possible exception of *Redondasuchus reseri*, possess a raised dorsal eminence (boss) on the dorsal surface of the paramedian plates. In most taxa this boss takes the form of a low pyramidal or rounded knob, but in others the eminence is dorsoventrally taller. Taller eminences take three distinct forms. In *Paratypothorax* they have the shape of a bulbous spike (although they tend to be larger in the German specimens). In *Lucasuchus hunti* (TMM 31100-361) , they are in the form of what Long and Murry (1995) described as an ‘inverted ice-cream cone’ in that they are extremely tall and conical with a broad rounded base.

The third form is found in *Rioarribasuchus chamaensis* (e.g., NMMNH P-32793), where the dorsal eminence in the posterior trunk and anterior pelvic areas is an elongate, gracile, anteromedially recurved spine. Presently each of these tall forms is found in separate taxa. I do not combine them into a single ‘tall’ character because although the presence of the boss itself is homologous, it is not clear that a tall boss is homologous because it has taken so many unique forms.

72. Lateral osteoderms: absent (0); present (1). New character.

All known aetosaurs preserve lateral osteoderms with the exception of *Redondasuchus reseri* (Hunt and Lucas, 1991) and *Aetobarbakinoides brasiliensis* (Desojo et al., 2012); however, despite this absence, the evidence that they completely lacked lateral osteoderms is unequivocal. Lateral osteoderms are not present in *Postosuchus kirkpatricki* (Nesbitt, 2011; Weinbaum, 2013).

73. Lateral osteoderms, distribution within carapace; absent (0); only present in the sacral and anterior caudal region (1); present through the entire carapace (2). New character.

In all aetosaurians that preserve lateral armor th~~is~~ osteoderms extend through the entire carapace and even in taxa with incomplete carapaces there is no evidence to the contrary. However, *Revueltosaurus callenderi* almost certainly had lateral osteoderms in the pelvic region (W. Parker, unpublished data).

74. Lateral osteoderms dorsolateral to the cervical vertebrae, form of the dorsal eminence: low keel or knob (0); moderate length dorsoventrally flattened slightly recurved spine (1); moderate length faceted, slightly recurved spine (2); greatly elongated horn (3). Figures B12g; B13h.

Taxa such as *Aetosaurus ferratus* (Schoch, 2007) and *Coahomasuchus kahleorum* (Heckert and Lucas, 1999) possess cervical lateral osteoderms bearing dorsal eminences in the form of a low keel or knob. In other taxa such as *Longosuchus meadei* (TMM 31185-84B) and *Paratypothorax* sp. (VRPH 2) the eminence takes the form of a moderately elongate spine; however, in the former the spine is distinctly faceted. The facets, *sensu* Hunt and Lucas (1990), provide the spine with a trihedral cross-section (Lucas, 1998b). The extreme is seen in *Desmatosuchus* (e.g., UMMP 7476) where the eminence is an enormous posteriorly recurved horn.

75. Lateral osteoderms dorsolateral to the anterior trunk vertebrae, dorsal eminence form knob or spine (0); large and hemispherical (1). Modified from Parker (2007), character 37. Figure B13e.

In *Desmatosuchus* the dorsal eminences on the first three dorsal trunk lateral osteoderms, situated just posterior to the large hornlike dorsal eminence of the posterior cervical laterals, are in the forms of a large, but low, ovate mounds (Brady, 1958:fig. 3; Long and Ballew, 1985:fig. 6a; Parker, 2008b:figs. 24a-c). Long and Ballew (1985) considered this shape for osteoderms of the pelvic region; however, the articulated specimen MNA V9300 demonstrated that they are instead from the anterior dorsal region (Parker, 2008b).

76. Lateral osteoderms dorsolateral to the trunk vertebrae, shape of dorsal flange: broad rectangle (0); triangular (1); highly reduced in size and a narrow triangle ("tongue-shaped") (2). [Ordered]. Parker (2007), character 36. Figures B13b-c, g, i-k.

The dorsal flange of the lateral osteoderms is the portion of the osteoderm that is medial to the dorsal eminence. The lateral flanges of many of the dorsal lateral osteoderms in *Calyptosuchus wellesi* (e.g., UCMP 27225) are distinctly triangular in dorsal view. This differs significantly from the dorsal flanges in *Tecovasuchus chatterjeei* (TTU P-545) and *Paratypothorax* sp. (PEFO 3004), which are much reduced and 'tongue-like' (Martz and Small, 2006), as well as the rectangular dorsal flanges of *Desmatosuchus spurensis* (MNA V9300) and *Longosuchus meadei* (TMM 31185-97). The triangular dorsal flange in *Calyptosuchus wellesi*, results from the elongate anterolateral process of the adjacent paramedian osteoderm projecting into the 'space' of the lateral osteoderm. Some of the lateral osteoderms of *Calyptosuchus wellesi* are sub-rectangular in dorsal view (e.g., UCMP 27225), however, these co-occur in the same carapace with the triangular osteoderms and differ from taxa such as *Desmatosuchus spurensis* where all of the lateral osteoderms in the carapace bear rectangular flanges. Thus *Calyptosuchus wellesi* is scored for state 1, as at least some of the osteoderm lateral flanges are distinctly triangular.

Although the dorsal trunk lateral osteoderms of *Typothorax coccinarum* (e.g., NMMNH P-56299) share many characters with *Paratypothorax* sp., rather than *Calyptosuchus wellesi* (e.g., strongly acute angle of flexion, 'blade-like' flanges forming a curved spine in ventral view), the dorsal flange is clearly triangular in dorsal view and not 'tongue-like' as in *Paratypothorax*, thus I have scored *Typothorax coccinarum* as possessing state 1.

77. Lateral osteoderms dorsolateral to the trunk vertebrae, ventralmost 1/3 of the posterior face of the dorsal eminence (spine) ventral margin straight (0); distinct ventrally concave embayment ('emarginated') (1). Heckert and Lucas (1999a), character 48. Figures B12g; B13b, j.

In taxa where the dorsal eminence of the dorsal trunk lateral osteoderms forms a spine, there is a deep ventral, triangular emargination of the posterior face of the spine in some (e.g., *Longosuchus meadei*). This emargination is lacking in other taxa such as *Lucasuchus hunti* (Parker and Martz, 2010). This character is scored as inapplicable for taxa lacking a spine-like dorsal eminence, because absence of the spine is not the same as absence of the ventral emargination.

78. Lateral osteoderms dorsolateral to the mid-trunk region, form of the dorsal eminence: triangular boss or keel, not elongated (0); elongated flattened horn (1); conical spike (2). Parker (2007), character 30. Figures B13a-d, f-g, i-k.

A number of aetosaurians (e.g., *Calyptosuchus wellesi*, *Aetosaurus ferratus*) lack the extension of the dorsal eminence of the dorsal trunk lateral osteoderms into an elongate conical spike as in *Desmatosuchus spurensis* (UMMP 7476) and *Lucasuchus hunti* (TMM 31185-66). In *Typothorax coccinarum* (e.g., AMNH 2713) and *Paratypothorax andressorum* (SMNS uncatalogued, L18) the dorsal and lateral (ventral) flanges are mediolaterally elongate and meet along an extended transverse edge. This edge continues laterally and terminates in a slightly recurved point. Thus it is more like an elongate flattened horn than a conical spine.

79. Lateral osteoderms dorsolateral to the mid-trunk region, angle of flexion between dorsal and lateral flanges of the osteoderms obtuse (0); approximately 90 degrees (1); strongly acute (2). [Ordered] Modified from Heckert et al. (1996), character 14. Figures B14a, d, j.

This character is variable through the anteroposterior extent of the carapace and thus is restricted to the mid-lateral to posterior dorsal trunk lateral osteoderms. Aetosaurians with obtuse angles of flexion between the dorsal and lateral flanges include *Aetosaurus ferratus* (Schoch, 2007) and *Coahomasuchus kahleorum* (Heckert and Lucas, 1999). Heckert and Lucas (1999) considered the dorsal trunk lateral osteoderms of the holotype of *Coahomasuchus kahleorum* (NMMNH P-18496) to be completely flat with not sign of a division into dorsal and lateral flanges. This would be autapomorphic for Aetosauria; however, in NMMNH P-18496, the lateral osteoderms have small, triangular dorsal flanges as in *Aetosaurus ferratus* and *Calyptosuchus wellesi* (UCMP 27225) and flattening of the carapace because of crushing has pushed the dorsal flanges downward and partially obscuring them. However, they can be seen in the holotype (Heckert and Lucas, 1999: fig. 3) on the right side in the waist narrowing and anterior to it. Note also that the width of the lateral flange increases significantly anterior to the waist compared to the very reduced dorsal flange and this helps to create the illusion that these is no discrete dorsal flange. The presence of a discrete triangular flange and obtuse flexion of the lateral osteoderms is also confirmed by isolated osteoderms in TMM 31100-437. Specimens that possess an obtuse angle of flexion retain this through the entire carapace. *Calyptosuchus wellesi* has been described as possessing cervical laterals with an acute angle of flexion (Long and Ballew, 1985; Long and Murry, 1995); however, these are dorsal lateral osteoderms of a ‘*Tecovasuchus*-like’ taxon (Parker, 2005a).

Desmatosuchus spurensis (e.g., MNA V9300) and *Longosuchus meadei* (TMM 31185-97) possess distinct dorsal and lateral flanges that meet at an angle of around 90 degrees. This varies little throughout the carapace. *Typothorax coccinarum* (e.g., NMMNH P-56299) and *Paratypothorax andressorum* (SMNS unnumbered, L18) have dorsal and lateral flanges that meet at an acute angle and are scored as such; however, other lateral osteoderms in these taxa are anteroposteriorly shorter and have flanges that meet at right angles (e.g., *Paratypothorax andressorum* (SMNS unnumbered, L9, R10). It is not entirely certain where in the carapace this character state occurs but scoring of disarticulated, incomplete material needs to be done with caution. If a specimen possesses the acute angle in at least one osteoderm, I code the taxon as possessing that state even if the angle of flexion in other osteoderms in the same carapace may trend closer to 90 degrees. Completion of preparation and description of SMNS 19003 should reveal these changes in angle of flexion in an aetosaur with the acute osteoderm type.

80. Lateral osteoderms dorsolateral to the mid-trunk region, symmetry of dorsal and lateral flanges: weakly or strongly asymmetrical, with lateral flange the longest (0); strongly asymmetrical with dorsal flange longest (1). Modified from Heckert et al. (1996), character 15. Figures B14a,c, i.

This character considers size differences (symmetry) of the lateral and dorsal flanges of the dorsal trunk lateral osteoderms as divided by the axis of the dorsal eminence. No aetosaurian lateral osteoderm is perfectly symmetrical; however, in taxa where the symmetry is close the lateral flange is still larger than the dorsal flange (e.g., *Aetosauroides scagliai*). Where the flanges are strongly asymmetrical, some taxa such as *Coahomasuchus kahleorum* (NMMNH P-18496), have greatly reduced dorsal flanges where the dorsal flange is a small triangle and the lateral flange is a wide rectangle (see Heckert and Lucas, 1999: fig. 3). In *Desmatosuchus spurensis* (MNV V9300), the mid-dorsal trunk lateral osteoderms possess elongate dorsal flanges, and reduced lateral flanges (Parker, 2008b).

81. Lateral osteoderms dorsolateral to the sacral and anterior caudal vertebrae, lateral flange shape: roughly rectangular and lateral to a sharp medially situated keel (0); roughly triangular in lateral view with a semicircular ventrolateral border and a hook-like eminence (1); rectangular and ventral to a well-developed spine (2). Parker (2007), character 28. Figures B13c, f, j.

This character attempts to capture the anatomical variation in the lateral flange of the pelvic and anterior caudal lateral osteoderms. A roughly triangular osteoderm with a semicircular ventrolateral border and a hook-like eminence is shared by several taxa including *Typothorax coccinarum* (NMMNH P-56299) and *Paratypothorax sp.*(PEFO 3004)*,* and differs strikingly from the spiked plate found in *Desmatosuchus spurensis* (MNA V9300) and *Longosuchus meadei* (TMM 31185-84b). A somewhat similar form occurs in *Aetosaurus ferratus* (Schoch, 2007)*, Stagonolepis robertsoni* (Walker, 1961)*, Aetosauroides scagliai* (PVL 2073)*,* and *Neoaetosauroides engaeus* (PVL 3525)*,* but these plates are more rectangular rather than triangular (Parker, 2007).

82. Carapace, overall shape in dorsal view: presence of narrow waist anterior to sacrum (0); moderate spinose carapace (1); broad discoidal carapace (2). Modified from Heckert et al. (1996), character 16.

The aetosaur carapace comes in three general forms, a narrow carapace with a distinct narrowing (waist) just anterior to the pelvis (e.g., *Aetosaurus ferratus*), a broader carapace that lacks the narrow waist and is generally spinose (e.g., *Desmatosuchus spurensis*), and a very broad discoid form (e.g., *Typothorax coccinarum*) (Desojo et al., 2013:fig. 1).

83. Osteoderms ventral to the trunk vertebrae, shape and arrangement: absent (0); irregular, non-touching (1); square, overlapping (2). New character.

Previous characters regarding the ventral osteoderms focused on number of rows or the type of ornament; however, these were difficult to score given the incomplete preservation of the ventral osteoderms in many taxa. Instead, this new character focuses on the shape and arrangement of the ventral osteoderms in light of the recent discovery of *Stenomyti huangae*, which has a unique arrangement of the ventral osteoderms (Small and Martz, 2013). In aetosaurians such as *Stagonolepis robertsoni* (Walker, 1961) and *Coahomasuchus kahleorum* (Heckert and Lucas, 1999) the associated ventral osteoderms consists of rows and columns of overlapping, equant osteoderms. However, in *Stenomyti huangae* the ventral osteoderms are round to oval and non-overlapping (Small and Martz, 2013). Despite the recovery of several nearly complete skeletons of *Desmatosuchus* and *Longosuchus meadei*, no ventral osteoderms are known for the taxa and it is hypothesized here that these forms lacked ventral armor (Parker, 2008b).

APPENDIX C

Tree support

Character state transformations were evaluated under both the accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) options. Synapomorphies recovered under each option are listed for each node and character states placed at the same node under both ACCTRAN and DELTRAN criteria are considered to be unambiguous synapomorphies. Underlined numbers represent characters with a C.I. of 1.000 and can be considered to be robust synapomorphies.

Unnamed node (*Revueltosaurus callenderi* + Aetosauria)

Unambiguous synapomorphies -- 1) lateral surface of maxilla bears a sharp longitudinal ridge (7-1); 2) ventrolateral margin of the nasal forms part of the dorsal border of the antorbital fossa (10-1); 3) postfrontal-parietal contact is restricted by a posterolateral process of the frontal (14-1); 4) anterior process of the quadratojugal forms the ventral margin of lateral temporal fenestra (16-1); 5) transverse width of frontals greater than that of the parietals at their anteroposterior mid-points (19-1); 6) basal tubera of the basicranial are clearly separated in ventral view (24-1); 7) The crown bases of the maxillary teeth are anteroposteriorly oval, but not strongly mediolaterally compressed in occlusal view (34-1); 8) articular face of the cervical centrum is round (38-1); 9) trunk vertebrae lack well-developed intervertebral articulations (hyposphene/hypantrum) (43-1); 10) anterior bar present and strongly raised om osteoderms (52-1); 11) lateral osteoderms only present in the sacral and anterior caudal regions (73-1); and 12) ventral osteoderms square and overlapping (83-2).

Other possible synapomorphies -- ACCTRAN: 1) shape of the maxillary tooth crown in labial/lingular view is bulbous with pointed or slightly recurved tips (35-2); 2) subglenoid 'pillar' absent on coracoid (46-1); and 3) acetabulum of ilium opens opens fully or mostly laterally (49-1). DELTRAN: none.

Aetosauria Marsh, 1884 *sensu* Parker, 2007. Modified by Nesbitt, 2011.

Definition -- The most inclusive clade containing *Aetosaurus ferratus* and *Desmatosuchus spurensis*, but not *Rutiodon carolinensis*, *Postosuchus kirkpatricki*, *Prestosuchus chiniquensis*, *Poposaurus gracilis*, *Crocodylus niloticus*, *Gracilisuchus stipanicicorum*, and *Revueltosaurus callenderi*.

Unambiguous synapomorphies -- 1) premaxillary teeth restricted to posterior portion of the element (3-1); 2) external nares longer than or equal to the antorbital fenestra (6-1); 3) prefrontal-parietal contact is extensive (14-2); 4) supratemporal fenestra is dorsolaterally or laterally oriented and visible in lateral view (20-1); 4) posterodorsal process of dentary more elongate than the posteroventral process (26-1); 5) anterior portion of dentary edentulous (28-1); 6) radiate patterning on paramedian osteoderms (53-1); 7) dorsal eminence of paramedian osteoderm contacts the posterior margin of osteoderm in most osteoderm rows (54-1); 8) the dorsal eminence of the anterior caudal paramedian osteoderms are low and pyramidal or rounded and knob-like (71-1); and 9) lateral osteoderms present along the entire dorsal carapace (73-2).

Other possible synapomorphies -- ACCTRAN: 1) dorsally projecting tuber present on articular (33-1). DELTRAN: none.

Stagonolepididae Lydekker, 1887 *sensu* Heckert and Lucas, 2000.

Definition -- The last common ancestor of *Desmatosuchus spurensis* and *Aetosaurus ferratus* and all of their descendants.

1) maxilla contributes to the margin of the external naris (2-1); 2) premaxilla has prominent dorsal tubercle that extends dorsally into the external naris (5-1); 3) anterior ends of the dentary prolonged into an acute rostrum (slipper-shaped) (30-1); and 4) maxillary teeth are conical in cross section (34-2).

Other possible synapomorphies -- ACCTRAN: 1) A ventral 'chin' is present on the mandibular ramus formed by a ventral inflexion of the dentary, which covers the splenial (29-2) and 2) subglenoid pillar present on coracoid (46-1). DELTRAN: 1) dorsally projecting tuber present on articular (33-1); and 2) shape of the maxillary tooth crown in labial/lingular view is bulbous with pointed or slightly recurved tips (35-2).

Aetosaurinae Marsh 1884, *sensu* Heckert and Lucas, 2000.

Revised Definition – The least inclusive clade containing *Aetosaurus ferratus* but not *Desmatosuchus smalli*.

Unambiguous synapomorphies -- 1) transverse width of parietals greater than transverse width of the frontals (19-0); and 2), the anteroposterior diameter of the supratemporal fenestra is roughly half the size of the orbit (22-1).

Other possible synapomorphies -- ACCTRAN: 1) pubis symphysis short, less than one-half of element length (51-1). DELTRAN: none.

Typothoracinae Huene, 1915 *sensu* Parker, 2007. Emended clade name

Revised Definition – The least inclusive clade containing *Typothorax coccinarum* and *Paratypothorax andressorum,* but not *Aetosaurus ferratus*, *Stagonolepis robertsoni* or *Desmatosuchus smalli.*

Note: This clade was first named Typothoracisinae (Parker, 2007); however, the formation of this name is incorrect as the root for 'thorax' is 'thorac' not 'thoracis' so the proper formation of this clade name is Typothoracinae. The family name Typothoracidae was first proposed by Huene (1915), so he should also be credited for the name Typothoracinae.

Unambiguous synapomorphies -- 1) width/length ratio of widest paramedian osteoderms (rows 9-11) in dorsal trunk series is greater than 3.5 (64-2); and 2) carapace is broad and discoidal in dorsal view (82-2).

Other possible synapomorphies -- ACCTRAN: 1) anterior projection of quadratojugal underlies the posterior process of the jugal and excluded from the lateral temporal fenestra (16-2); 2) articular lacks strong dorsally projecting tuber (33-0); 3) cervical vertebrae with a transversely oval articular face of the centrum (38-0); 4) transverse processes of the trunk vertebrae are elongate, more than twice as wide as the centrum (40-1); 5) neural spine height of the mid-trunk vertebrae is equal to or less than the height of the centrum (41-1); 6) proximal head of the humerus is broadly expanded transversely, with significant lateral expansion (48-1); 7) acetabulum on ilium opens fully or mostly ventrally (49-0); 8) strongly developed ventral keel on the paramedian osteoderms (56-2); 9) dorsal eminence of cervical lateral osteoderms is a moderate length, dorsoventrally flattened, slightly recurved spine (74-1); 10) mid-trunk lateral osteoderms with a strongly acute angle of flexion between the dorsal and lateral flanges (79-2); and 11) lateral flange of pelvic and anterior caudal lateral osteoderms is roughly triangular in lateral view with a semicircular ventrolateral border and a hook-like eminence (81-1). DELTRAN: none.

Unnamed node ((Paratypothoracini + (*Typothorax coccinarum* + *Redondasuchus rineharti*)).

Unambiguous synapomorphy -- lateral edge of the dorsal paramedian osteoderms in dorsal view are strongly sigmoidal with a strongly posteromedially oriented posterolateral corner (63-1). *Other possible synapomorphies* – ACCTRAN: none. DELTRAN: 1) anterior projection of quadratojugal underlies the posterior process of the jugal and excluded from the lateral temporal fenestra (16-2); 2) transverse processes of the trunk vertebrae are elongate, more than twice as wide as the centrum (40-1); 3) neural spine height of the mid-trunk vertebrae is equal to or less than the height of the centrum (41-1); 4) dorsal eminence of cervical lateral osteoderms is a moderate length, dorsoventrally flattened, slightly recurved spine (74-1); 5) mid-dorsal lateral osteoderms with a strongly acute angle of flexion between the dorsal and lateral flanges (79-2); and 6) lateral flange of pelvic and anterior caudal lateral osteoderms is roughly triangular in lateral vie with a semicircular ventrolateral border and a hook-like eminence (81-1).

Unnamed node (*Typothorax coccinarum* + *Redondasuchus rineharti*)

Unambiguous synapomorphies -- 1) cervical vertebrae extremely shortened anteroposteriorly (37-1); and 2) surface pattern of dorsal paramedian osteoderms is reticulate (53-2).

Other possible synapomorphies -- ACCTRAN: 1) premaxilla lacks a prominent dorsal tubercle that extends dorsally into the external naris (5-0); 2) lateral surface of the maxilla is smooth, lacking longitudinal ridge (7-2); 3) lateral margin of the nasal does not form part of the dorsal border of the antorbital fossa (10-0); 4) supratemporal fenestra larger than or nearly same size as the orbit (22-0); 5) retroarticular process is longer than high (32-1); 6) ectepicondyle of the humerus proximodistally oriented foramen present on its lateral side (47-1); and 7) ratio of cervical vertebrae/paramedian osteoderms significantly less than 1:1 (58-1). DELTRAN: 1) ventral strut of paramedian osteoderms strongly developed (56-2).

Paratypothoracini Parker, 2007. Emended clade name.

Revised Definition -- The least inclusive clade containing *Tecovasuchus chatterjeei, Rioarribasuchus chamaensis,* and *Paratypothorax andressorum*.

Note: This clade was first named Paratypothoracisini (Parker, 2007); however, the formation of this name is incorrect as the root for ‘thorax’ is ‘thorac’ not ‘thoracis’ so the proper formation of this clade name is Paratypothoracini.

Unambiguous synapomorphies -- 1) caudal ribs of the caudal vertebrae attach near the base of the centrum (45-1); 2) anterior bar present, but weakly raised (52-2); 3) dorsal eminence of the paramedian osteoderms does not contact the posterior margin of the osteoderm in most rows (54-0); 5) dorsal eminence of the dorsal paramedian osteoderms is strongly offset medially (66-2); 5) dorsal flange of the dorsal lateral osteoderms is highly reduced and ‘tongue-shaped’ (76-2); and 6) dorsal eminence of the anterior and mid-dorsal lateral osteoderms is in the form of an elongate flattened horn (78-1).

Other possible synapomorphies -- ACCTRAN: 1) Transverse width of frontal wider than parietal (19-1); 2) strong posteroventral orientation of the posterior portion of the parietal forms a triangular supratemporal fenestra (21-1); 3) maxillary teeth are anteroposteriorly oval, but not strongly mediolaterally compressed in cross section (34-1); and 4) shape of the maxillary tooth crown in labial/lingular view is bulbous and partly recurved, anterior edge is concave, posterior edge straight (35-1). DELTRAN: none.

Unnamed node (SMNS 19003 + Paratypothoracini).

Unambiguous synapomorphy -- posterior margin of paramedian osteoderms bears a transverse, posteroventrally sloping flange (bevel) (57-1).

Other possible synapomorphies -- none.

Unnamed node (*Tecovasuchus chatterjeei* + *Paratypothorax*).

Unambiguous synapomorphy -- distinct sharp raised mediolateral ridge extends medially from dorsal eminence of paramedian osteoderm to medial osteoderm margin (65-1).

Other possible synapomorphy -- ACCTRAN: none. DELTRAN: ventral strut of paramedian osteoderms strongly developed (56-2).

Paratypothorax (*Paratypothorax andressorum* + *Paratypothorax* sp.).

Unambiguous synapomorphies -- 1) lateral faces of the posterior trunk vertebrae meet to form a sharp ventral edge or keel (44-1); and 2) dorsal eminence of the posterior trunk – anterior caudal paramedian osteoderms is a moderate, bulbous spike (71-2).

Other possible synapomorphies -- none.

Stagonolepidoidea Hoffstetter, 1955. New clade name.

Definition -- The most inclusive clade containing *Stagonolepis robertsoni* and *Desmatosuchus smalli*, but not *Aetosaurus ferratus* and *Paratypothorax andressorum*.

Unambiguous synapomorphies -- 1) anterior portion of the premaxilla laterally expanded in dorsal view (1-1); 2) anterior portion of nasal maintains an equal width in dorsal view (9-1); 3) triangular depression on the midline suture area of the nasals absent (11-1); 4) jugal contributes to the margin of the antorbital fenestra (13-1); 5) basal tubera are nearly or completely connected (24-0); and 6) surangular bears prominent dorsal tuber (31-1).

Other possible synapomorphies – ACCTRAN: none. DELTRAN: 1) A 'chin' is present on the mandibular ramus formed by a ventral inflexion of the dentary, which covers the splenial (29-2); and 2) acetabulum on ilium opens fully or mostly laterally (49-1).

Stagonolepidinae Huene 1936*, sensu* Heckert and Lucas, 2000.

Revised Definition – The most inclusive clade containing *Stagonolepis robertsoni*, but not *Desmatosuchus spurensis* or *Paratypothorax andressorum*.

Unambiguous synapomorphies – 1) proximal portion of pubis bears two foramina' (50-1).

Other possible synapomorphies -- ACCTRAN: 1) Postfrontal-parietal contact restricted by a posterolateral process of the frontal (14-1). DELTRAN: none.

Desmatosuchinae Huene 1936, *sensu* Heckert and Lucas, 2000.

Revised Definition – The most inclusive clade containing *Desmatosuchus smalli,* but not *Stagonolepis robertsoni*, *Aetosaurus ferratus*, or *Paratypothorax andressorum*.

Unambiguous synapomorphies -- 1) lateral surface of the maxilla is smooth, lacking longitudinal ridge (reversed in *Longosuchus meadei*) (7-2); 2) lateral margin of the nasal does not form part of the dorsal border of the antorbital fossa (10-0); 3) quadrate foramen entirely within quadrate bone (18-1), and 4) fewer than nine tooth positions in the dentary (27-1).

Other possible synapomorphies -- ACCTRAN: 1) ventral margin of the jugal strongly anterodorsally inclined in lateral view (12-1); and 2) proximal head of the humerus broadly expanded transversely, with significant lateral expansion (48-1). DELTRAN: None.

Unnamed node (*Neoaetosauroides engaeus* + Desmatosuchinae).

Unambiguous synapomorphies -- 1) supratemporal fenestra is roughly half the size of the orbit (22-1); 3) dorsal and ventral posteroventral processes of the dentary are roughly equal in length (26-0); and 4) anterolateral projection of the anterior bar of the dorsal paramedian osteoderms is present and elongate (reversed in Desmatosuchini) (68-1).

Other possible synapomorphies -- ACCTRAN: 1) ventral portion of the antorbital fossa on the maxilla is very shallow or absent (8-1); 2) retroarticular process is longer than high (32-1); and 3) ectepicondyle of the humerus proximodistally oriented foramen present on its lateral side (47-1). DELTRAN: 1) ventral margin of the jugal strongly anterodorsally inclined in lateral view (12-1).

Unnamed node (((*Adamanasuchus eisenhardtae* + *Scutarx deltatylus*) + *Calyptosuchus wellesi*)) + Desmatosuchini))).

Unambiguous synapomorphies -- 1) basal tubera and basipterygoid processes widely separated anteroposteriorly (reversed in *Desmatosuchus smalli* and *Scutarx deltatylus*; convergent with *Tecovasuchus chatterjeei*) (25-1); and 2) cervical vertebrae with a transversely oval articular face of the centrum (38-0).

Other possible synapomorphies -- ACCTRAN: 1) edentulous premaxilla (3-2); 2) edentulous premaxilla (4-2); 3) postfrontal/parietal contact absent (14-0); and 4) ratio of cervical vertebrae/paramedian osteoderms significantly less than 1:1 (58-1). DELTRAN: none.

Desmatosuchini. Case, 1920. New clade name.

Definition – The most inclusive clade containing *Desmatosuchus smalli,* but not *Neoaetosauroides engaeus*, *Scutarx deltatylus, Stagonolepis robertsoni*, *Aetosaurus ferratus*, *Calyptosuchus wellesi*, and *Paratypothorax andressorum*.

Unambiguous synapomorphies -- 1) random surface patterning of paramedian osteoderms (reversed in *Lucasuchus hunti*) (53-0); 2) in the dorsal trunk paramedian osteoderms the anterior edge of the lateral osteoderm overlaps the anterior edge of the paramedian osteoderm (62-1); 3) lacks the sharp anteromedial projection of the anterior bar (reversed in *Lucasuchus hunti*) (67-1); 4) anterior bar of the dorsal trunk paramedian osteoderms lacks scalloping of the anterior margin on the medial side of the osteoderm (69-1); 5) dorsal eminence of the cervical lateral osteoderms is in the form of a moderately long, faceted, slightly recurved spine (74-2); 6) rectangular dorsal flange of the dorsal lateral osteoderms (76-0); 7) approximately 90 degree angle between the dorsal and lateral flanges of the mid-trunk lateral osteoderms (79-1); 8) dorsal trunk lateral osteoderms strongly asymmetrical with the dorsal flange longest (80-1); and 9) overall shape in of the dorsal carapace in dorsal view is moderately spinose (82-1).

Other possible synapomorphies- ACCTRAN: 1) post-temporal fenestra is absent (23-1); 2) ventral ‘chin’ of the mandibular ramus present and formed by a ventral inflexion of the splenial (29-1); 3) in the paramedian osteoderms dorsal to the cervical and anterior trunk vertebrae, lateral edge articulation with lateral osteoderms is dorsoventrally thickened, angled contact, with deeply incised interdigitation (='tongue and groove') (60-1); 4) dorsal eminence shape in the cervical paramedian osteoderms are a low pyramidal or rounded boss, or elongate keel (61-1); 5) the anterior bar of the trunk distal paramedian osteoderms lacks an anterolateral pro69-jection (68-2); 6) dorsal eminence in the mid-trunk osteoderms is a conical spike (78-2); 7) lateral flange of the pelvic and anterior caudal lateral osteoderms are rectangular and ventral to a well-developed spine (81-2); and 8) ventral osteoderms absent (83-0). DELTRAN: ratio of cervical vertebrae/paramedian osteoderms significantly less than 1:1 (58-1).

Unnamed node (*Longosuchus meadei* + Desmatosuchini).

Unambiguous synapomorphies -- 1) cervical paramedian osteoderms are longer than wide (57-1); and 2) adjacent paramedian and lateral cervical osteoderms are often fused (59-1).

Other possible synapomorphies – ACCTRAN: none. DELTRAN: 1) ventral portion of the antorbital fossa on the maxilla is very shallow or absent (8-1); 2) post-temporal fenestra is absent (23-1); 3) ventral ‘chin’ of the mandibular ramus present and formed by a ventral inflexion of the splenial (29-1); 4) proximal head of humerus broadly expanded transversely with a significant lateral expansion (48-1); 5) in the paramedian osteoderms dorsal to the cervical and anterior trunk vertebrae, lateral edge articulation with lateral osteoderms is dorsoventrally thickened, angled contact, with deeply incised interdigitation (='tongue and groove') (60-1); 6) dorsal eminence shape in the cervical paramedian osteoderms are a low pyramidal or rounded boss, or elongate keel (61-1); 7) the anterior bar of the trunk dirsal paramedian osteoderms lacks an anterolateral projection (68-2); 8) dorsal eminence in the mid-dorsal osteoderms is a conical spike (78-2); 9) lateral flange of the pelvic and anterior caudal lateral osteoderms are rectangular and ventral to a well-developed spine (81-2); and 10) ventral osteoderms absent (83-0).

Unnamed node (*Sierritasuchus macalpini* + Desmatosuchini).

Unambiguous synapomorphies -- 1) neural spine height of the mid-dorsal vertebrae is low, equal to or less than the height of the centrum (41-1) and 2) dorsal eminence of dorsal paramedian osteoderms is centralized (66-0).

Other possible synapomorphies -- ACCTRAN: 1) quadrate foramen positioned between the quadrate and quadratojugal (18-0); 2) supratemporal fenestra larger than or nearly same size as the orbit (22-0); 3) lower posteroventral process of the dentary is longer than the upper process (26-2); 4) dorsal tuber of surangular is absent (31-0); 5) articular lacks strong dorsally projecting tuber (33-0); and 6) hyposphene/hypantrum present in dorsal vertebrae (43-0). DELTRAN: none.

Unnamed node (*Lucasuchus hunti* + *Desmatosuchus*).

Unambiguous synapomorphies -- 1) dorsal eminence of the paramedian osteoderms almost never contacts the posterior osteoderm margin (54-0); and 2) posterior face of the dorsal trunk lateral osteoderms lack a ventral emargination (77-0).

Other possible synapomorphy -- ACCTRAN: 1) articular face of the cervical vertebral centrum is subrectangular (38-2). DELTRAN: none.

Desmatosuchus Case 1920 (= *Desmatosuchus smalli* + *Desmatosuchus spurensis*).

Unambiguous synapomorphies -- 1) osteoderms possess a depressed anterior lamina rather than a raised anterior bar (52-3); 2) dorsal eminence of the cervical lateral osteoderms is a greatly elongated horn (<u>74-3</u>); and 3) anteriormost dorsal trunk lateral osteoderms bear a mound-like dorsal eminence (<u>75-1</u>).

Other possible synapomorphies – ACCTRAN: none. DELTRAN: 1) postfrontal-parietal contact absent (14-0); 2) retroarticular process is longer than high (32-1); 3) articular lacks strong dorsally projecting tuber (33-0); 4) articular face of the cervical vertebral centrum is subrectangular (38-2); and 5) hyposphene/hypantrum present in trunk vertebrae (43-0).

<u>Unnamed node (*Calyptosuchus wellesi* + (*Adamanasuchus eisenhardtae* + *Scutarx deltatylus*)).</u>

Unambiguous synapomorphies -- 1) acetabulum on ilium opens fully or mostly ventrally (49-0); 2) ventral strut of the paramedian osteoderms weakly developed (56-1); and 3) width/length ratio of widest paramedian osteoderms is between 3.01 and 3.5 (64-1).

Other possible synapomorphies -- ACCTRAN: 1) dentary tooth count of nine or more (27-0); and 2) two pubic foramina (50-1). DELTRAN: none.

<u>Unnamed node (*Adamanasuchus eisenhardtae* + *Scutarx deltatylus*).</u>

Unambiguous synapomorphies -- 1) anterolateral projection of the anterior bar of the dorsal paramedian osteoderms is present and elongate (70-1).

Other possible synapomorphies -- ACCTRAN: none. DELTRAN: none.

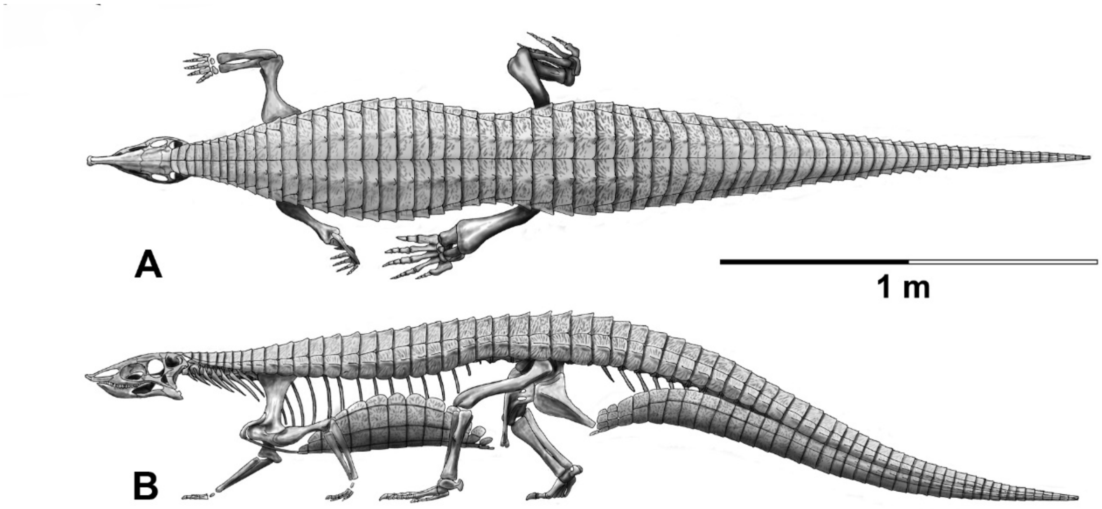

Figure 1: Skeletal reconstruction of an aetosaur (*Stagonolepis robertsoni*) showing the extensive carapace and associated armor in dorsal (A) and lateral (B) views. Courtesy of Jeffrey Martz.

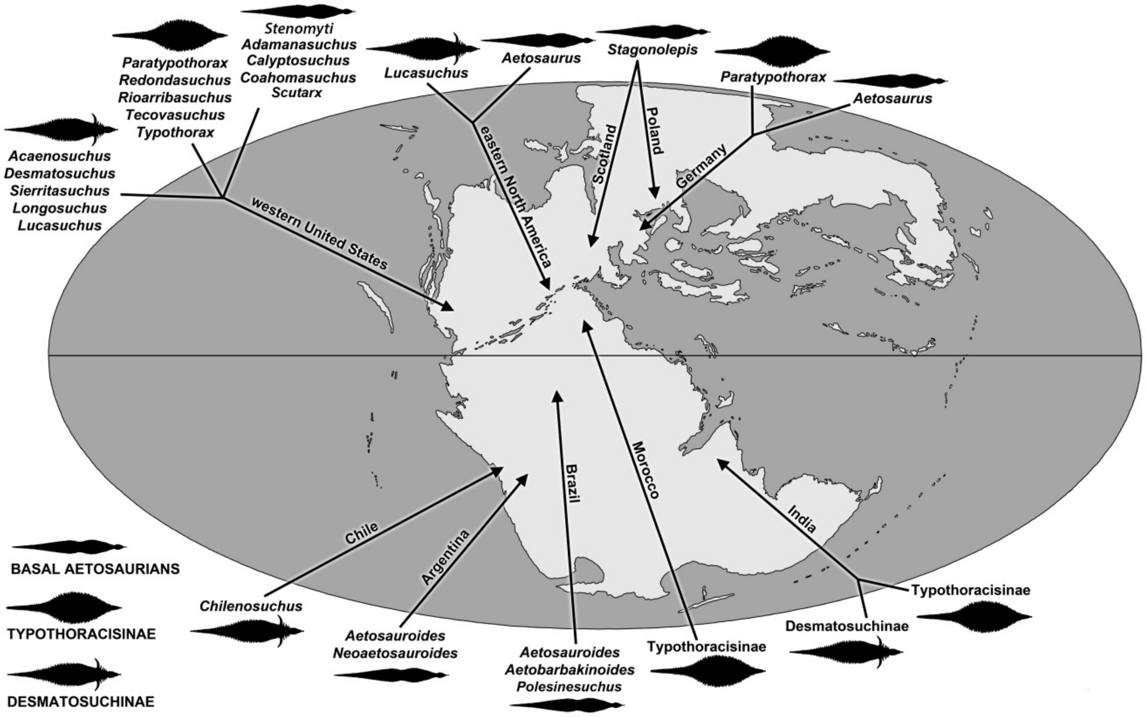

Figure 2: Global distribution of known aetosaurian taxa and specimens throughout Pangaea during the Late Triassic. Modified from Desojo et al., 2013.

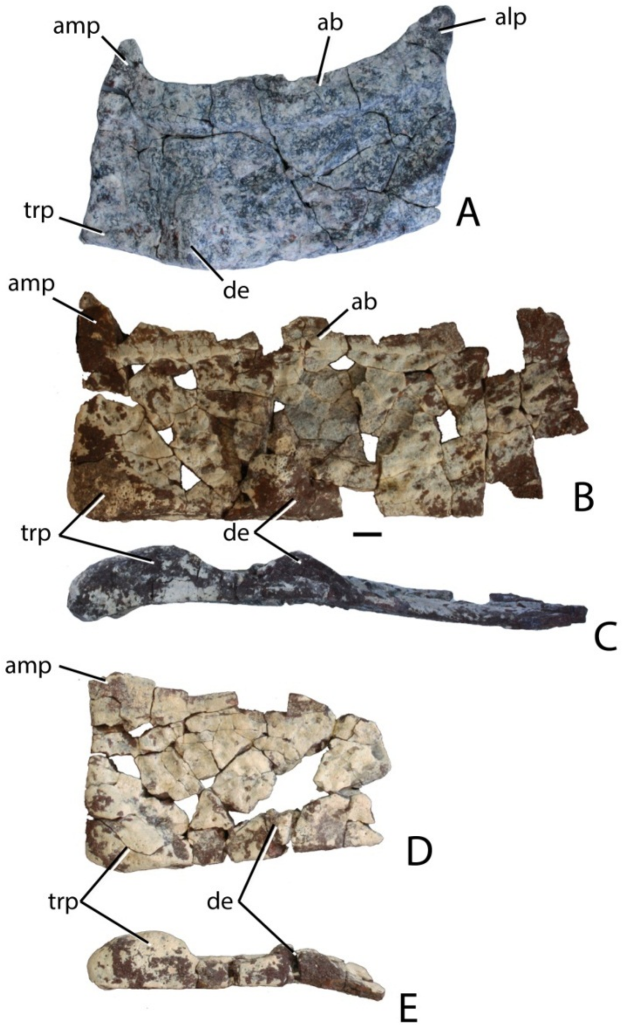

Figure 3: Holotype paramedian osteoderms of *Scutarx deltatylus* from PEFO 34616. A, posterior cervical osteoderm in dorsal view. B-C, right dorsal trunk paramedian osteoderm in dorsal (B) and posterior (C) views. D-E, partial right dorsal trunk paramedian osteoderm in dorsal (D) and posterior (E) views. Note the prominence of the triangular protuberance in the posterior views. Scale bar equals 1 cm. Abbreviations: ab, anterior bar; alp, anterolateral process; amp, anteromedial process; de, dorsal eminence; trp, triangular protuberance.

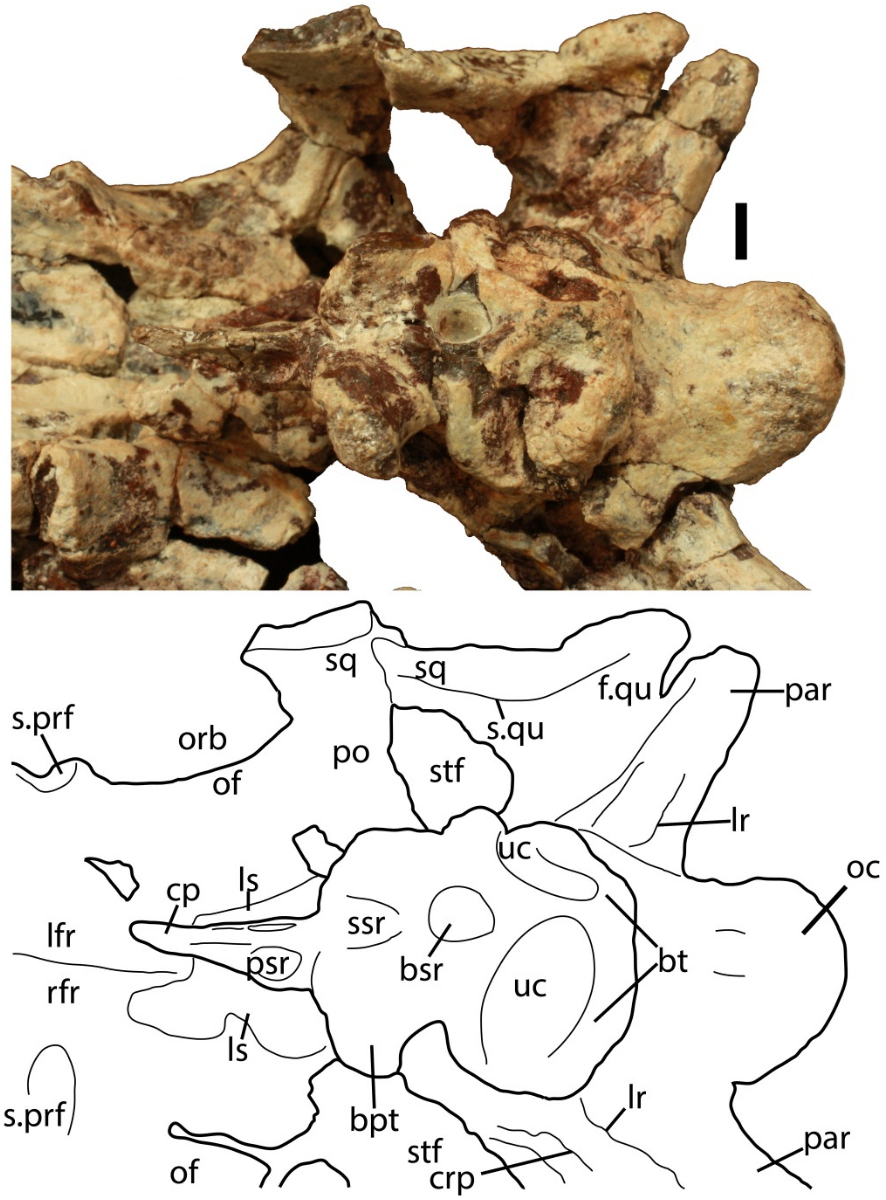

Figure 4: Parabasisphenoid of *Scutarx deltatylus* (PEFO 34616) in ventral view. Scale bar equals 1 cm. Abbreviations: **bpt**, basipterygoid processes; **bsr**, basisphenoid recess; **bt**, basal tubera; **cp**, cultriform process; **crp**, crista prootica; **f.**, fossa for specified element; **lfr**, left frontal; **lr**, lateral ridge; **ls**, laterosphenoid; **of**, orbital fossa; **orb**, orbit; **par**, paroccipital process of the opisthotic; **po**, postorbital; **prf**, prefrontal; **pr**, prootic; **prf**, prefrontal; **psr**, parasphenoid recess; quadrate; **rfr**, right frontal; **sq**, squamosal; **ssr**, subsellar recess; **stf**, supratemporal fenestra; **uc**, unossified cleft of the basal tubera.

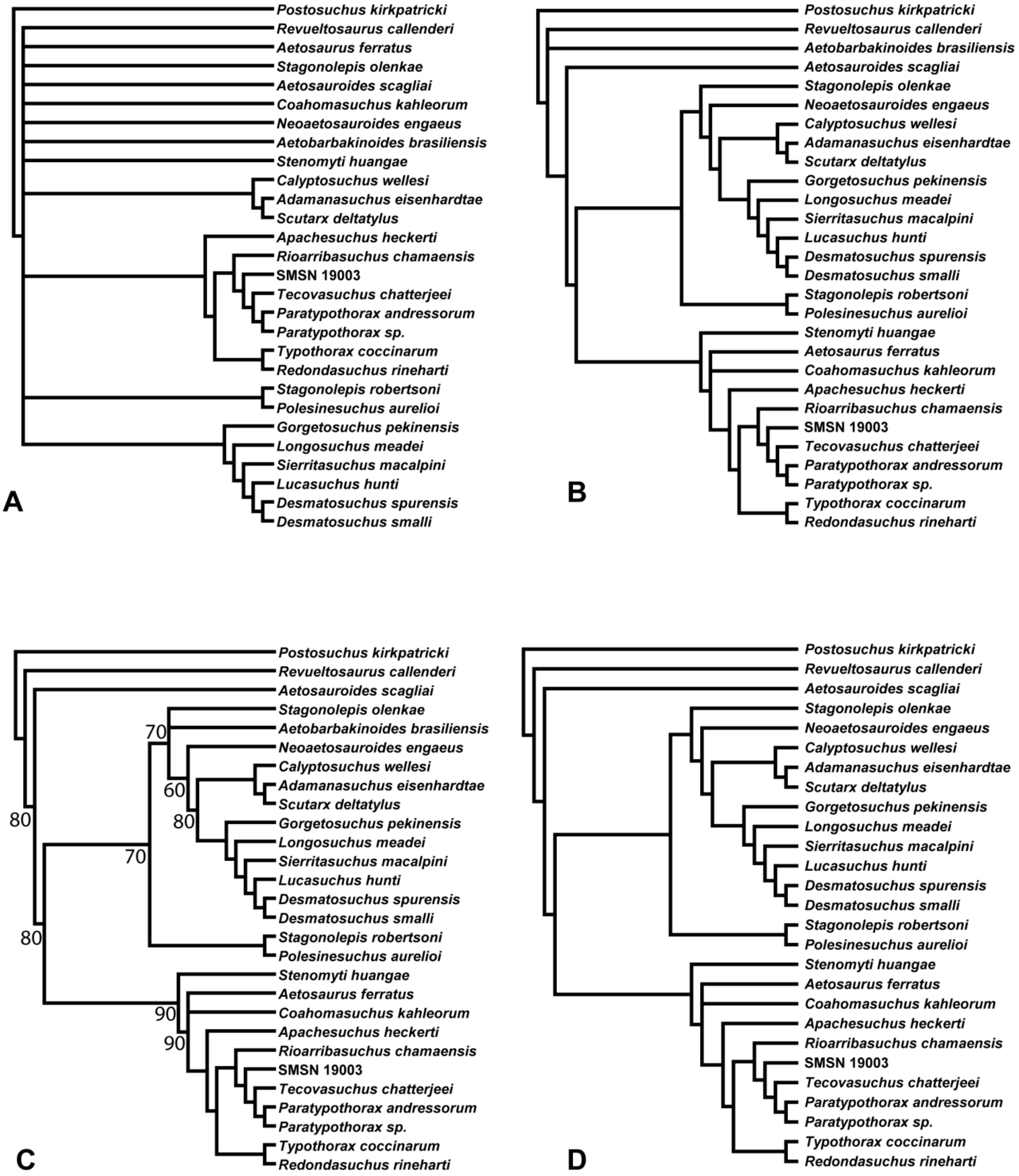

Figure 5: Phylogenetic trees recovered from the initial run of the main dataset. A, Strict component consensus of 30 MPTs; B, Adams consensus of 30 MPTs; 50% Majority Rule consensus of 30 MPTs. Only values under 100% are shown; D, Maximum agreement subtree after *a priori* pruning of *Aetobarbakinoides brasiliensis*.

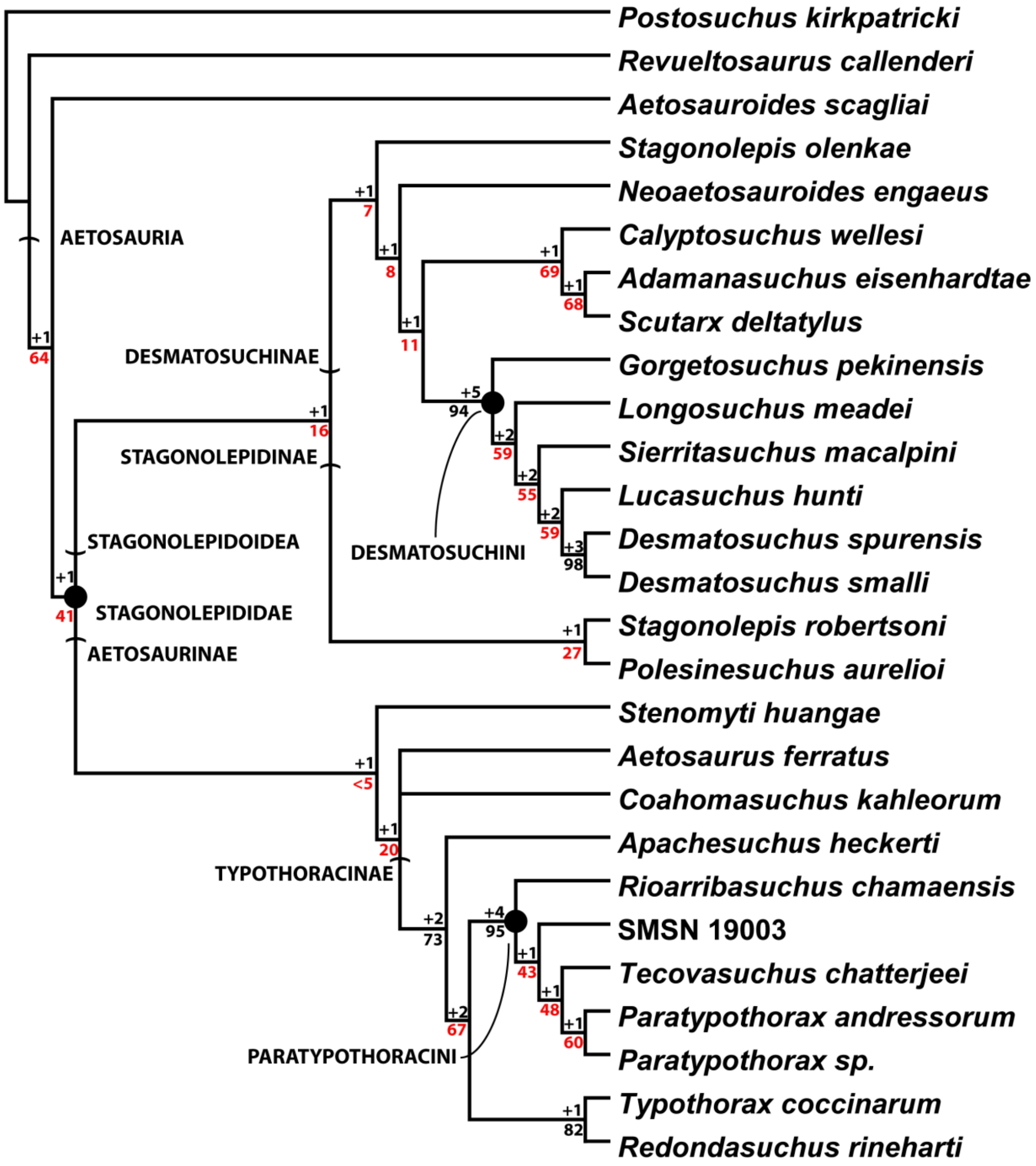

Figure 6: The reduced strict consensus of 3 MPTs used for this study with *Aetobarbakinoides brasiliensis* removed, with all named clades. Decay indices and bootstrap values are shown for all nodes, with bootstrap values under 70% (the confidence threshold of Hillis and Bull, 1993) shown in red.

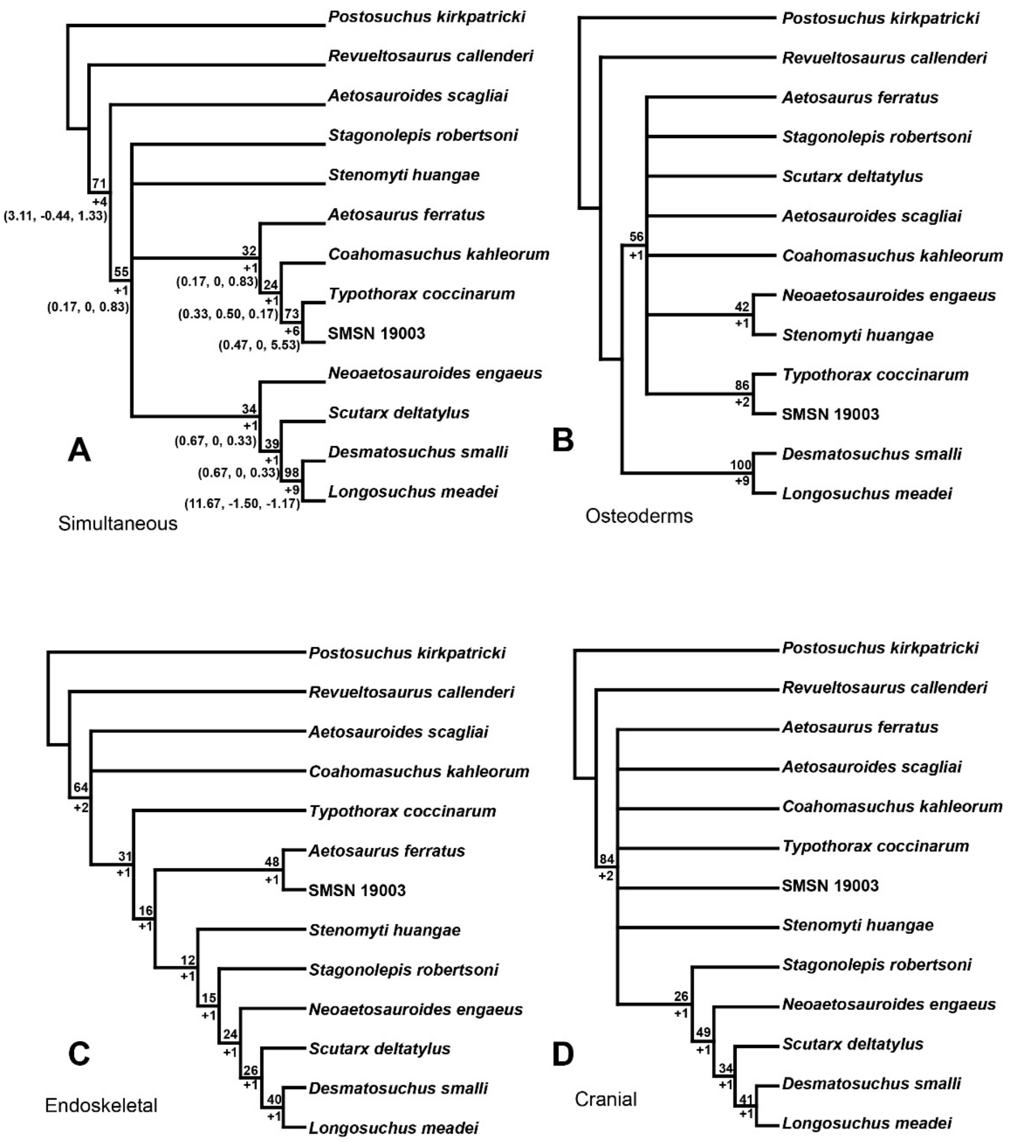

Figure 7: Phylogenetic trees recovered from partitioning the main dataset. Decay indices and bootstrap values (1000 replicates) listed for all nodes. A, Topology of a three MPTs from the simultaneous (13 taxa, 83 characters) dataset. Partitioned Bremer Support values for nodes are given in parentheses. The first value pertains to the cranial only characters, the second from the postcranial characters, and the third from the osteoderm characters; B, Topology of a three MPTs recovered for the osteoderm dataset; C, Strict consensus tree from two MPTs from the complete non-osteoderm (endoskeletal) dataset (cranial, axial, appendicular); D) Strict consensus of 13 MPTs from analysis of the cranial dataset.

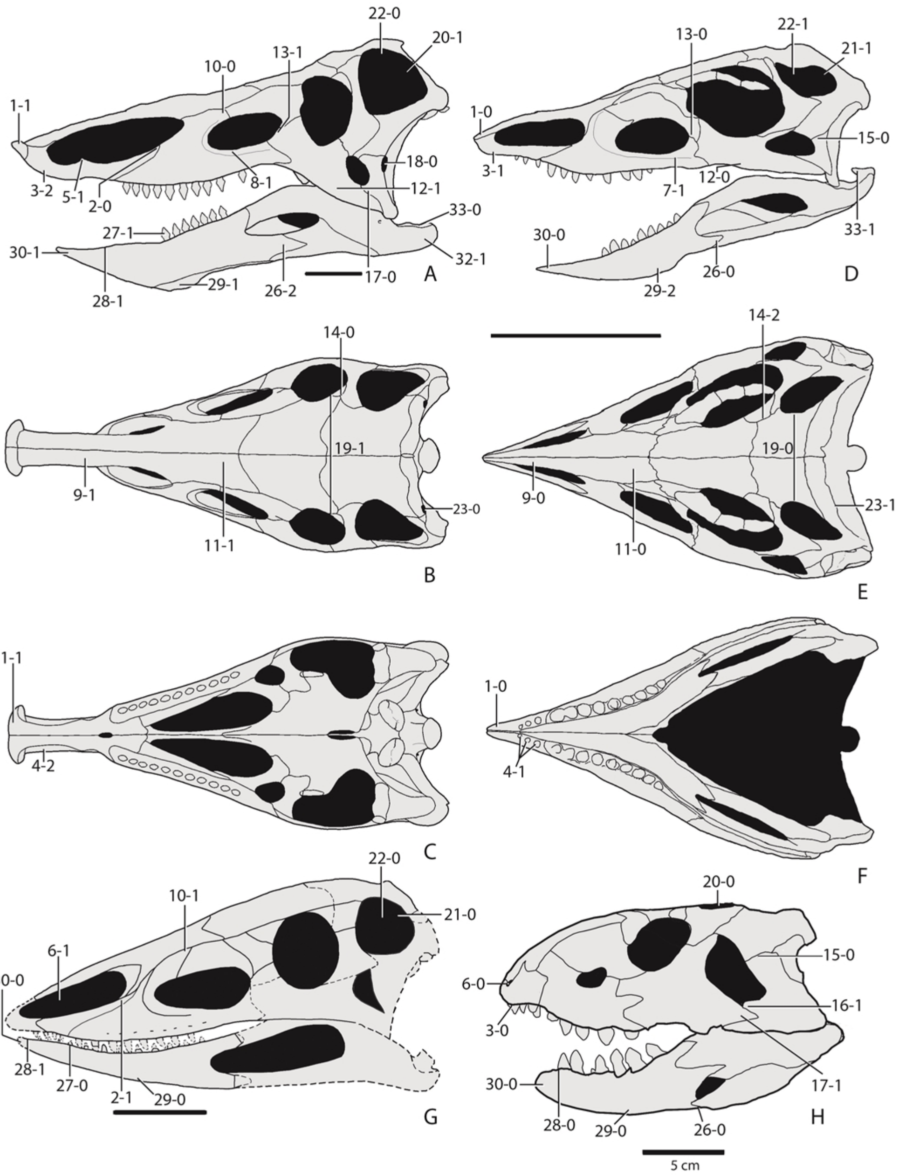

Figure B1: Skull reconstructions of suchian archosaurs showing defined character states. A, B, C, *Desmatosuchus smalli* in lateral, dorsal and ventral views (redrawn from Small, 2002); D, E, F, *Stenomyti huangae* in lateral, dorsal, and ventral views (redrawn from Small and Martz, 2013); G, *Aetosauroides scagliai* in lateral view (redrawn from Desojo and Ezcurra, 2011); H, *Revueltosaurus callenderi* (based on PEFO 34561) in lateral view. Scale bars equal 5 cm.

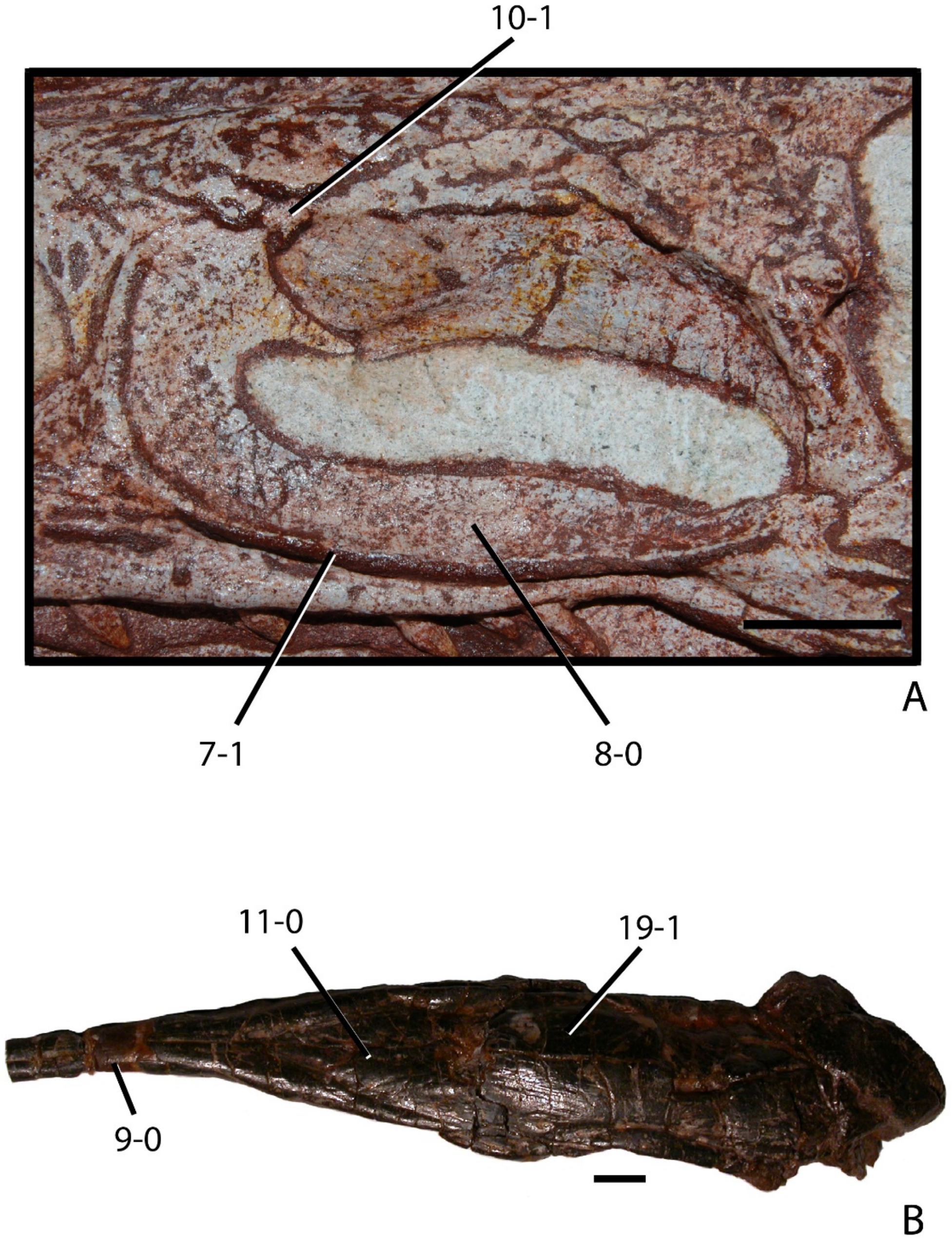

Figure B2: Photos of aetosaurian crania showing defined character states. A, close-up view of the antorbital fenestra in SMNS 19003, showing the extent of the antorbital fossa and the upper contact with the frontal; B, skull of *Aetosauroides scagliai* (PVL 2073) in dorsal view. Scale bars equal 1 cm.

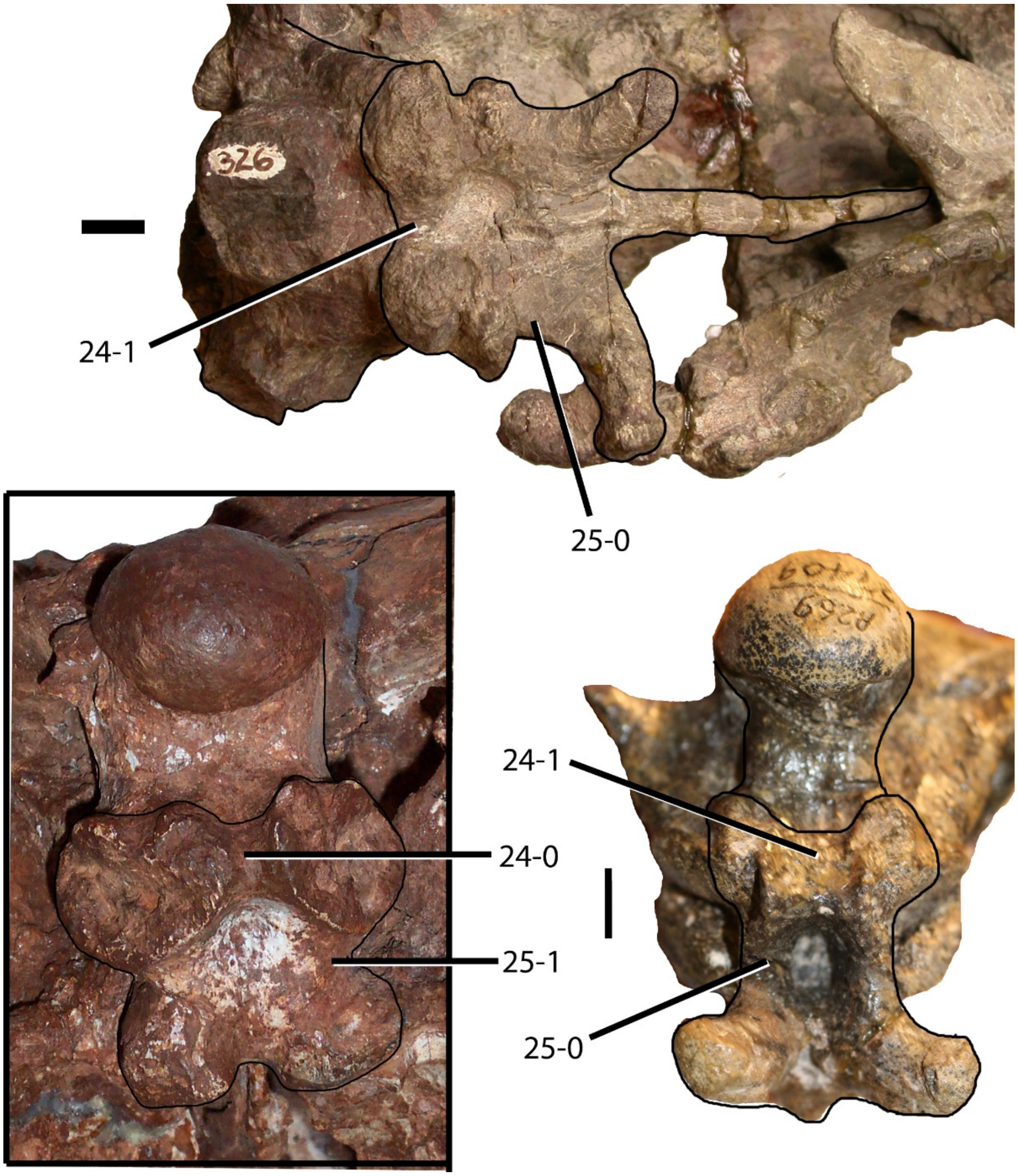

Figure B3: Photos of aetosaurian basicrania showing defined character states. A, PVSJ 326, parabasisphenoid of *Aetosauroides scagliai* in ventral view; B, TTU P-9024, parabasisphenoid of *Desmatosuchus smalli* in ventral view; C, UCMP 27409, parabasisphenoid of an aetosaurian, possibly *Calyptosuchus wellesi,* in ventral view; Scale bars equal 1 cm.

Figure B4: Posterior portion of the left mandible of *Stagonolepis olenkae* (ABIII 578/34) in lateral view showing defined character states. Scale bar equal 1 cm.

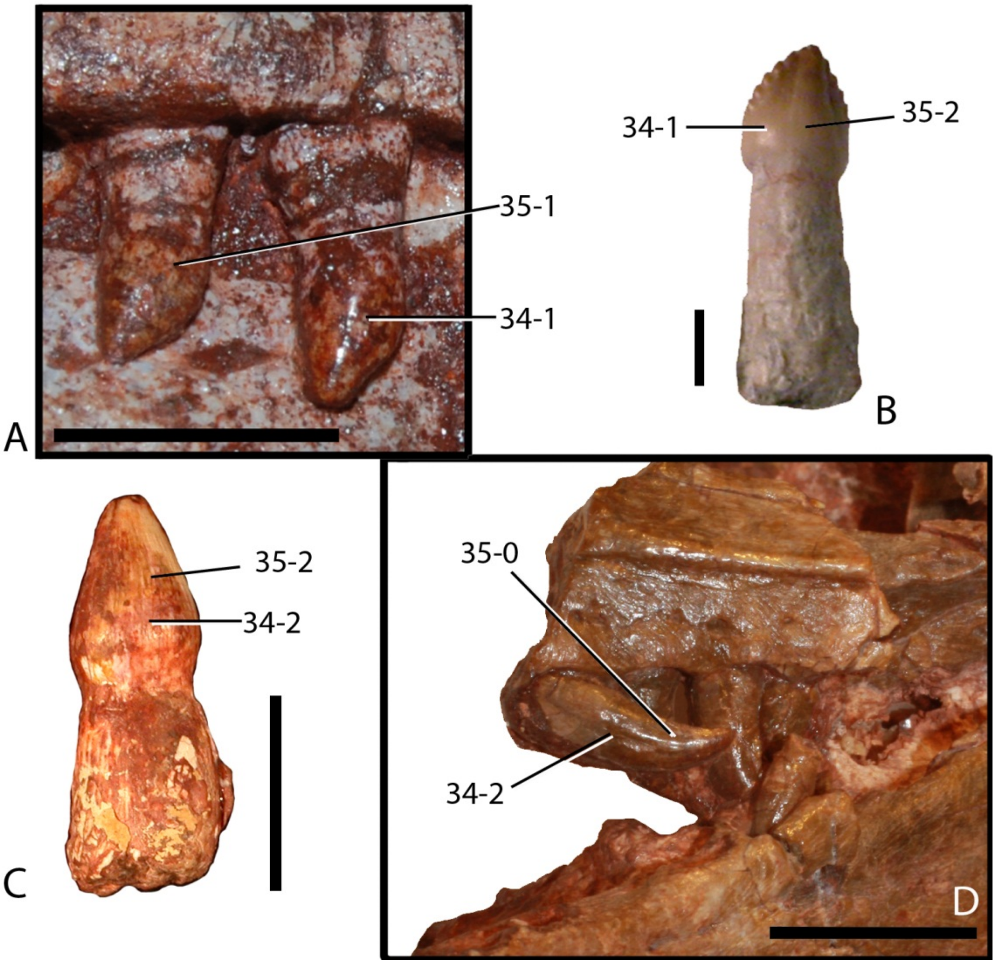

Figure B5: Maxillary teeth of various aetosaurians and *Revueltosaurus callenderi* showing defined character states. A, SMNS 19003; B, *Revueltosaurus callenderi* (PEFO 34561); C, *Desmatosuchus smalli* (TTU P-9024); D, *Coahomasuchus kahleorum* (TMM 31100-437). Scale bars equal 1 cm.

Figure B6: Cervical series centra of aetosaurians showing defined character states. A, *Desmatosuchus spurensis* (UMMP 7504) in anterior view; B, *Redondasuchus rineharti* (MDM 20080809BDM006RRF 34561) in lateral view; C, *Sierritasuchus macalpini* (UMMP V60817) in ventral view; D, *Calyptosuchus wellesi* (UMCP 139837) in posterior view; E, *Calyptosuchus wellesi* (UCMP 139794) in lateral view; F, *Calyptosuchus wellesi* (UCMP 78714) in ventral view. Scale bars equal 1 cm.

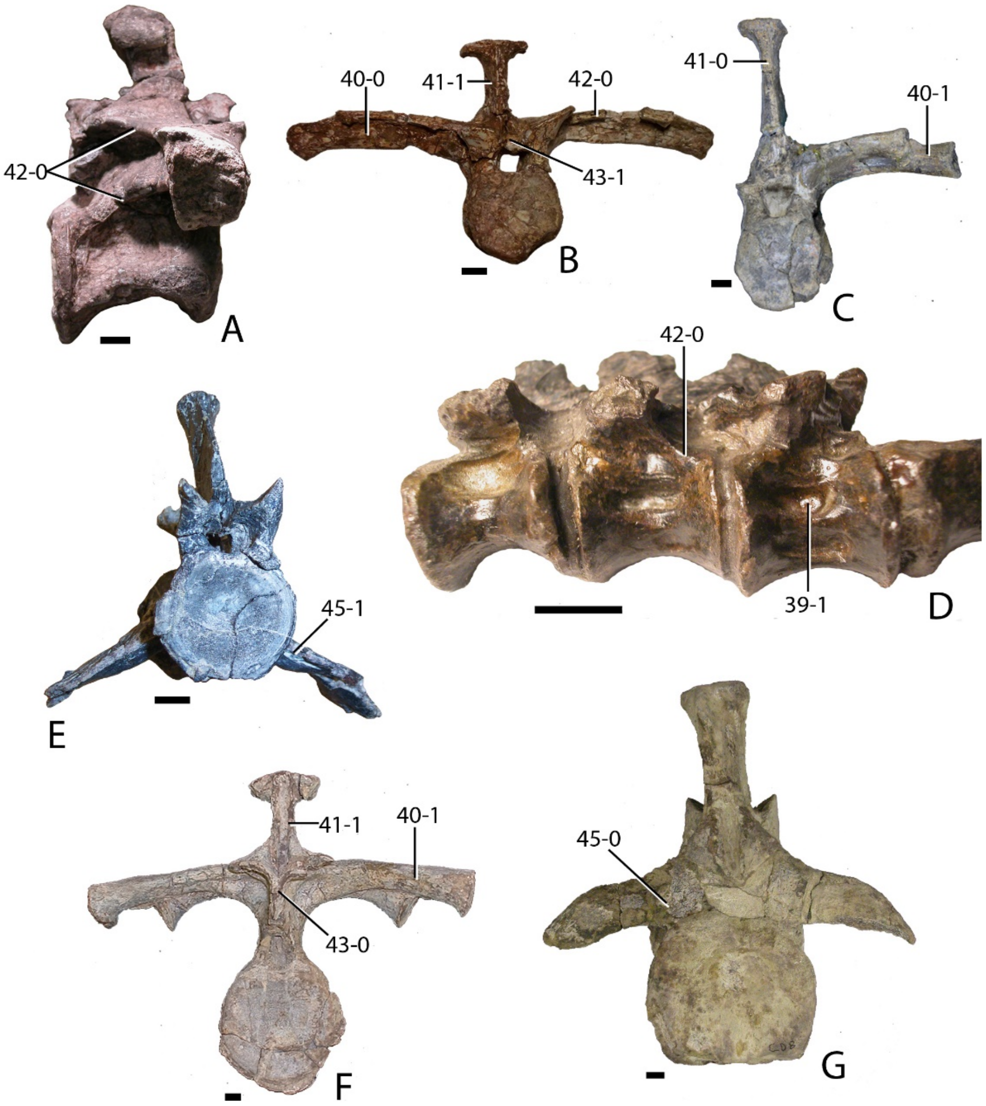

Figure B7: Dorsal and caudal series vertebrae of aetosaurians showing defined character states. A, *Desmatosuchus spurensis* (MNA V9300) anterior dorsal vertebra in lateral view; B, *Typothorax coccinarum* (TTU P-09214) posterior dorsal vertebra in anterior view; C, *Calyptosuchus wellesi* (UMCP 139702) mid-dorsal vertebra in anterior view; D, *Aetosauroides scagliai* (PVL 2073) dorsal vertebrae in lateral view; E, *Paratypothorax* sp. (PEFO 3004) anterior caudal vertebra in anterior view; F, *Desmatosuchus spurensis* (MNA V9300) mid-dorsal vertebra in posterior view; G, *Desmatosuchus spurensis* (MNA V9300) anterior mid-caudal vertebra in posterior view. Scale bars equal 1 cm.

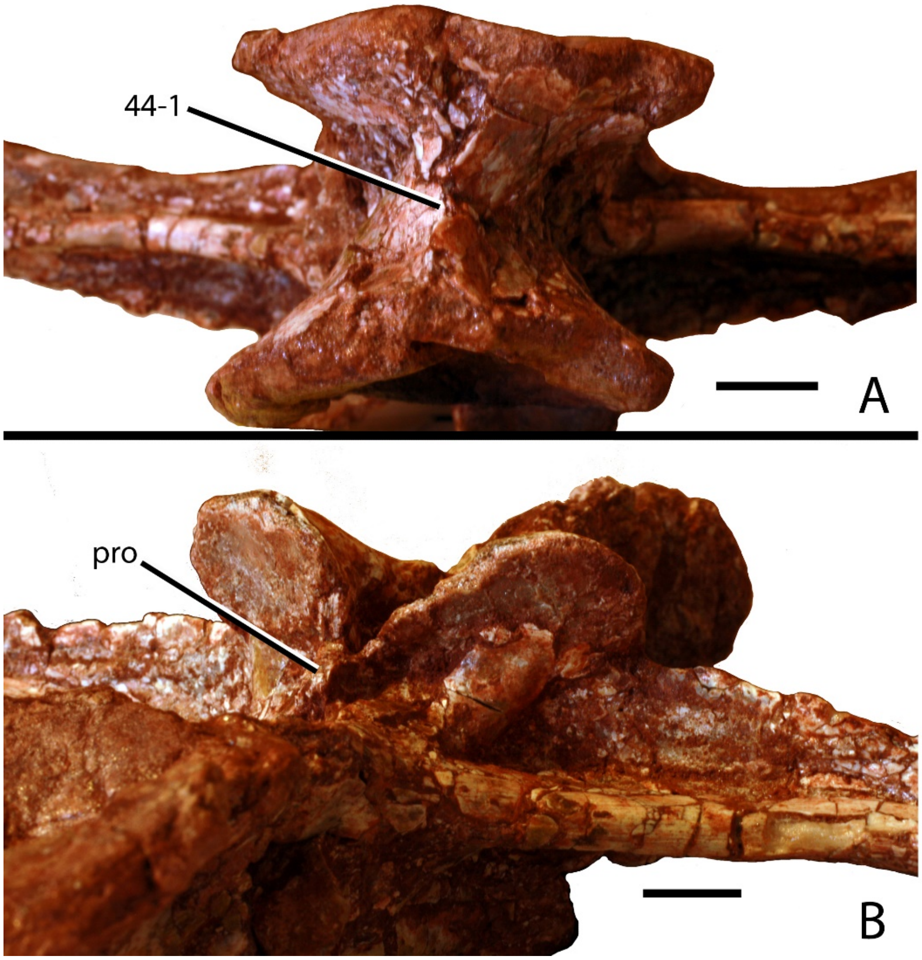

Figure B8: TTU P-9416, posterior dorsal vertebra of *Paratypothorax* sp. showing defined character states. A, centrum in ventral view; B, neural arch in posterolateral view showing posterior projection (pro). Scale bars equal 1 cm.

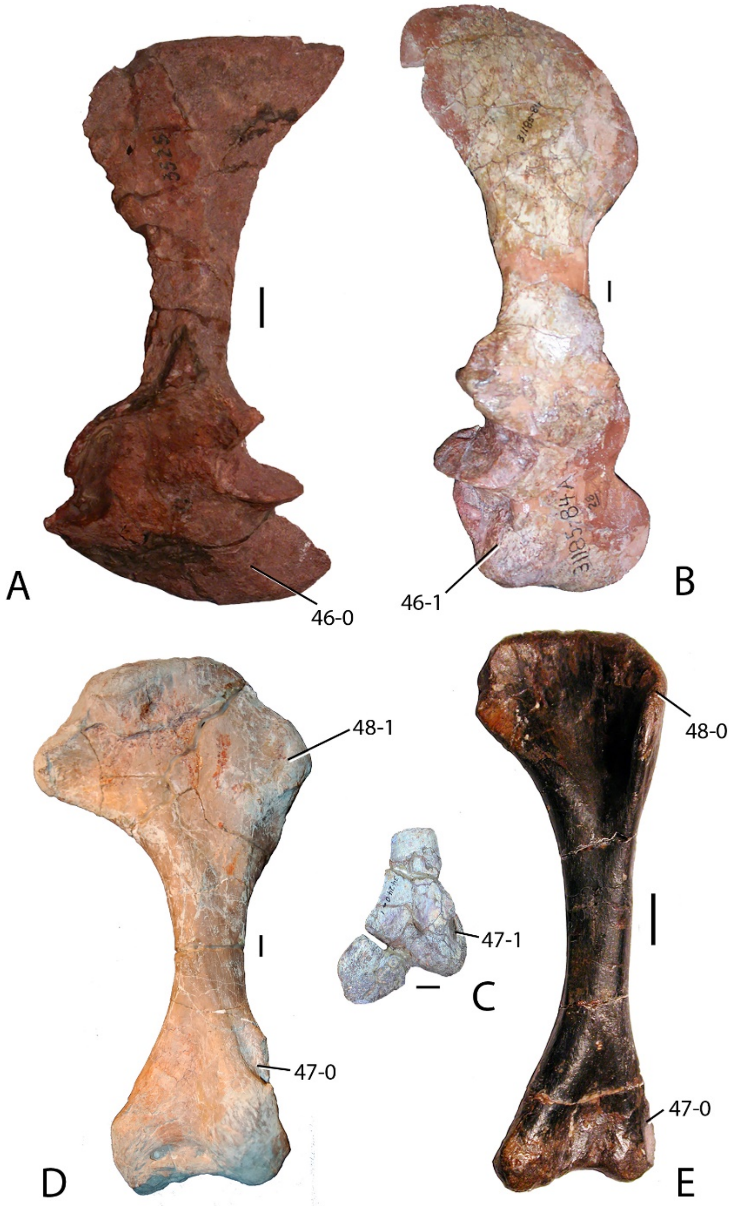

Figure B9: Scapulocoracoids and humeri of aetosaurians showing defined character states. A, *Neoaetosauroides engaeus* (PVL 3525) left scapulocoracoid in lateral view; B, *Longosuchus meadei* (TMM 31185-84a) right scapulocoracoid in lateral view; C, *Typothorax coccinarum* (UCMP 34240) distal end of left humerus in anterior view; D, *Stagonolepis olenkae* (ABIII 1175) right humerus in posterior view; E, *Aetosauroides scagliai* (PVL 2073) left humerus in anterior view. Scale bars equal 1 cm.

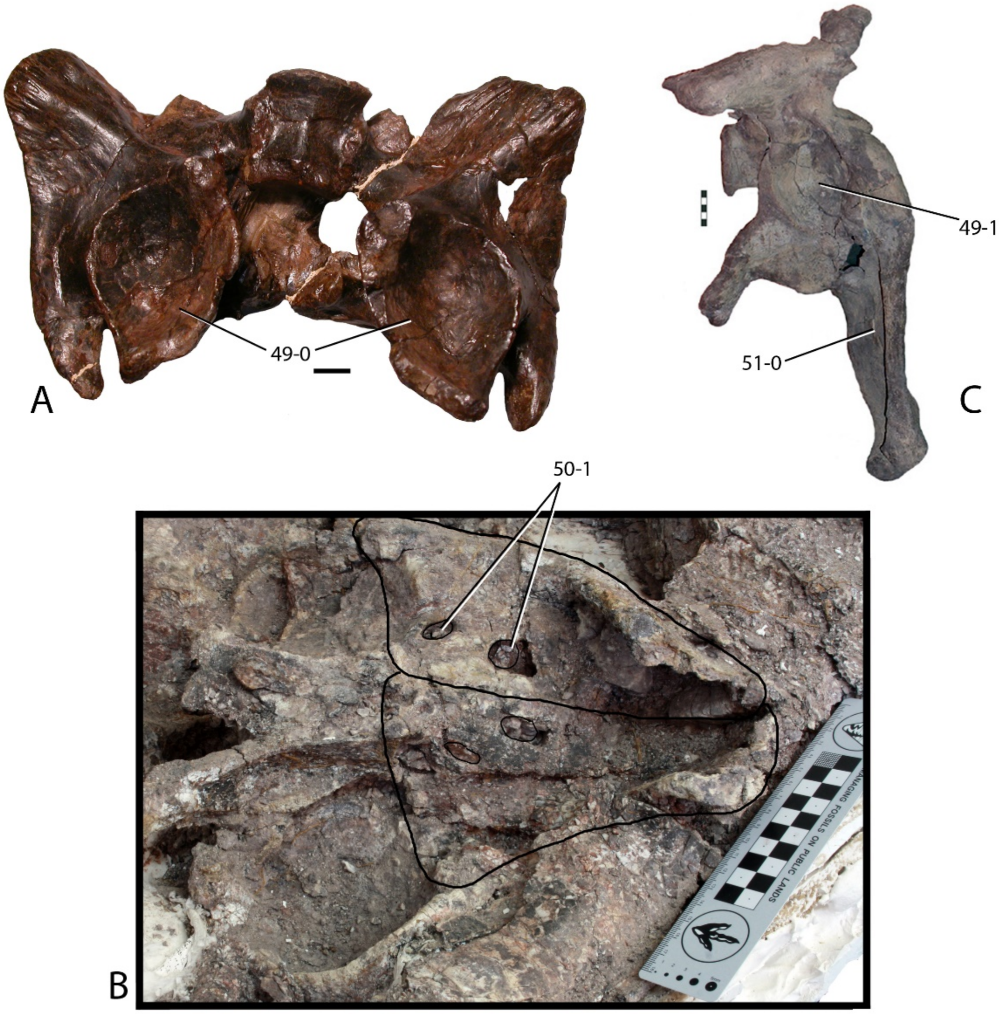

Figure B10: Sacra of aetosaurians showing defined character states. A, *Aetosauroides scagliai* (PVL 2073) ventral view; B, *Desmatosuchus spurensis* (MNA V9300) right lateral view; C, *Scutarx deltatylus* (PEFO 31217) ventral view. Scale bar for A equals 1 cm, for B equals 5 cm.

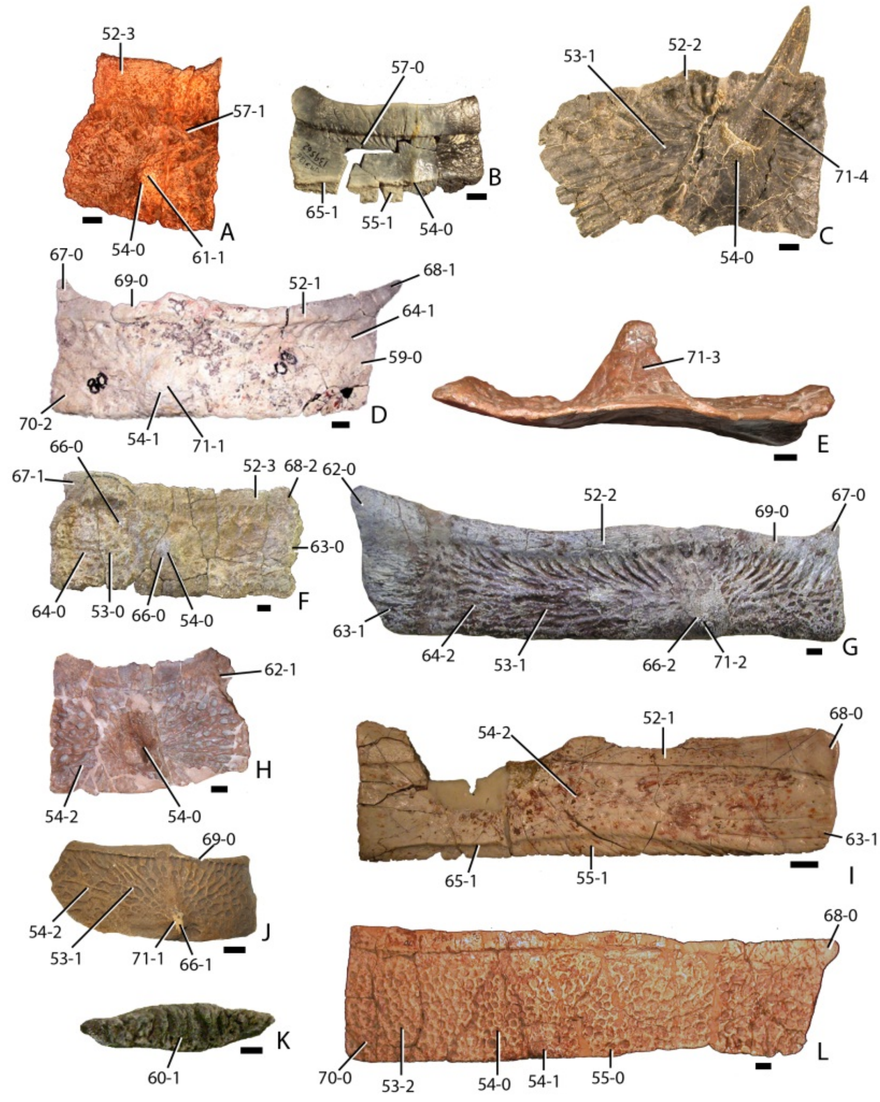

Figure B11: Paramedian osteoderms of aetosaurians showing defined character states. A, *Desmatosuchus smalli* (TTU P-9024) left posterior cervical osteoderm in dorsal view; B, Paratypothoracini (UCMP 139562) left cervical osteoderm in dorsal view; C, *Rioarribasuchus chamaensis* (NMMNH P-35459) left anterior caudal paramedian in dorsal view; D, *Scutarx deltatylus* (PEFO 34045) right dorsal trunk paramedian in dorsal view; E, *Lucasuchus hunti* (TMM 31100-361) right dorsal trunk osteoderm in posterior view; F, *Desmatosuchus spurensis* (MNA V9300) right dorsal trunk osteoderm in dorsal view; G, *Paratypothorax andressorum* (SMNS numbered L16) left dorsal trunk osteoderm in dorsal view; H, *Lucasuchus hunti* (TMM 31100-361) right dorsal trunk osteoderm in dorsal view; I, *Tecovasuchus chatterjeei* (TTU P-00545) right dorsal trunk osteoderm in dorsal view; J, *Stagonolepis robertsoni* (NHMUK 4789a) cast of left dorsal trunk osteoderm in dorsal view; K, *Desmatosuchus spurensis* (PEFO 26668) left dorsal trunk osteoderm in lateral view; L, *Paratypothorax* sp. (UCMP 34227) right dorsal trunk osteoderm in dorsal view. Scale bars equal 1 cm.

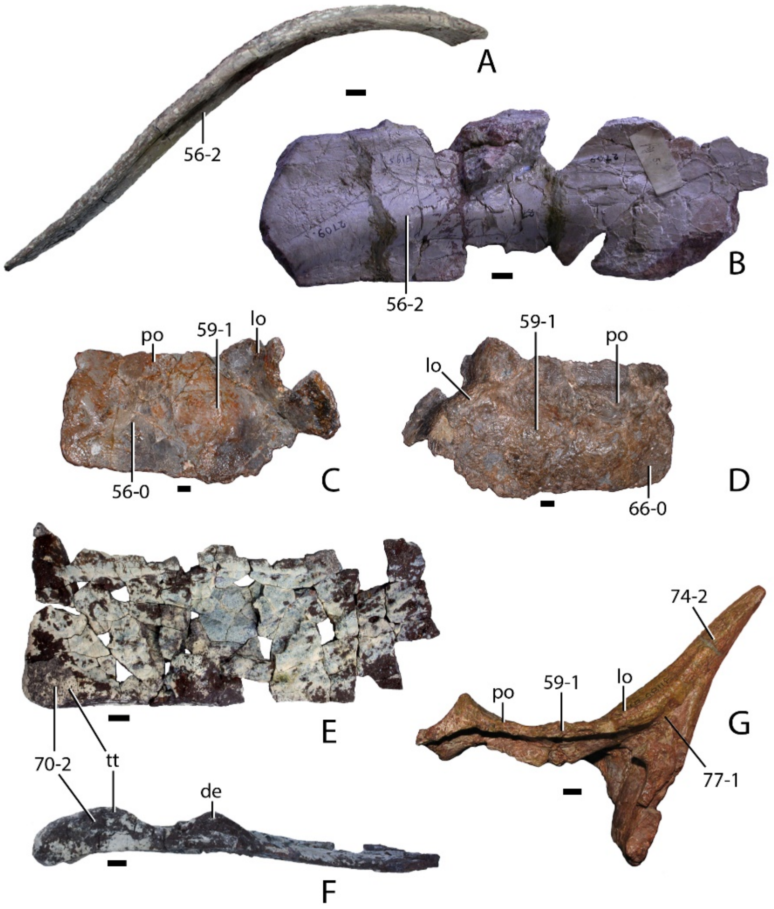

Figure B12: Paramedian and lateral osteoderms of aetosaurians showing defined character states. A, *Typothorax coccinarum* (PEFO 34848) left dorsal trunk paramedian osteoderm in posterior view; B, *Typothorax coccinarum* (AMNH FR 2709) left paramedian osteoderm in ventral view; C-D, *Desmatosuchus spurensis* (MNA V687) fused left anterior dorsal trunk paramedian and lateral trunk osteoderms in ventral (C) and dorsal (D) views; E-F, *Scutarx delatatylus* (PEFO 34045) right dorsal trunk paramedian osteoderm in dorsal (E) and posterior (F) views; G, *Longosuchus meadei* (TMM 31185-84B) fused right anterior dorsal trunk and lateral trunk osteoderms in posterior view. Scale bars equal 1 cm. Abbreviations: de, dorsal eminence, lo, lateral osteoderm, po, paramedian osteoderm, tt, triangular tuber.

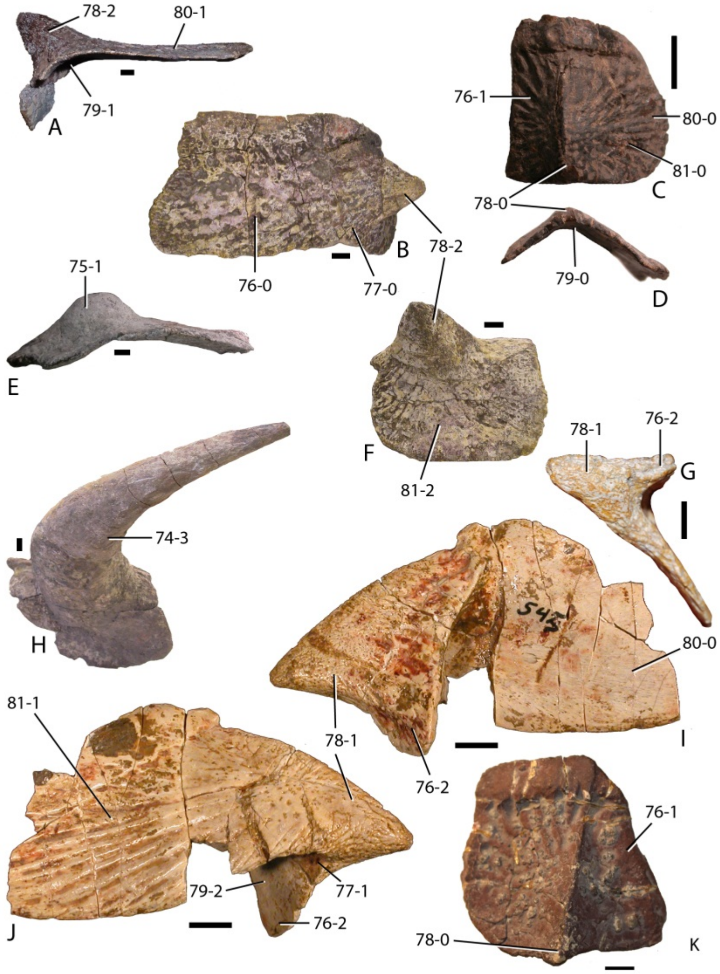

Figure B13: Lateral osteoderms of aetosaurians showing defined character states. A, *Desmatosuchus spurensis* (MNA V9300) right dorsal trunk osteoderm in anterior view; B, *Desmatosuchus spurensis* (MNA V9300) right dorsal trunk osteoderm in dorsal view; C-D, *Aetosauroides scagliai* (PVL 2073) right dorsal trunk osteoderm in dorsolateral (C) and posterior (D) views; E, *Desmatosuchus spurensis* (MNA V9300) left anterior dorsal trunk osteoderm in posterior view; F, *Desmatosuchus spurensis* (MNA V9300) right dorsal trunk osteoderm in lateral view; G, *Redondasuchus rineharti* (MDM 20110607RRBW006#2) left dorsal trunk osteoderm in posterior view; H, *Desmatosuchus spurensis* (MNA V9300) left cervical osteoderm in lateral view; I-J, *Tecovasuchus chatterjeei* (TTU P-00545) left dorsal trunk osteoderm in dorsomedial (I) and lateral views; K, *Calyptosuchus wellesi* (UCMP 27225) left dorsal trunk osteoderm in dorsolateral view. Scale bars equal 1 cm.

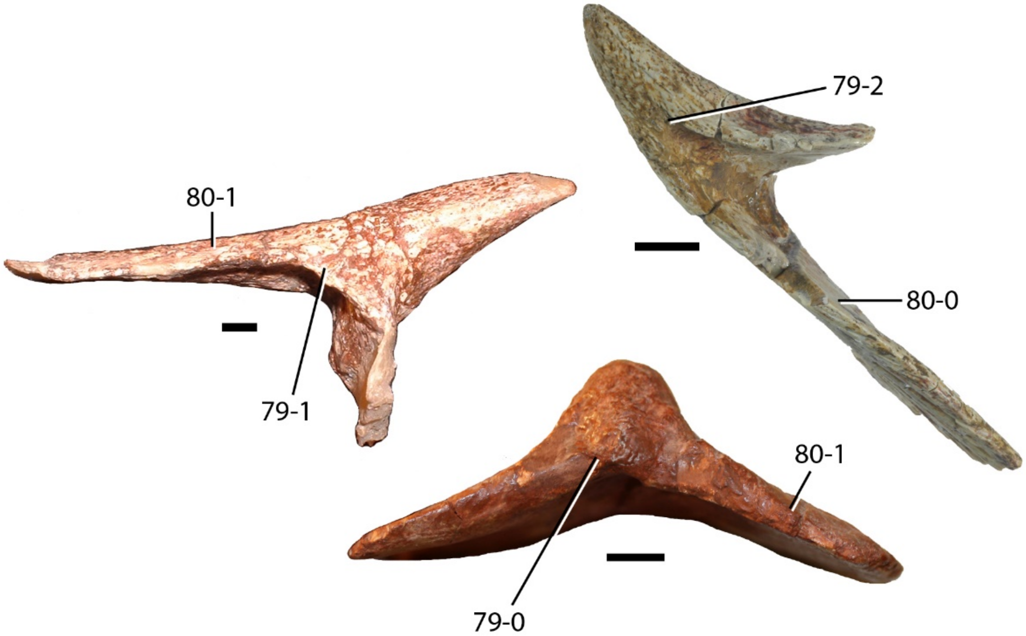

Figure B14: Lateral osteoderms of aetosaurians showing defined character states. A, *Desmatosuchus smalli* (TTU P-9024) right posterior dorsal trunk osteoderm in posterior view; B, *Tecovasuchus chatterjeei* (TTU P-00545) left dorsal trunk osteoderm in posterior view; C, *Scutarx deltatylus* (UCMP 35738) right dorsal trunk osteoderm in posterior view. Scale bars equal 1 cm.