Osteology of the Late Triassic aetosaur *Scutarx deltatylus* (Archosauria: Pseudosuchia)

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Aetosaurians are some of the most common fossils collected from the Upper Triassic Chinle Formation of Arizona, especially at the Petrified Forest National Park. Aetosaurians collected from lower levels of the park include *Desmatosuchus spurensis*, *Paratypothorax*, *Adamanasuchus eisenhardtae*, *Calyptosuchus wellesi*, and *Scutarx deltatylus*. Four partial skeletons collected from the park from 2002 through 2009 represent the holotype and referred specimens of *Scutarx deltatylus*. These specimens include much of the carapace, as well as the vertebral column, and shoulder and pelvic girdles, and a new naming convention proposed for osteoderms descriptions better differentiates portions of the carapace and ventral armor. A partial skull from the holotype specimen represents the first aetosaur skull recovered and described from Arizona since the 1930s. The key morphological feature distinguishing *Scutarx deltatylus* is the presence of a prominent, triangular boss located in the posteromedial corner of the dorsal surface of the dorsal paramedian osteoderms. *Scutarx deltatylus* can be distinguished from closely related forms *Calyptosuchus wellesi* and *Adamanasuchus eisenhardtae* not only morphologically, but also stratigraphically. Thus, *Scutarx deltatylus* is potentially an index taxon for the upper part of the Adamanian biozone.
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Abstract

Aetosaurians are some of the most common fossils collected from the Upper Triassic Chinle Formation of Arizona, especially at the Petrified Forest National Park. Aetosaurians collected from lower levels of the park include Desmatosuchus spurensis, Paratypothorax, Adamanasuchus eisenhardtae, Calyptosuchus wellesi, and Scutarx deltaylus. Four partial skeletons collected from the park from 2002 through 2009 represent the holotype and referred specimens of Scutarx deltaylus. These specimens include much of the carapace, as well as the vertebral column, and shoulder and pelvic girdles, and a new naming convention proposed for osteoderms descriptions better differentiates portions of the carapace and ventral armor. A partial skull from the holotype specimen represents the first aetosaur skull recovered and described from Arizona since the 1930s. The key morphological feature distinguishing Scutarx deltaylus is the presence of a prominent, triangular boss located in the posteromedial corner of the dorsal surface of the dorsal paramedian osteoderms. Scutarx deltaylus can be distinguished from closely related forms Calyptosuchus wellesi and Adamanasuchus eisenhardtae not only morphologically, but also stratigraphically. Thus, Scutarx deltaylus is potentially an index taxon for the upper part of the Adamanian biozone.

Introduction

The Triassic Period is a key transitional point in Earth history when remnants of Paleozoic terrestrial biotas were replaced by a Mesozoic biota including components of recent ecosystems (e.g., Fraser 2006). Prominent in this new radiation were the archosaurs, which include the common ancestor of birds and crocodylians and all of their descendants (Gauthier 1986). The early appearance and diversification of this important clade is of interest because, beginning in the Triassic, the archosaurs almost completely dominated all continental ecosystems.
throughout the entire Mesozoic (e.g., Nesbitt 2011). Because the Triassic globe had a coalesced supercontinent, Pangaea, the Laurasian and Gondwanan continental faunas are often considered to be cosmopolitan in their distribution, presumably because of a lack of major oceanic barriers (Colbert 1971). Thus, many Triassic taxa have been considered widespread and widely applicable for global biostratigraphy (e.g., Lucas 1998a).

More recent work suggests that this is a gross oversimplification of the taxonomic diversity present at the time (e.g., Irmis et al. 2007a; Nesbitt, Irmis & Parker 2007; Nesbitt et al. 2009a; Nesbitt et al. 2009b) and new research on many Triassic groups is showing evidence for endemism of species-level taxa (e.g., Martz & Small 2006; Parker 2008a; Parker 2008b; Stocker 2010), with distinct patterns of radiation of more inclusive clades into new areas (e.g., Nesbitt et al. 2010). Key to this change in thinking are the utilization of testable techniques such as apomorphy-based identification of fossils (Irmis et al. 2007b; Nesbitt & Stocker 2008) and improved phylogenetic approaches to archosaur relationships and paleobiogeography (e.g., Irmis 2008; Nesbitt 2011; Nesbitt et al. 2010). The apomorphy-based approach reveals hidden diversity in faunal assemblages resulting in the recognition of distinct taxa (Nesbitt & Stocker 2008).

Aetosaurians are quadrupedal, heavily armored, suchian archosaurs with a global distribution, restricted to non-marine strata of the Late Triassic (Desojo et al. 2013). Aetosaurians are characterized by their specialized skull with partially edentulous mandibles, an upturned premaxillary tip, and laterally facing supratemporal fenestrae. Another key feature of aetosaurians is a heavy carapace consisting of four columns of rectangular dermal armor, two paramedian columns that straddle the midline, and two lateral columns (Walker 1961). Ventral and appendicular osteoderms are also present in most taxa. Aetosaurian osteoderms possess
detailed ornamentation on the dorsal surface, the patterning of which can be diagnostic for taxa
(Long & Ballew 1985). Thus, the type specimens of several aetosaurian taxa consist solely of
osteoderms (e.g., Typothorax coccinarum Cope 1875; Paratypothorax andressorum Long and
Ballew 1985; Lucasuchus hunti Long and Murry 1995; Rioarribasuchus chamaensis Zeigler,
Heckert & Lucas 2003; Apachesuchus heckerti Spielmann & Lucas 2012) or consist chiefly of
osteoderms (e.g., Calyptosuchus wellesi Long & Ballew 1985; Typothorax antiquus Lucas,
Heckert & Hunt 2003; Tecovasuchus chatterjeei Martz & Small 2006; Adamanasuchus
eisenhardtae Lucas, Hunt, & Spielmann 2007; Sierritasuchus macalpini Parker, Stocker & Irmis
2008). Aetosaurian osteoderms and osteoderm fragments are among the most commonly
recovered fossils from Upper Triassic strata (Heckert & Lucas 2000). Because of this abundance,
in concert with the apparent ease of taxonomic identification, global distribution in non-marine
strata, and limited stratigraphic range (e.g., Upper Triassic), aetosaurs have been proposed as
key index fossils for use in regional and global non-marine biostratigraphy (Long & Ballew
1985; Lucas & Hunt 1993; Lucas & Heckert 1996; Lucas et al. 1997; Lucas 1998; Heckert et al.
2007a; Heckert et al. 2007b; Lucas et al. 2007; Parker & Martz 2011). Four Land Vertebrate
Faunachrons (LVF) were erected that use aetosaurs to divide the Late Triassic Epoch (Lucas
& Hunt 1993); from oldest to youngest, these are the Otischalkian (middle Carnian); Adamanian
(late Carnian); Revueltian (Norian), and the Apachean (Rhaetian). These were redefined as
biozones by Parker and Martz (2011).

Aetosaurs are one of the most commonly recovered vertebrate fossils in the Upper
Triassic Chinle Formation at Petrified Forest National Park (PEFO), Arizona. Paleontological
investigations in the park between 2001 and 2009 resulted in the discovery of four partial
skeletons that are considered a new taxon (Parker 2016). The first specimen (PEFO 31217),
discovered in 2001 and collected in 2002 from Petrified Forest Vertebrate Locality (PFV) 169 (Battleship Quarry; Figure 1), was initially assigned to *Calyptosuchus (=Stagonolepis) wellesi* based on characters of the armor and vertebrae (Parker & Irmis 2005). The second partial skeleton was collected in 2004 from PFV 304 (Milkshake Quarry), at the south end of the park (Figure 1). That specimen (PEFO 34045) was also mentioned by Parker and Irmis (2005), who noted differences in the armor from *Calyptosuchus wellesi* and suggested that might represent a distinct species. The other two specimens were collected in 2007 and 2009. The first (PEFO 34616), from the Billings Gap area (PFV 355; Figure 1) is notable because it included the first aetosaurian skull to be recovered in the park. The second specimen (PEFO 34919) was recovered from the Saurian Valley area of the Devils Playground (PFV 224; Figure 1). All four of these specimens were originally assigned to *Calyptosuchus wellesi* by Parker and Martz (2011) and used to construct the stratigraphic range for that taxon. *Calyptosuchus* is considered to be an index taxon of the Adamanian biozone (Lucas & Hunt 1993; Parker & Martz 2011).

Subsequent preparation and more detailed examination of these four specimens led to the discovery that they all shared a key autapomorphy, the presence of a prominent, raised triangular protuberance in the posteromedial corner of the paramedian osteoderms. The protuberance is not present on any of the osteoderms of the holotype of *Calyptosuchus wellesi* (UMMP 13950). It is also absent on the numerous paramedian osteoderms of *Calyptosuchus wellesi* recovered from the *Placerias* Quarry of Arizona in collections at the UCMP and the MNA. That autapomorphy and several features of the cranium and pelvis differentiate these specimens (PEFO 31217; PEFO 34045; PEFO 34616; PEFO 34919) from all other known aetosaurs and form the basis for assigning these materials to a new taxon, *Scutarx deltatylus* (Parker 2016). The goal of this contribution is to provide a detailed osteological description of the holotype and paratype
material of *Scutarx deltatylus*, and to discuss the potential biostratigraphic utility of the taxon locally and regionally.

**Institutional abbreviations** – DMNH [PMNH], Perot Museum of Natural History, Dallas, Texas, USA; DMNH [DMNS], Denver Museum of Nature and Science, Denver, Colorado, 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 Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina; TMM, Texas Vertebrate Paleontology Collections, University of Texas, Austin, Texas, USA; TTU P, Museum of Texas Tech, Lubbock, Texas, USA; UCMP, University of California, Berkeley, California, USA; UMMP, University of Michigan, Ann Arbor, Michigan, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; VPL, Vertebrate Paleontology Lab, University of Texas at Austin, Austin, Texas, USA; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Warsaw; Poland.
GEOLOGICAL SETTING

The four localities from which the material of *Scutarx deltatylus* was collected all occur in the lower part of the Sonsela Member of the Chinle Formation (Martz & Parker 2010) (Figure 2). In the PEFO region the Sonsela Member can be divided into five distinct beds, the Camp Butte, Lot’s Wife, Jasper Forest, Jim Camp Wash, and Martha’s Butte beds (Martz & Parker 2010). The Lot’s Wife, Jasper Forest, and Martha’s Butte beds are sandstone dominated, cliff forming units with source areas to the south and west (Howell & Blakey 2013), whereas the Lot’s Wife and Martha’s Butte beds are slope forming units with a higher proportion of mudrocks than sandstones (Martz & Parker 2010). All of these localities represent proximal floodplain facies associated with a braided river system (Howell & Blakey 2013; Martz & Parker 2010; Woody 2006).

PFV 169 and PFV 224 occur in the upper part of the Lot’s Wife beds, PFV 355 is situated in the base of the Jasper Forest bed, and PFV 304 marks the highest stratigraphic occurrence, located in the lower part of the Jim Camp Wash beds (Figure 2). All of these sites are below the ‘persistent red silcrete,’ a thick, chert, marker bed that approximates the stratigraphic boundary between the Adamanian and Revuelitian biozones (Martz & Parker 2010; Parker & Martz 2011). Exact locality information is available at Petrified Forest National Park to qualified researchers. Non-disclosure of locality information is protected by the Paleontological Resources Preservation Act of 2009.

A high concentration of volcanic material in mudrocks of the Chinle Formation includes detrital zircons and allows for determination of high precision radioisotopic dates for studied beds (Figure 2; Ramezani et al. 2011). Zircons from the top of the Lot’s Wife beds provided an age of 219.317 ± 0.080 Ma (sample SBJ; Ramezani et al. 2011). The base of the unit is constrained
by a maximum depositional age of 223.036 ± 0.059 Ma for the top of the underlying Blue Mesa Member (sample TPs; Ramezani et al. 2011). Maximum depositional ages of 218.017 ± 0.088 Ma (sample GPL) and 213.870 ± 0.078 (sample KWI) are known from the Jasper Forest bed and the overlying Jim Camp Wash beds further constraining the upper age for the fossil specimens (Ramezani et al. 2011).

MATERIALS AND METHODS

All specimens were excavated utilizing small hand tools, although a backhoe tractor was used initially to remove overburden at PFV 304. B-15 Polyvinyl Acetate “Vinac” (Air Products & Chemicals, Inc.) and B-76 Butvar (Eastman Chemical Company) dissolved in acetone were used as a consolidant in the field. PEFO 31217 was discovered partly in unconsolidated, heavily weathered sediment with numerous plant roots growing over and through the bones. Small handtools, including brushes, caused damage to the bone surface so plastic drinking straws were used to blow away sediment from the bone surface, which was then quickly hardened with a consolidant. In the lab the same specimen (PEFO 31217) quickly deteriorated upon exposure and applications of Polyvinyl Acetate (Vinac™, Air Products and Chemicals, Inc.) proved to result in a flexible specimen, therefore liberal amounts of extremely thin Paleobond™ Penetrant Stabilizer PB002 (Uncommon Conglomerates) were applied to stop disintegration and provide rigidity of the bone. Because of the delicate nature of this specimen and the application of the cyanoacrylate, many of the bones cannot be prepared further or removed from the original field jackets. Furthermore, during collection the condition of the bones and surrounding matrix proved to be so poor that a portion of the jacket with the scapulocoracoid in it was lost during turning. This lost material consisted mostly of trunk vertebrae, ribs, and osteoderms. Unfortunately, this block of material is too large to CT scan to obtain more information for these elements.
The other three skeletons (PEFO 34045; PEFO 34616; PEFO 34919) were consolidated in
the lab using B-72 Butvar™ (Eastman Chemical Company), with Paleobond™ PB40 and PB100
(Uncommon Conglomerates) cyanoacrylate used in many cases for permanent bonds.
Paleobond™ PB304 (Uncommon Conglomerates) aerosol activator was originally used on some
of the bones in PEFO 34045, but was halted because it was causing discoloration of the bone
surface during the curing process. PEFO 34919 is coated with thin layers of hematite as is
common for fossil specimens recovered from sandy facies in the Devils’ Playground region of
PEFO. Mechanical preparation with pneumatic tools damaged the bone surface upon removing
the coating and revealed that the hematite had permeated numerous microfractures in the bones,
expanding them slightly, or in some bones significantly. As a result, the non-osteoderm bones
from PFV 224 are highly deformed and often ‘mashed’ into the associated osteoderms. Further
preparation to remove the hematite coating was not attempted.

**Naming Conventions for Aetosaurian Osteoderms**

Traditionally, identification and naming of aetosaurian osteoderms, which cover the
dorsal, ventral, and appendicular areas, utilizes terms first originated by Long & Ballew (1985).
In this convention the dorsal armor (carapace) consists of two midline ‘paramedian’ columns
flanked laterally by two ‘lateral’ columns (Long & Ballew 1985; Heckert & Lucas, 1999; Desojo
et al. 2013). By convention, osteoderms of the dorsal region are named from the type of vertebrae
they cover [e.g., cervical, dorsal, and caudal; (Long & Ballew 1985)]. However, the anteriormost
paramedian osteoderms lack equivalent lateral osteoderms causing a potential numbering offset
between the presacral paramedian and lateral rows (Heckert et al. 2010). Aetosaurians also
possess ventral armor at the throat, as well as ventral armor that underlies the ‘dorsal’ (=trunk)
and caudal vertebrae. The presence of ventral armor of the ‘dorsal’ series creates the awkward
combination of ‘ventral-dorsal’ osteoderms. Therefore there is a need to standardize the positional nomenclature for aetosaurian osteoderms.

The term carapace properly refers only to the dorsally situated network of osteoderms, thus the term ‘dorsal carapace’ is incorrect and redundant. In this study, the term carapace refers only to the dorsally situated osteoderms and the term ventral osteoderms is used for all ventrally situated osteoderms (Heckert & Lucas 1999).

The carapace can be divided into four anteroposteriorly trending columns of osteoderms (Heckert & Lucas 1999; Heckert et al. 2010). Those that straddle the mid-line are referred to as the paramedians and the flanking osteoderms are called the lateral armor (Long & Ballew 1985). Each column is divided into rows (Figure 3) and as noted above these have traditionally been given names based on the vertebral series they cover (in most taxa there is a 1:1 ratio between osteoderms and vertebrae, except in the cervical series of desmatosuchines where six osteoderms cover the nine cervical vertebrae).

The two anteriormost paramedian osteoderms fit into the back of the skull and are generally mediolaterally oval and lack corresponding lateral osteoderms. These osteoderms are termed the nuchal series (Figure 3; Sawin 1947; Desojo et al. 2013; Schoch & Desojo 2016).

Posterior to these are roughly five, six, or nine rows of paramedian and lateral osteoderms that cover the entire cervical vertebral series, termed cervical osteoderms (Figure 3; Long & Ballew 1985). The patch of osteoderms beneath the cervical vertebrae in the throat area would be called the gular osteoderms, based on the name given to these osteoderms in phytosaurs (Long & Murry 1995).

The next vertebral series initiates with the 10th presacral vertebra. On this vertebra the parapophysis has moved up to the top of the centrum, just below the level of the neurocentral suture. In the previous nine vertebrae (the cervical series), the parapophysis is situated at the base of the centrum, and in the eleventh vertebra the parapophysis is situated on the transverse process. Thus the 10th presacral is transitional in form and has been considered to be the first of the ‘dorsal’ series (Case 1922; Walker 1961; Parker 2008a), and that convention is followed here.
Historically in aetosaurians these vertebrae have been referred to as the dorsal series and osteoderms covering these vertebrae are the ‘dorsal osteoderms’ (e.g., Long & Ballew 1985; Long & Murry 1995; Heckert & Lucas 2000; Desojo et al. 2013); however, this term has become problematic because whereas all of the osteoderms below the vertebral column are termed the ventral osteoderms, only those of above the vertebral column in the trunk region are called the dorsals. Thus technically the osteoderms beneath the caudal vertebrae would be the caudal ventral osteoderms and those beneath the ‘dorsal’ vertebrae would be the dorsal ventral osteoderms. This is nonsensical so I suggest a new term be used for what have been known as the dorsal vertebrae and osteoderms in aetosaurians. The terms “thoracic” and “lumbar” vertebrae reflect the chest and loin areas respectively and are assigned depending on the presence or absence of free ribs. This is not readily applicable to pseudosuchians which have ribs through the entire series. Instead the term trunk vertebrae is used, which is commonly used for amphibians and lepidosaurs, which also tend to have a ribs throughout the entire series (e.g., Wake 1992).

The osteoderms above the trunk vertebrae are the dorsal trunk paramedian and dorsal trunk lateral osteoderms. The osteoderms located beneath the trunk vertebrae are the ventral trunk osteoderms and consists of numerous columns of osteoderms (Figure 3; Walker 1961). Heckert et al. (2010) utilized the term ventral thoracic osteoderms, which effectively solves the ‘ventral dorsal’ problem; however, the term ventral trunk osteoderms is preferred here to maintain consistency with the term dorsal trunk osteoderms.

The osteoderms above the caudal vertebrae are termed the dorsal caudal osteoderms and consist of paramedian and lateral columns (Figure 3; Long & Ballew 1985). The osteoderms beneath the caudal vertebrae are the ventral caudal osteoderms (Heckert et al. 2010) and also consist of paramedian and lateral columns behind the cloacal area (fourth row) to the tip of the tail (Jepson 1948; Walker 1961), the first two lateral rows bear spines in *Typothorax coccinarum* (Heckert et al. 2010). An assemblage of irregular shaped osteoderms located anterior to the cloacal area is preserved in *Stagonolepis robertsoni, Aetosaurus ferratus*, and *Typothorax coccinarum* (Walker 1961; Schoch 2007; Heckert et al. 2010), which can be called the cloacal osteoderms. Small masses of irregular shaped osteoderms cover the limb elements of aetosaurians.
(e.g., Heckert & Lucas 1999; Schoch 2007; Heckert et al. 2010). These have collectively been termed as simply appendicular osteoderms. However, when found in articulation they can be differentiated by the limb that is covered, including the humeral, radioulnar, femoral, and tibiofibular osteoderms (Hill 2010).

**SYSTEMATIC PALEONTOLOGY**

Archosauria Cope 1869 *sensu* Gauthier & Padian 1985.

Pseudosuchia Zittel 1887-90 *sensu* Gauthier & Padian 1985.

Aetosauria Marsh 1884 *sensu* Parker, 2007.

Stagonolepididae Lydekker 1887 *sensu* Heckert & Lucas 2000.

*Scutarx deltatylus* Parker 2016

(Figs. 4 – 29)

1985  *Calyptosuchus wellesi*: Long and Ballew, p. 54, figs. 13a, 15. Pl. 5.
1995  *Stagonolepis wellesi*: Long and Murry, p. 82, figs. 71b, 72b, e.
2005  *Stagonolepis wellesi*: Parker and Irmis, p. 49, fig. 4a.
2005a *Stagonolepis wellesi*: Parker, p. 44.
2005b *Stagonolepis wellesi*: Parker, p. 35.
2006  *Stagonolepis wellesi*: Parker, p. 53.
2011  *Calyptosuchus wellesi*: Parker and Martz, p. 242.
2013  *Calyptosuchus wellesi*: Martz et al., p. 342, figs. 7a-d.
2014  *Calyptosuchus wellesi*: Roberto-Da-Silva et al., p. 247.
2016  *Scutarx deltatylus*: Parker, p. 27, figs. 2-5.

**Holotype** – PEFO 34616, articulated posterior portion of a skull with the braincase; detached left nasal; cervical and dorsal trunk paramedian and dorsal trunk lateral osteoderms; ventral osteoderms, rib fragments, and paired gastral ribs.
Paratypes -- 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, girdle fragments, ilium; PEFO 34045, much of a postcranial skeleton including vertebrae, ribs, and osteoderms.

Referred Specimens – UCMP 126844, 10 partial dorsal trunk paramedian osteoderms (PFV 162, Lot’s Wife beds, Sonsela Member, Chinle Formation, PEFO, Arizona); UCMP 84916, partial left dorsal trunk paramedian osteoderm (PFV 146, lower part of the Sonsela Member, Chinle Formation, Billings Gap, Arizona; UCMP 36656, UCMP 35738, dorsal trunk paramedian and dorsal trunk lateral osteoderms (UCMP locality V3205; lower part of the Sonsela Member, Chinle Formation, 11 km north of Nazlini, Arizona); TTU P-09240, left and right dorsal trunk paramedian osteoderms (Post Quarry, Cooper Canyon Formation, Dockum Group, Texas).

Locality, Horizon, and Age -- PFV 255 (The Sandcastle), Petrified Forest National Park, Arizona; lower part of the Sonsela Member, Chinle Formation; Adamanian biozone, Norian, ∼217 Ma (Ramezani et al. 2011).

Diagnosis – From Parker (2016): 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; the occipital condyle lacks a distinct neck because the condylar stalk is mediolaterally broad; 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. An additional possible autapomorphy is that the base of the cultriform process of the parabasisphenoid bears deep lateral fossae; however, in more complete, articulated aetosaur skulls (e.g., SMNS 19003) the parabasisphenoid is articulated with the pterygoids making this
difficult to observe. *Scutax deltatylylus* can also be differentiated from other aetosaurs a unique combination of characters including moderately wide (W:L ~2.7/1) dorsal trunk paramedian osteoderms with a strongly raised anterior bar that possesses anteromedial and anterolateral processes (shared with all aetosaurs 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 distinct obturator and thyroid 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 (shared with *Desmatosuchus*).

**DESCRIPTION**

**Skull**

Much of the posterodorsal portion of the skull is present in PEFO 34616 (Figures 4-10). Elements preserved include much of the left nasal, both frontals (the right is incomplete), both postfrontals, the left parietal (badly damaged), the left and right squamosals, the right postorbital, a portion of the left postorbital, and a nearly complete occipital region and braincase. The skull was already heavily eroded when discovered and although the skull roof/braincase portion was collected in situ, the remaining elements had to be carefully pieced together from many fragments collected as float. Accordingly many of the skull roof elements are incomplete.

Much of the skull appears to have separated originally along some of the sutures, notably those between the prefrontal-frontal, squamosal-quadrade, and postorbital-quadratojugal contacts.
The left frontoparietal suture is also visible because of bone separation, and the sockets in the squamosals for reception of the proximal heads of the quadrates are well-preserved. Thus, the skull appears to have mostly fallen apart before burial and many of the anterior and ventral elements were presumably scattered and lost during disarticulation, with the exception of the left nasal, which is represented as an isolated piece. The skull of *Scutarx deltatylus* includes a well-preserved braincase, which is described in detail below. Sutures are difficult to observe because of the state of preservation of the specimen, and the skull of *Longosuchus meadei* (TMM 31185-98) was used to infer the locations of various sutures, based on observable landmarks present in PEFO 34616.

**Nasal**

The proximal half of the left nasal is preserved, consisting of the main body and the posterior portion of the anterior projection through the mid-point of the external naris (Figure 4). The main body is dorsoventrally thick and the entire element is slightly twisted dorsomedially so that the dorsal surface is noticeably concave. Any surface ornamentation is obscured by a thin coating of hematite. The midline symphysis is straight and slightly rugose (Figure 4). The lateral surface is damaged along the lacrimal suture; however, more anteriorly, the sutural surface for the ascending process of the maxilla is preserved and is strongly posterovertrally concave (Figure 4). Anteriorly the nasal narrows mediolaterally where it forms the dorsal margin of the external naris. The ventral process of the nasal that borders the posterior edge of the naris is missing its tip but it is clear from what is preserved that it was not elongate as in *Aetosauroides scagliai* (PVL 2059), but rather short as in *Stagonolepis olenkae* (ZPAL AbIII/346).
Frontal

Both frontals are present, with the left nearly complete and the right missing the posterior portion (Figure 5). The extreme dorsoventral thickness of the element is evident, as the dorsoventral thickness is 0.35 times the midline length of the element. The frontals appear to be hollow; however, this is most likely from damage during deposition and subsequent weathering before the skull roof was collected and pieced back together. In dorsal view the posterior margin of the frontal is slanted posterolaterally as in Stagonolepis robertsoni (Walker 1961) so that the lateral margin of the frontal is longer than the medial margin, forming a distinct posterolateral process (Figure 5). The anterior portion of that process meets the postfrontal laterally and the parietal posteriorly as in Stagonolepis olenkae (Sulej 2010). Just anterior to the posterolateral process the frontal forms the dorsal margin of the orbit. The position of the suture with the postfrontal is not clear, but it should have been present as in all other aetosaurians.

The dorsal surfaces of the frontals are rugose, ornamented with deep pits, some associated with more elongate grooves. Laterally above the round orbits and anteriorly there are wider, anteroposteriorly oriented grooves as in Stagonolepis olenkae (Sulej 2010). These grooves demarcate a raised central portion of the frontals as described for Stagonolepis robertsoni by Walker (1961). The anterolateral margins of the frontals are dorsoventrally thick, rugose, anteromedially sloping areas that are bounded posteriorly by a thin curved ridge. These are the sutures for the prefrontals (Figures 5-6). There is no clear evidence for articulation of a palpebral bone at this position as in Stenomyti huangae (Small & Martz 2013), but the posteriormost portion of the articular surface (Figure 6) is probably a suture for a palpebral as in Longosuchus meadei (TMM 31184-98). The anterior margins of the frontals are thick and rugose for articulation with the nasals (Figures 5, 7). The frontal/nasal suture is nearly transverse. The
frontal also lacks the distinct, raised midline ridge present in *Stenomyti huangae* (Small & Martz 2013).

The ventral surfaces of the frontals are broadly ventrally concave and smooth (Figure 7). Medial to the orbital fossa is a distinct, slightly curved ridge that is the articulation point with the laterosphenoid.

**Postfrontal**

The postfrontals are small, roughly triangular bones that form the posterodorsal margin of the orbit. Both are certainly preserved in PEFO 34616, as in all aetosaurians, but the positions of their sutures cannot be determined.

**Parietal**

The dorsal portions of both parietals are mostly missing, although the posterolateral corner of the left one remains as well as a small fragment of the posterior portion of the right where it contacts the dorsal process of the squamosal (Figure 5). The frontal/parietal suture is visible along the posterior margin of the frontals, so it is clear that these elements were not fused. The posterolateral portion forms the dorsal border of the supratemporal fenestra, but few other details are visible.

The posterior flanges of both parietals are preserved (Figure 8). Their posteroventrally sloping surfaces form the upper portion of the back of the skull. Ventrally, they contact the paroccipital processes of the opisthotics. There is no evidence for the posttemporal fenestrae, which may have been obliterated by slight ventral crushing of the skull roof. The parietal flanges contact the supraoccipital medially and the posterior process of the squamosal laterally. The upper margins are damaged so that the presence of a shelf for articulation of the nuchal paramedian osteoderms cannot be confirmed.
**Squamosal**

The majority of both squamosals is present. As is typical for aetosaurians the squamosals are elongate bones that are fully exposed in lateral view, forming the posterior corner of the skull, as well as the posteroventral margin of the supratemporal fenestra (Figure 6). The anterior and posterior portions are separated by a dorsoventrally thin neck. The anterior portion divides into two distinct rami, a large, but mediolaterally thin, ventral lobe that presumably contacted the upper margin of the quadratojugal, and a much smaller triangular dorsal ramus that forms much of the anteroventral margin of the supratemporal fenestra. These two rami are separated by a posterior process of the postorbital. On the right side of PEFO 34616, the dorsal ramus is broken, clearly showing the articulation with the postorbital and exposing the prootic in this view (Figure 6). The ventral margin of the main body is concave and bears a flat surface that is the articulation surface with the quadrate (s.qu; Figure 7). Anterior to that articular surface the ventral margin of the anterior portion of the squamosal is confluent with the ventral margin of the postorbital. This arrangement suggests that the squamosal contributed little if anything to the margin of the infratemporal fenestra. This is similar to the condition in *Stagonolepis robertsoni* (Walker 1961) and differs from that in *Stenomyti huangae* (Small & Martz 2013) in which the ventral margin of the squamosal is situated much lower that the ventral margin of the postorbital, and the squamosal contributes significantly to the margin of the infratemporal fenestra.

The posterior portion of the squamosal expands posterodorsally into dorsal and ventral posterior processes. The dorsal process forms the posterior border of the supratemporal fenestra and is mediolaterally thickened with a smooth anterior concave area that comprises the supratemporal fossa. The apex of the upper process contacts the parietal. The ventral posterior
process forms a small hooked knob that projects off of the back of the skull. Medial to this is a deep pocket in the medial surface of the squamosal that receives the dorsal head of the quadrate. Dorsomedial to this pocket is the contact between the squamosal and the distal end of the paroccipital process of the opisthotic (Figures 5, 7).

**Postorbital**

A portion of the left and almost the complete right postorbital are preserved in PEFO 34616 (Figures 5-7). They are mediolaterally thin, triradiate bones that contact the postfrontal and parietal dorsally, the jugal anteriorly, and the squamosal posteriorly. The upper bar forms the posterior margin of the orbit and the anterior margin of the supratemporal fenestra. The posterior process is triangular and inserts into a slot in the anterior portion of the squamosal. The ventral margin is flat, and forms the dorsal border of the infratemporal fenestra and more anteriorly that edge bears an articular surface with the jugal. The tip of the anterior process is broken, but it would have overlain the posterior process of the jugal and formed the posteroventral margin of the orbit. The postorbital of *Scutarx* appears to lack to broad ventral contact with the quadratojugal (Figure 6) as in *Paratypothorax* (SMNS 19003) and *Aetosaurus* (Schoch, 2007), and instead was like *Desmatosuchus spurensis* (Small, 2002) and *Stagonolepis* (Walker, 1961; Sulej, 2010) where an anterior process of the squamosal separates the postorbital from the quadratojugal.

**Supraoccipital**

The supraoccipital is present but poorly preserved (Figure 8). A median element, it forms much of the dorsal portion of the occiput, but appears to be at least partially excluded from the roof of the foramen magnum. Laterally it contacts the parietal flanges and ventrally the otooccipitals.
**Exoccipital/ opisthotic**

The exoccipitals and opisthotics are fused into a single structure, the otooccipital. The exoccipital portions form the lateral margins of the foramen magnum (Figure 8). A protuberance, or prong, is present on the left exoccipital at the dorsolateral corner of the foramen magnum (Figures 5, 8). The presence of similar structures in *Neoaetosauroides engaeus* (e.g., PVL 5698) was noted by Desojo and Báez (2007), and interpreted by them to be facets for reception of the proatlantes. Those authors considered the facets located on the supraoccipital; however, in *Longosuchus meadei* (TMM 31185-84) they are located on the exoccipital and the same appears to be true for PEFO 34616.

Anteriorly, a strong lateral ridge forms the posteroventral margin of the ‘stapedial groove’ as is typical for aetosaurs (Gower & Walker 2002). In aetosaurians there are typically two openings for the hypoglossal nerve (XII) that straddle the lateral ridge (Gower & Walker 2002); however, they are not apparent in PEFO 34616, and where the posterior opening of the left side should be situated there is a fragment of bone missing.

Both paroccipital processes are present and well-preserved (Figures 5-8). They are mediolaterally short (14 mm) and stout, dorsoventrally taller than anteroposteriorly long (8 mm tall, 4 mm long), and contact the parietal flanges dorsally and the squamosal laterally. The distal end expands slightly dorsoventrally (Figure 8). The posterior surface is flat and distally the process forms the posterior border of the pocket for reception of the quadrate head, therefore there was a sizeable contact between the opisthotic and the quadrate.

The proximoventral portion of the paroccipital process opens into the ‘stapedial groove’. That groove continues into the main body of the opisthotic, bounded by the lateral ridge of the exoccipital posteroventrally and the crista prootica anterodorsally Figure 9). Here there is a large opening for the fenestra ovalis and the metotic foramen; however, the two cannot be
distinguished because the ventral ramus of the opisthotic that divides the two openings in aetosaurians (Gower & Walker 2002) is not preserved (Figure 9). It is not clear if the ventral ramus was never originally preserved or if it was removed during preparation of the braincase. Thus the perilymphatic foramen is not preserved as well. The embryonic metotic fissure is undivided in aetosaurs and therefore the glossopharyngeal, vagal, and accessory (IX, X, XI) nerves and the jugular vein would have exited the braincase via a single opening, the metotic foramen (Gower & Walker 2002; also see Rieppel 1985; Walker 1990). Just lateral to the metotic foramen on the ventral surface of the crista prootica there should be a small opening for the facial nerve (VII); however, it is not visible through the hematite build-up on the lateral wall of the cranium.

A second distinct groove extends from the ventral border of the fenestra ovalis anteroventrally along the lateral face of the parabasisphenoid to the posterodorsal margin of the basipterygoid process, and is bordered anterodorsally by the anteroventral continuation of the crista prootica (Figure 9). The termination of that groove houses the entrance of the cerebral branch of the internal carotid artery (Gower & Walker 2002; Sulej 2010).

**Prootic**

The entire braincase is slightly crushed and rotated dorsolaterally so that the left side of the otic capsule is easier to view (Figure 9). Both prootics are preserved. Posteriorly, the prootic overlaps the opisthotic medially, and ventrolaterally forms a thin ridge (crista prootica), which is bounded ventrally by the upper part of the ‘stapedial groove’ and the groove in the parabasisphenoid leading to an opening for the internal carotid. Anteroventrally, the prootic meets the anterior portion of the parabasisphenoid, just posterior to the hypophyseal fossa. Anteriorly and anterodorsally, the prootic meets the laterosphenoid and dorsally it is bounded by
the parietal. The uppermost margin is deformed by a thick anteroposteriorly oriented mass of
bone, which could represent crushing of the parietal margin. Just posterior to the anterior suture
with the laterosphenoid is the opening for the trigeminal nerve (V) which is deformed and closed
by crushing (Figure 9). In PEFO 34616 the opening for the trigeminal nerve is completely
enclosed by the prootic. This is similar to the condition in *Stagonolepis olenkae* (Sulej, 2010),
*Stagonolepis robertsoni* (Walker, 1961), and *Longosuchus meadei* (TMM 31185-98) and appears
to be typical for all aetosaurs; however, Small (2002) shows the trigeminal opening subdivided in
the skull of *Desmatosuchus smalli* although he does not describe it.

**Laterosphenoid**

The laterosphenoids are ossified but poorly preserved. On the left side anterodorsal to the
opening for the trigeminal nerve (V), there is the cotylar crest, which is crescentic and opens
posteriorly (Figure 9). No other details of the laterosphenoid can be determined.

**Basioccipital/Parabasisphenoid**

The basioccipital and parabasisphenoid are complete and together comprise the best
preserved and most distinctive portion of the braincase in *Scutax deltatylus* (Figure 10). The
occipital condyle is transversely ovate in posterior view rather than round like in other aetosaurs
such as *Longosuchus meadei* (TMM 31185-98) and *Desmatosuchus smalli* (TTU P-9024). The
dorsal surface is broad with a wide shallow groove for the spinal cord.

The condylar stalk is also broad (25 mm wide), and wider than the condyle. Thus there is
no distinct ‘neck,’ nor does a sharp ridge delineate the condyle from the stalk as in *Longosuchus
meadei* (TMM 31185-98; Parrish 1994) or *Desmatosuchus smalli* (TTU P-9024; Small 2002).

The ventral surface of the condylar stalk bears two low rounded ‘keels’ separated by a shallow,
but distinct, oblong pit. The broad stalk, lack of a distinct neck, and ventral keels all appear to be
autapomorphic for *Scutarx deltatylus*. Anterolaterally the condylar stalk expands laterally to form the ventral margin of the metotic fissure. The contacts with the exoccipitals are dorsal and posterior to that margin.

The right basal tuber of the basioccipital is present, but the left is missing. The basioccipital tuber is separated from the crescentic basal tuber of the parabasisphenoid by an unossified cleft, typical for aetosaurians and other suchians (Figure 10; Gower & Walker 2002). The basal tubera of the basioccipital are divided medially by an anteroposteriorly oriented bony ridge that bifurcates anteriorly to form the crescentic basal tubera of the parabasisphenoid and enclose the posterior portion of the basisphenoid recess (*sensu* Witmer 1997). Posteriorly that bony ridge is confluent with the posteriorly concave posterior margin of the basioccipital basal tubera (Figure 10). The short, anterolaterally directed basipterygoid processes are located anteriorly and in contact posteriorly with the anterior margin of the basal tubera of the parabasisphenoid. The upper portion of the distal end of the left basipterygoid process is broken, but the right is complete and bears a slightly expanded and slightly concave distal facet that faces anterolaterally to contact the posterior process of the pterygoid.

The basipterygoid processes and the basal tubera are positioned in the same horizontal plane (Figure 9), which is typical for aetosaurians and differs significantly from the condition in *Revueltosaurus callenderi* (PEFO 34561) and *Postosuchus kirkpatrickorum* (TTU P-9000; Weinbaum 2011; emend Parker 2016) in which the basicranium is oriented more vertically, with the basipterygoid processes situated much lower dorsoventrally than the basal tubera.

*Scutarx deltatylus* differs from aetosaurians such as *Stagonolepis robertsoni* (MCZD 2), *Neoaetosauroides engaeus* (PVL 5698), and *Aetosauroides scagliai* (PVSJ 326) in that there is a broad contact between the basal tubera and the basipterygoid processes and that the basipterygoid
processes are not elongate (Figure 10). This is nearly identical to the condition in *Desmatosuchus smalli* (TTU P-9023) and *Desmatosuchus spurensis* (UMMP 7476; Case 1922). There are two basicrania (UCMP 27414, UCMP 27419) from the *Placerias* Quarry with widely separated (anteroposteriorly) basal tubera and (elongate) basipterygoid processes that apparently do not pertain to either *Desmatosuchus* or *Scutarx deltatlulus*, and may belong to *Calyptosuchus wellesi*. This would demonstrate a potential important braincase difference between *Calyptosuchus wellesi* and *Scutarx deltatlulus*, despite the nearly identical structure of the osteoderms shared between these two taxa.

In the anteroposteriorly short area between the basal tubera and the basipterygoid processes, a deep, subrounded fossa (Figure 10) comprises the basisphenoid recess (=median pharyngeal recess of Gower and Walker, 2002; =parabasisphenoid recess of Nesbitt, 2011), which is formed by the median pharyngeal system (Witmer 1997). The presence of a ‘deep hemispherical fontanelle’ (= basisphenoid recess) between the basal tubera and the basipterygoid processes has been proposed as a synapomorphy of *Desmatosuchus* and *Longosuchus* (Parrish 1994), but, as discussed by Gower and Walker (2002), that condition is present in many archosauriforms. The number of aetosaurian taxa with this feature was expanded by Heckert and Lucas (1999), who also reported that a ‘hemispherical fontanelle’ is absent in *Typothorax* and *Aetosaurus*. Unfortunately they did not list catalog numbers for examined specimens, and scoring of character occurrences cannot be replicated. The basisphenoid recess is actually present in *Aetosaurus* (Schoch 2007), *Paratypothorax* (SMNS 19003), *Neoaetosauroides* (PVL 5698), and *Typothorax* (TTU P-9214; Martz 2002). Thus, the presence of that recess is an aetosaurian synapomorphy.
Small (2002) found the shape and size of the basisphenoid recess to be variable in his hypodigm of *Desmatosuchus haplocerus*, and recommended that the character be dropped from phylogenetic analysis pending further review. However, rather than utilizing the presence or absence of the structure, it has been proposed that the shape and depth may be of phylogenetic significance (Gower & Walker 2002). As noted above, it appears that there are two types of aetosaurian basicrania, those with anteroposteriorly short parabasisphenoids and those with long parabasisphenoids. These differences were used as rationale for splitting *Desmatosuchus haplocerus* into two species (Parker 2005b). Among taxa with short parabasisphenoids, *Scutarx deltatylus* (PEFO 34616) and *Desmatosuchus spurensis* (UMMP 7476) have deep, more or less round basisphenoid recesses, and *Desmatosuchus smalli* has a shallow subtriangular recess. In *Longosuchus meadei* (TMM 31185-98) the recess is round and shallow. Among taxa with elongate basisphenoids, *Aetosauroides scagliai* (PVSJ 326) has a shallow, round recess and *Tecovasuchus chatterjeii* (TTU P-545) has a deep, round recess. However, in *Coahomasuchus kahleorum* (NMMNH P-18496; TMM 31100-437), which has an elongate basisphenoid, the recess has the form of a moderately deep, anteroposteriorly elongate oval (Desojo & Heckert 2004; pers. obs. of TMM 31100-437). Thus, the shape of this structure is highly variable and most likely not phylogenetically informative, although the elongate form of the recess in *C. kahleorum* may prove autapomorphic.

Anterior to the basisphenoid recess and between the bases of the basipterygoid processes there is another shallow, anteroventrally opening recess (Figure 10). This recess is at the base of the parasphenoid process, in the same position as the subsellar recess in theropod dinosaurs (Witmer 1997; Rauhut 2004) and may be homologous to the latter. However, the function and
origin of the recess are not understood (Witmer 1997). It is also present in *Neoaetosauroides engaeus* (PVL 5698) and may have a broader distribution within Aetosauria.

Dorsal to the basipterygoid processes, two crescentic and dorsally expanding clinoid processes flank the circular, concave hypophyseal fossa, which housed the pituitary gland (Figure 9). No openings are visible because of poor preservation, but the dorsum sellae should be pierced by two canals for the abducens (VI) nerves (Hopson 1979; Gower & Walker 2002). At the base of the hypophyseal fossa in *Stagonolepis robertsoni* (MCZD 2) and *Longosuchus meadei* (TMM 31185-98) there is a triangular flange of bone termed the parabasisphenoid prow (Gower & Walker 2002). This structure is mostly eroded in PEFO 34616, although its base is preserved as a small dorsal protuberance.

Anterior to this, the cultriform process of the parasphenoid is completely preserved (Figures 9-10). This structure is delicate and usually missing, obscured, or in articulation with the pterygoids in the few known aetosaur skulls, making comparisons difficult. However, the process is notably short in PEFO 34616, barely extending past the anterior margins of the orbits (Figure 9). In PEFO 34616 the basisphenoid has a length of 34.2 mm, whereas the cultriform process measures 20.2 mm in length (cultriform process/basisphenoid ratio = 0.59). This is noticeably different from the parabasisphenoid in *Aetosauroides scagliai* (PVSJ 326) which has a basisphenoid length of 51 mm and a cultriform process length of at least 63 mm, although the anterior end of the process is concealed (ratio = 1.23) beneath the left pterygoid. The cultriform process is also preserved in *Desmatosuchus spurensis* (UMMP 7476), which has a relatively short parabasisphenoid and a cultriform process/basisphenoid ratio of 0.96.

The cultriform process is elongate and tapers anteriorly. It is Y-shaped in cross-section with a ventral ridge, and dorsal trough for the ethmoid cartilage. Its posterolateral margins bear
distinct oval recesses bound posterodorsally by strong ridges that are confluent with the 
posterodorsal edge of the process (Figures 9-10). Thus the process is broader posteriorly, with 
these recesses contributing greatly to the thinning of the element anteriorly. The parasphenoid 
recesses appear to be unique to PEFO 34616, although the general lack of known aetosaurian 
cultriform processes, or their preservation articulated with the pterygoids, makes it difficult to 
determine this with certainty.

**Postcranial skeleton**

**Vertebrae**

**Cervical Series**

**Post-axial Cervicals**

Two articulated cervical vertebrae are preserved in PEFO 31217 (Figure 11). Although 
both are crushed mediolaterally, they are nearly complete and preserve many details. The centra 
are taller than long (Figure 11a) suggesting they represent part of the anterior (post-axial) series 
(i.e., positions 3-6). Most notably, the difference in dimensions is not as pronounced as in 
*Typothorax coccinarum* and *Neoaetosauroides engaeus*, in which the centra are greatly reduced 
in length (Long & Murry 1995; Desojo & Báez 2005; Heckert et al., 2010). The centrum faces 
are subcircular in anterior and posterior views and slightly concave, with slightly flared rims 
(Figures 11b-c). The ventral surface of each centrum consists of two concave, ventromedially 
inclined, rectangular surfaces divided by a sharp and deep mid-line keel (Figure 11d).

The short parapophyses are oval in cross-section and situated at the anteroventral corners 
of the centrum. The parapophyses are directed posteriorly, and each forms the beginning of a 
prominent ridge that extends to the posterior margin of the centrum. The lateral faces of the 
centra are concave mediolaterally and dorsoventrally form discrete, but shallow, lateral fossae
that contact the neural arch dorsally (Figure 11a). However, PEFO 31217 lacks the deep lateral
fossae, which are considered an autapomorphy of *Aetosauroideos scagliai* (Desojo & Ezcura
2011). The neurocentral sutures are not apparent on this specimen, suggesting closure of the
sutures and that this individual is osteologically ‘mature’ although this cannot be completely
confirmed without histological sectioning of the sutural contact (Brochu 1996; Irmis 2007).

The diapophyses are centrally located at the base of the neural arch (Figure 11b). The best
preserved vertebra shows that they are slightly elongate, oval in cross-section, and curved
ventrolaterally. Because none of the diapophyses appears to be complete their exact length cannot
be determined. The neural canal is round in posterior view (Figure 11c) rather than rectangular as
in *Desmatosuchus spurensis* (UMMP 7504). The entire neural arch is taller than the
corresponding centrum face. The zygapophyses are well-formed, elongate, and oriented at
approximately 45 degrees from the horizontal.

Aetosaurian vertebrae bear several vertebral laminae and associated fossae. The
terminology for these structures follows Wilson (1999) and Wilson et al. (2011). There is a
weakly developed posterior centrodiapophyseal lamina (pcdl) that originates at the posteroventral
corner of the diapophysis and continues posteroventrally to the posterior edge of the neurocentral
suture. The only other apparent vertebral laminae are paired intrapostzygapophyseal laminae
(tpol) that originate on the posteroventral surface of the postzygapophyses and form two sharp
ridges (laminae) that meet at the dorsomedial margin of the neural canal (Figure 11b). Those
laminae delineate the medial margins of a pair of distinct lateral fossae, called the
postzygapophyseal centrodiapophyseal fossae (pocdf), as well as a sizeable medial fossa, called
the spinopostzygapophseal fossa (spof). This represents the first recognition of distinct
intrapostzygapophyseal laminae in an aetosaurian. *Desmatosuchus spurensis* (MNA V9300) has
struts of bone from the dorsomedial margins of the postzygapophyses that join medially and then 
extend ventrally as a single thickened unit to form a Y-shaped hyposphene (Parker 2008a: fig.
10a), similar to the pattern formed by the intrapostzygapophyseal laminae in *Scutarx deltatylus*.
Thus, it is possible that the structure of the hyposphene in aetosaurs is homologous (i.e., the 
hyposphene is actually formed by paired vertebral laminae) with the presence of paired (but not 
joined) intrapostzygapophyseal laminae, but this interpretation requires further investigation.
The neural spines are not complete; however, the base of the one on the second preserved 
vertebra shows that the spine was anteroposteriorly elongate, with prominent 
spinopostzygapophyseal laminae (spol) that are confluent with the dorsal surfaces of the 
postzygapophyses (Figure 11b). Spinopostzygapophyseal laminae are also present on the cervical 
vertebrae of *Desmatosuchus spurensis* (Parker 2008a).

**Trunk Series**

*Mid-trunk vertebrae*

Four mid-trunk vertebrae are preserved in PEFO 34045. In aetosaurs the cervical to trunk 
transition occurs when the parapophysis fully migrates from the base of the neural arch, laterally 
on to the ventral surface of the transverse process (Case 1922; Parker 2008a). PEFO 34045/FF-51 
is well preserved, missing only the postzygapophyses (Figures 12a-c). The articular faces of the 
centra are round and slightly concave with broad flaring rims. The centrum is longer (45.78 mm) 
than tall (41.81 mm), its lateral faces are deeply concave, and its ventral surface is narrow and 
smooth. The neural canal is large and in anterior view, the margins of the neural arch lateral to 
the canal are mediolaterally thin with sharp anterior edges.
The prezygapophyses are inclined at about 45 degrees from the horizontal and are 
confluent laterally with a short horizontally oriented prezygadiapophyseal lamina (prdl) that
terminates laterally at the parapophysis (Figure 12b). Between the prezygapophyses and ventral
to the base of the neural spine there is a well-developed broad, sub-triangular
spinoprezygapophyseal fossa (sprf). In combination with the flat prezygapophyses this creates a
broad shelf for reception of the posterior portion of the neural arch of the preceding vertebra
(Figure 12b). There is a horizontal, ventral bar that roofs the opening of the neural canal between
the ventromedial edges of the prezygapophyses (Figure 13a); thus, there is no developed
hypantrum as in *Desmatosuchus spurensis* or *Aetobarbakinoides brasiliensis* (Desojo, Ezcurra &
Kischlat 2012; Parker 2008a). The ventral bar also occurs in *Stagonolepis robertsoni* (Walker
1961: fig 7j). Ventrolateral to the prezygapophysis there is a deep centroprezygapophyseal fossa
(cprf), which is bordered posteriorly by the main strut of the transverse process (Figure 12b).
Although the positions of these fossae appear homologous with those of saurischian dinosaurs
because they share distinct topological landmarks, it is not clear if these features are similarly
related to the respiratory system as they are in saurischians (Butler, Barrett & Gower 2012;
Wilson et al. 2011).

In posterior view, the postzygapophyses (best preserved in PEFO 34045/14-R) are also
oriented about 45 degrees above the horizontal. They are triangular in posterior view with a well-
developed lateral postzygadiapophyseal lamina (podl). That lamina extends laterally to the
diapophysis and forms a broad dorsal shelf of the transverse process in dorsal view (Figure 12a).
The shelf is wider proximally and narrows distally along the transverse process. Along the dorsal
surface of the shelf, between the postzygapophyses and the neural spine is a pair of shallow
postzygapophyseal spinodiapophyseal fossae (posdf).

The neural spine is short (32.3 mm) relative to the centrum height as in *Desmatosuchus
spurensis* (MNA V9300) and *Typothorax coccinarum* (TTU P-9214). The spine is
anteroposteriorly elongate, equal in length to the proximal portion of the neural arch, and the
distal end is mediolaterally expanded (spine table). The anterior and posterior margins of the
neural spine possess paired vertical spinoprezygapophyseal (sprl) and spinopostzygapophyseal
(spol) laminae as in *Desmatosuchus spurensis* (MNA V9300).

The postzygapophyses bound deep oval spinopostzygapophyseal fossae (spof). These
fossae are much taller than wide and are bounded laterally by thin, nearly vertical
intrapostzygapophyseal laminae (tpol). These laminae meet medially at a thickened triangular
area dorsal to the neural canal. Here the vertebra bears a strong posteriorly pointed projection that
inserts into the ventral portion of the spinoprezygapophyseal fossa (sprf) just above the ventral
bar. This projection is also present in *Calyptosuchus wellesi* (e.g., UCMP 139795). Ventrolateral
to the postzygapophyses there are two deep centropostzygapophyseal fossae (cporf) in the
proximal portions of the transverse processes.

The transverse processes extend laterally with a length of 81.6 mm in PEFO 34045/FF-51.
However, in two of the other vertebrae (PEFO 34045/14-R; PEFO 34045/19-V) the transverse
processes are directed more dorsolaterally (Figures 13a-b). This difference also occurs in
*Stagonolepis robertsoni* (Walker 1961) in the more anteriorly positioned trunk vertebrae.
Furthermore, the ventral surface of the centrum in these two vertebra (PEFO 34045/14-R; 19-V)
is more constricted forming a blunt ventral 'keel'. The keel and the orientation of the transverse
process are the only visible differences between and anterior and mid-trunk vertebrae in *Scutarx
deltatylus*.

**Posterior trunk vertebrae**

The currently available material of *Scutarx deltatylus* includes seven posterior trunk
vertebrae; three from PEFO 34045, three from PEFO 31217, and one from PEFO 34919. As in
*Desmatosuchus spurensis* (MNA V9300; Parker 2008a), the posterior trunk vertebrae are much more robust than the anterior and mid-trunk vertebrae (Figures 13c-d; 14a-c). Notable differences between the mid- and posterior trunk vertebrae in *Scutax deltatylus* include an increase in the height of the neural spines and a lengthening of the transverse processes, which coincide with the loss of distinct parapophyses and diapophyses along the series. Furthermore, the centra become anteroposteriorly shorter than they are dorsoventrally tall (Figure 13e). The neural spine characteristics are identical to those of the mid-trunk vertebrae with regard to the presence of the various vertebral laminae and associated fossae. An isolated posterior trunk vertebra from PEFO 31217 (Figure 14c) shows that the prezygadiapophyseal laminae are even more strongly developed and extend farther laterally than in the more anterior trunk vertebrae. In the more posterior vertebra, the length ratio between the transverse process length (86.84 mm) and centrum width (53.26 mm) equals 1.63, thus the process is more than 1.5 times the width of the centrum. This is comparable to a ratio of 1.58 for the mid-trunk vertebrae. This same vertebra from PEFO 31217 also lacks distinct diapophyses and parapophyses and a single-headed rib is fused onto the distal end of the process (Figure 14c). This is also seen in *Desmatosuchus spurensis* (Parker 2008a), *Stagonolepis robertsoni* (Walker 1961), and *Calyptosuchus wellesi* (UMMP 13950). An isolated posterior trunk vertebra from PEFO 34045 (Figures 13a-b) preserves the entire transverse processes and the associated fused ribs. However, the specimen differs from the previously described vertebra from PEFO 31217 in that the parapophysis and diapophysis are distinct and the rib is double-headed (Figures 14a-b). Although the ribs and transverse processes are fused, the fusion is incomplete; gaps are present within the individual articulations and another gap is apparent between the anterior surface of the distal end of the transverse process and the medial surface of the capitulum of the rib (Figure 14b). This
suggests that several vertebrae in the posterior trunk series fuse with the ribs, and loss of a
distinct parapophysis and diapophysis of the transverse process and of the tuberculum and
capitulum of the dorsal ribs only occurred in the last one or two presacrals. Examination of
UMMP 13950 (Case 1932; Long & Murry 1995) suggests that this loss occurs in the last three
presacrals. In *Stagonolepis robertsoni* that condition occurs in the final two presacral vertebrae
(Walker 1961). There is no evidence in *Scutax deltatylus* that the last presacral was incorporated
into the sacrum as in *Desmatosuchus spurensis* (Parker 2008a). The last presacral in PEFO 31217
also shows a distinct vertical offset in the ventral margins of the articular faces of the centra with
the anterior face situated more ventrally. This is also the case in *Stagonolepis robertsoni* (Walker
1961) and *Desmatosuchus spurensis* (Parker 2008a).

Another posterior trunk vertebra, PEFO 34045/22 (Figures 13d-e), lacks the transverse
processes, but preserves other key characteristics of the posterior presacrals. Its neural spine is
taller (81.94 mm) than the height of the centrum (61.24 mm), differing from the condition in the
anterior and mid-trunk vertebrae where the neural spine is shorter than the centrum (Figure 13d).
This transition occurs at the beginning of the posterior trunk vertebrae series, because the
specimen from PEFO 34045 with the fused ribs, but distinct rib facets (Figures 14a-b), has a
centrum and neural spine of equal height. PEFO 34045/22 also preserves the pointed posterior
projection above the neural arch that is present throughout the trunk series (Figure 13e).

*Sacral vertebrae*

A sacral vertebra, probably the second, is visible in ventral view in PEFO 31217 in
articulation with the rest of the pelvis (Figure 15). It is recognizable by the presence of a strong,
broad sacral rib that expands laterally and anterodorsally to contact the posterodorsal margin of
the left ilium. Unfortunately no other details are available for that specimen.
Caudal series.

Vertebrae

Eight vertebrae occur in semi-articulation in PEFO 31217 posterior to the sacral vertebra described previously (Figure 15). The first two are robust with thick flaring rims on the centra. The first vertebra has a length of 57.3 mm, and its anterior face is indistinguishable from the posterior face of the preceding sacral vertebra. Furthermore, the centrum is constricted which is unusual for an aetosaur, because the sacrals and anterior caudals usually have wide ventral surfaces (e.g., *Desmatosuchus spurensis*, MNA V9300). The vertebra in PEFO 31217 lacks a ventral groove and chevron facets. It is possible that this is a sacral vertebra that has been forced backwards, but the poor preservation of the specimen does not allow a firm determination. The second caudal vertebra (assuming the first described is from the caudal series) has a centrum length of 52.2 mm and a width of 61.6 mm, thus it is wider than long as is typical for the anterior caudals of aetosaurians (Long & Murry 1995). The centrum is ventrally broad and a chevron is articulated to the posterior margin. The base of the caudal rib originates from the base of the neural arch, but laterally the rib is incomplete.

Two anterior caudal vertebrae are also known from PEFO 34045, which roughly correspond in morphology to the second and third caudal centra of PEFO 31217 (Figures 16a-f). These two vertebrae have blocky centra that are wider (flared centrum faces) than long. The ventral surfaces are broad, with a deep median trough bordered by two lateral ridges. These ridges terminate posteriorly into two posteroventrally facing hemispherical chevron facets (Figures 16d-e). The articular faces of the centra are round in anterior and posterior views, and in lateral view these faces are offset from each other (Figure 16f). The ventral margin of the posterior face is situated much farther ventrally than that of the anterior face, as is typical for aetosaurs (e.g., *Desmatosuchus spurensis*, MNA V9300). Although the neural spines are missing,
it is apparent that the neural arch complex was much taller than the height of the centrum (Figure 16c). The neural canal is oval with a taller dorsoventral axis.

The pre- and postzygapophyseal stalks are thickened and the facets are closely situated medially. They are oriented at about 30 degrees from the horizontal. The neural arch is directed posterodorsally and the postzygapophyses project posteriorly significantly beyond the posterior centrum face (Figure 16c). The caudal vertebrae lack diapophyseal and zygapophyseal laminae, but spinozygapophyseal fossae occur between the prezygapophyses (Figures 16a-b). The caudal ribs are fully fused to the centrum. They are anteroposteriorly broad and dorsoventrally thin with flat dorsal surfaces and buttressed ventral margins. The ribs are directed slightly posteriorly and laterally they arc ventrally (Figures 16a-c). Unfortunately their lateral extent is unknown.

The third and fourth caudal vertebrae in PEFO 31217 are longer than wide, with the centrum narrowing mediolaterally and with reduced flaring of the rims as in the previous vertebrae (Figure 15). The posteroventral margins possess chevron facets. The caudal ribs are broad, flat, and were elongate, as in Desmatosuchus spurensis (MNA V9300), even though the distal ends are not preserved. The third centrum has a length of 56.4 mm and the fourth has a length of 56.4 mm. Details of the neural arches and spines are buried in the block and irretrievable by mechanical preparation.

The fifth and sixth caudal vertebrae are mostly concealed beneath armor, bone fragments, and what are probably the eighth and ninth caudal vertebrae. Only the left caudal ribs are apparent, jutting out of the block. They are dorsoventrally flat and laterally elongate, typical for aetosaurs, but they are poorly preserved and no other details are apparent.

The anterior face of what is probably the seventh caudal vertebra is visible underneath matrix and an osteoderm about six centimeters behind where the sixth caudal vertebra is buried in
the block, breaking the line of articulation. The neural canal is prominent on this vertebra and
what is visible of the neural arch shows that it was tall. The centrum is amphicoelous and
mediolaterally constricted. The ventral surface consists of a median ventral groove bounded
laterally by two sharp ridges. The ridges would terminate posteriorly with the chevron facets, but
the relevant area is obliterated. A vertebra from approximately the same position is preserved in
PEFO 34919 (Figures 17a-c) and provides more details.

The centrum is much longer than wide (57 mm to ~30 mm), mediolaterally compressed,
and grooved ventrally. Its rims flare minimally, but the articular faces are deeply concave (Figure
17b-c). The neural arch is dorsoventrally shorter than in the more anteriorly positioned caudal
vertebrae, but the neural spine was certainly tall in this position as well (Figure 17b). The
zygapophyses are reduced and each pair is closely situated medially. The postzygapophyses do
not project far posteriorly. The caudal rib is situated anteroventrally on the neural arch. It is broad
and flat, extends laterally (~50 mm), and is slightly arcuate in anterior view (Figure 17b).

What are probably the eighth and ninth caudal vertebrae are well-preserved at the edge of
the block in PEFO 31217 (Figure 15). The centra are much longer than wide. The ninth centrum
has a length of 66.3 mm and a width of 40.2 mm. The lateral faces of the centrum are concave
and, as on the preceding centra, the ventral face is narrow with a deep median groove terminating
at the chevron facets. The neural arches and spines are complete and tall, with a height of 100.9
mm in the eighth vertebra and 98.4 mm in the ninth. The neural spines are tall and roughly
triangular in lateral view, with an anteroposteriorly broad base and tapering distally. The
zygapophyses are closely situated medially and extend anteriorly and posteriorly beyond the
articular faces of the centra. The caudal ribs are greatly reduced in lateral length.
An isolated vertebra from PEFO 34045 represents the mid-caudal series (Figure 17d). The centrum is longer than tall (65 mm to 35 mm) and mediolaterally compressed. Its articular faces are deeply concave and oval with the longest axis situated dorsoventrally. The neural arch is dorsolaterally reduced and mediolaterally compressed. The caudal ribs are greatly reduced and eroded. The neural spine is elongate, but its full dorsal extent is unknown (Figure 17d).

**Chevrons**

Only half of a single chevron and part of the head of a second are preserved in PEFO 34045 (Figures 18a-b). A few are smashed beneath other elements in PEFO 34919 and a badly preserved chevron is present beneath the second caudal vertebra of PEFO 31217. Although the details are poor the latter suggests, in accordance with the lack of facets on the first caudal vertebra of PEFO 31217, that chevrons started on the second caudal centrum. This is different from the condition in *Desmatosuchus spurensis*, in which they first appear on the third caudal centrum (Parker 2008a), but similar to the condition in *Typothorax coccinarum* (Heckert et al. 2010). The two preserved chevrons in PEFO 34045 are of the ‘slim’ elongate type and, therefore, from the anterior portion of the tail (Parker 2008a).

**Ribs**

**Presacral**

No cervical ribs are preserved in any of the specimens, but trunk ribs are common. The sacral and caudal ribs have been described above along with their associated vertebrae. The anterior and mid-trunk ribs are double-headed (Figure 18c-d). They extend laterally for the first quarter of their total length and then turn sharply ventrolaterally, are straight for half of the total length, and then gently turn more ventrally. Proximally the rib body is oval in cross-section,
becoming ovate and then flattened more distally; it is broadest at the point of the sharp ventrolateral turn.

The capitulum is oval in cross-section, with a sharp posterior projection. The capitulum and tuberculum are separated by 44 mm. The dorsal surface of the neck is marked by a transverse groove that terminates at a fossa on the proximal surface of the tuberculum (Figure 18e). That groove probably hosted the ventral portion of the vertebrarterial canal as in *Alligator* (Reese 1915). A thin flange of bone originates on the dorsal surface of the tuberculum and extends laterally, becoming confluent with the rib body just lateral to the ventrolateral hook. That flange forms a deep, elongate groove along the posterodorsal surface of the rib. Dorsally the rib is flattened and forms a thin anterior blade. The posteriormost ribs are single headed and fused with the transverse processes of the trunk vertebrae (Figure 14c).

**Gastralia**

It has been suggested that aetosaurians lack gastralia (Nesbitt 2011), but they are present in *Typothorax coccinarum* and *Stenomyti huangae* (Heckert et al. 2010; Small and Martz, 2013). In *Typothorax coccinarum* (e.g., NMMNH P-56299), the gastralia are preserved in the posteroventral portion of the thoracic region, are medially fused and laterally elongate. The gastralia of *Stenomyti huangae* (DMNH [DMNS] 60708) are presently undescribed. A single gastralia set is preserved in PEFO 34616 demonstrating that they were present in *Scutarx deltatylus* as well (Figure 18f). This set consists of incomplete but medially fused ribs with a short anterior projection.
Appendicular Girdles

Scapulocoracoid
The left scapulocoracoid is preserved in PEFO 31217; unfortunately the coracoid is covered by osteoderms that cannot be removed without causing significant damage, so only the dorsal-most portion of the coracoid, where it sutures to the scapula, is visible. In lateral view the general outline of the scapula of PEFO 31217 (Figure 19a) strongly resembles the scapulocoracoid of Stagonolepis robertsoni (Walker 1961: fig. 12a); although it is broader anteroposteriorly. The proximal end is expanded anterolaterally with the posterior projection situated more dorsally than the anterior projection. The posterior projection has a rounded posterior margin, as in Stagonolepis robertsoni (Walker 1961) differing from the pointed projection in Stagonolepis olenkae (ZPAL AbIII/694). The anterior projection is poorly preserved but appears to be pointed as in Stagonolepis robertsoni (Walker 1961). The scapular blade is gently bowed medially and the posterior edge is straight except for a slight posterior projection (the triceps tubercle) about 62 mm above the glenoid lip (Figure 19a). The anterior edge of the blade is straight for most of its length until it strongly flares anteriorly, forming a prominent deltoid ridge (=acromion process; Brochu 1992; Martz 2002). Below this there is a prominent foramen, although its anterior edge is broken away. Likewise the ventral margin of the posterior edge of the scapular blade strongly flares posteriorly forming the supraglenoid buttress. The glenoid facet opens posteriorly. Laterally there is a sharp ridge, which probably represents deformation and crushing along the scapulocoracoid suture.

Ilium
Ilium are preserved in PEFO 34919 (right ilium; Figure 20) and PEFO 31217 (both ilia; Figures 15, 21). When articulated the ilia of Scutax deltatylus were oriented so that the acetabula faced ventrally as in some aetosaurs such as Aetosauroides scagliai (PVL 2073) and Typothorax
coccinarum (PEFO 33980); however, to avoid confusion in this description, the anatomical
directions will be provided as if the reader is viewing the ventral surface as the lateral surface
(see Figure 20a-b). The right ilium of PEFO 34919 is nearly complete, missing only a portion of
the anterior margin of the acetabulum (Figures 20a-b). As usual for the bones from this specimen,
the ilium is covered with a thin layer of weathered hematite that cannot be removed without
damaging the underlying bone. The iliac blade is complete, with a length of 196 mm and a mid-
height of 66.8 mm. The ‘dorsal’ margin of the iliac blade is mediolaterally narrow, expanding
anteriory so that the dorsal margin of the anterior process is thicker and more robust than the rest
of the blade. The anterior portion of the iliac blade is triangular in lateral view, and does not
extend anteriorly beyond the edge of the pubic peduncle as in Stagonolepis robertsoni (Walker,
1961). There is a prominent recess on the dorsal surface between the supraacetabular crest and
the posterior iliac blade (Figure 20a) that appears to be unique to Scutarx deltatylus.

The dorsoventral height of the posterior portion of the iliac blade diminishes posteriorly,
terminating in a point. From there the posterovertral margin slopes anterovertrally into a curving
posterior margin that distally hooks posteriorly and thickens to form the ischiadic peduncle. The
posterior projection of the ischiadic peduncle is proportionally larger and more pointed than the
same structure in Aetosauroides scagliai (PVL 2073) and Stagonolepis robertsoni (NHMUK
R479a), and more like that of TMM 31100-1, which represents a desmatosuchine aetosaurine
(unpublished data). The ventral margins of the pubic and ischiadic peduncles meet at an angle of
90 degrees ventral to the acetabulum, with the ilium contributing to the majority of the
acetabulum. In ventral view the margins of the peduncles are comma-shaped, thinning into the
ventral margin of the broadly concave acetabulum. The medial side of the acetabulum is smooth
and slightly convex.
Dorsal to the iliac neck, the medial side of the posterior portion of the iliac blade bears a prominent ventral ridge that forms a shelf for sacral rib articulation (Figure 20b). The rib scar is situated just above the ridge and forms a concave sulcus that extends anteriorly to just dorsal to the anterior margin of the neck.

Both ilia are present in PEFO 31217 as portions of a complete sacrum. Of the two the left is the better preserved. The acetabula are deeply concave and oriented ventrally (Figures 15, 21). Originally this was thought to be the result of crushing of the pelvis; however, the acetabula are oriented ventrally in many other uncrushed aetosaurian specimens including *Aetosauroïdes scagliai* (Heckert & Lucas 2002), the holotype of *Typothorax antiquus* (Lucas, Heckert & Hunt 2003), and *Typothorax coccinarum* (Heckert et al. 2010). The supraacetabular ridge in these ilia is strong, but not as strong as in rauisuchids. As in PEFO 34919, there is a deep fossa/recess on the dorsal surface between the supraacetabular ridge and the posterior portion of the iliac blade, a condition that appears to be autapomorphic for this taxon. That fossa is bordered posterovertrally by the thickened margin of the neck, a feature which is ventrally confluent with the ischiadic peduncle. The left iliac blade measures 188.6 mm in length and 67.4 mm in height, producing a relatively tall iliac blade. The posterior portion of the iliac blade has a posterior margin that projects well beyond the iliac peduncle. The extent of the ventral portions of the ilia is hard to determine because they are indistinguishably fused to the ischia and pubes; however, the left acetabulum is more or less rounded, 116.5 mm tall and 111 mm wide.

**Ischium**

The left ischium and part of the right are present, but poorly preserved (Figures 15, 21). The ischium consists of the main body with a sharp, rounded acetabular rim, and an elongate posterior process. The upper margin of the posterior process slopes gradually from the posterior
margin of the ischiadic peduncle, and the entire ischium measures 183 mm in length. The anteroventral margin is flat where the two ischia are fused, forming a wide, slightly concave ventral shelf. Overall the ischium is similar to that of other aetosaurians such as *Stagonolepis robertsoni* (Walker 1961), but lacks the prominent ventral kink found in *Desmatosuchus spurensis* (MNA V9300; Parker 2008a).

**Pubis**

Both pubes are present and in articulation with the pelvis, although they are moderately distorted by crushing and were damaged by weathering before collection (Figures 15, 21). The body of the pubis consists of an elongate, narrow rod that curves anteroventrally and expands medially into two broad sheets of bone that meet in a median symphysis. This pubic apron is convex anteriorly and concave posteriorly. It is dorsoventrally short, barely extending past the ventral margin of the puboischiadic plate, more like the condition in *Typothorax coccinarum* (Long & Murry 1995) rather than the extremely deep pubic apron found in *Desmatosuchus spurensis* (MNA V9300). Two distinct oval foramina pierce the pubic apron in the proximal part of the element. The bone is broken around the more anterior foramen of the right pubis, but it is clear that it was the larger of the two openings (Figure 21). Two pubic foramina are also described for *Stagonolepis robertsoni* (Walker 1961), and the upper (anterior) opening considered homologous to the single foramen found in other aetosaurs (e.g., MNA V9300, *Desmatosuchus spurensis*). The distal ends of the pubes are shaped like elongate commata, narrow and curving into the symphysis (Figure 21), different from the strong, knob-like projections (pubic boots) found in *Desmatosuchus spurensis* (MNA V9300).
Osteoderms

Paramedian osteoderms

Cervical

Cervical osteoderms are present in PEFO 31217, PEFO 34045, and PEFO 34616. All of the
osteoderms are wider than long (w/l ratio of 1.85). The cervical osteoderms are dorsoventrally
thick with well-developed anterior bars (sensu Long and Ballew, 1985), which bear prominent
anteromedial projections. The lateral edges are strongly sigmoidal, and lack anterolateral
projections (Figures 22a, c; 23a).

The dorsal surface is relatively featureless, with the ornamentation poorly developed. The
dorsal eminence is low, broad, and mounded, contacting the posterior plate margin (Figures 22a,
c). The eminence is also slightly offset medially, closer to the midline margin. The characteristic
triangular protuberance that diagnoses *Scutarx deltatylus* is present in the posteromedial corner of
the osteoderm, but is greatly reduced in area (Figures 22a, c, d; 23a). In the cervical paramedian
osteoderms the shape of that protuberance is more of a right triangle than the equilateral triangles
found in the trunk series (see below).

In posterior view, the osteoderms are gently arched (Figures 22b, d). The median margins
are sigmoidal in medial view and dorsoventrally thick as is typical for aetosaurians. *Scutarx
deltatylus* lacks the ‘tongue-and-groove’ lateral articular surfaces present in *Desmatosuchus* (e.g.,
MNA V9300) and *Longosuchus meadei* (TMM 31185-84b).

The more posterior cervical paramedian osteoderms are similar, but increase in width (w/l
ratio of 2.05) and lack the strongly sigmoidal lateral margin. The margin is still sigmoidal but
bears a strong anterolateral projection (Figure 23a). Moreover, the anterior and posterior plate
margins are gently curved anterolaterally. In posterior view, these osteoderms have a lesser
degree of arching and are dorsoventrally thinner than the more anteriorly situated osteoderms.
The dorsal eminence is strongly offset medially and slightly more developed, becoming raised
and more pyramidal in shape, although this could be an individual variation (see description of
caudal paramedian osteoderms).
Trunk

The osteoderm transition between the cervical and trunk series is difficult to identify, but anterior dorsal trunk osteoderms are considered here to have higher width/length ratios and be dorsoventrally thinner than the cervical paramedian osteoderms. Furthermore, the triangular protuberance is more equilateral. However, it is difficult to differentiate these osteoderms from those of the anterior caudal region.

Osteoderms with the maximum width/length ratio (2.72/1) are found in the mid-trunk region. They bear a strongly raised anterior bar with prominent anteromedial and anterolateral projections. Prominent (greatly elongate) anterolateral projections also occur in *Calyptosuchus wellesi* (UMMP 7470), *Adamanasuchus eisenhardtae* (PEFO 34638), and *Neoaetosauroides engaeus* (PVL 3525). The anterolateral projections are shorter in *Stagonolepis robertsoni* ((NHMUK 4790a) and *Aetosauroides scagliai* (PVL 2073). The dorsal eminence in *Scutarx deltatylus* is medially offset, and forms a broad, low mound. Anterior to this on the anterior bar is a prominent, pointed anterior projection. The area of the anterior bar medial to this process is ‘scalloped out,’ and as a result is deeply concave (Figure 22e, f, j, k). This ‘scalloping’ of the anterior bar is a synapomorphy of aetosaurine aetosaurs, occurring throughout the clade. The length of the anterior bar decreases significantly within the arc of this concavity. The triangular protuberance is prominent and equilateral (Figures 22e-k; 23b, d).

The lateral margin is sigmoidal, and the anterior portion just posterior to the anterior bar is slightly embayed for slight overlap of the associated lateral osteoderm. In posterior view the osteoderm is only slightly arched (Figure 22h). In what are presumed to be more posteriorly positioned osteoderms, the osteoderm is more strongly arched (Figures 22l-m). The triangular protuberances are particularly visible in posterior view, extending even further dorsally that the main dorsal eminence (Figures 23c, e). The ventral surface of the dorsal trunk paramedian osteoderms are smooth, with a slight embayment situated on the underside of the dorsal eminence.
The surface ornamentation of the dorsal trunk paramedian osteoderms is barely apparent in PEFO 34045, but much better developed in the other specimens. The ornament consists of pitting surrounding the dorsal eminence and radiating grooves and ridges over the rest of the surface.

There is no direct evidence for a constriction (‘waist’) in the carapace anterior to the pelvis as in *Aetosaurus ferratus* (Schoch 2007), *Calyptosuchus wellesi* (Case 1932), and *Aetosauroides scagliai* (Heckert & Lucas 2002); however, because the lateral osteoderm shapes in *Scutarx deltatylylus* are identical to those of *Calyptosuchus wellesi*, it is probable that *Scutarx deltatylylus* also possessed a ‘waisted’ carapace although this cannot be confirmed.

Overall the paramedian cervical and trunk osteoderms of *Scutarx deltatylylus* are similar to those of *Calyptosuchus wellesi* in all characteristics except for the presence of the posteromedial triangular protuberance (Figure 24). This character must be present to differentiate *Calyptosuchus wellesi* and *Scutarx deltatylylus* paramedian osteoderms and in osteoderms where this area is not preserved an alpha taxonomic assignment cannot be made.

### Caudal

Like the cervical-trunk transition, the trunk-caudal transition is also difficult to determine in unarticulated aetosaurian carapaces (Parker 2008a). The latter transition is generally characterized by reduction of osteoderm width-length ratios and greater development of the dorsal eminences (Heckert & Lucas 2000). The extreme is found in *Rioarribasuchus chamaensis*, in which the barely visible dorsal eminences in the mid-dorsal region transition posteriorly to elongate, anteromedially curved spines in the anterior caudal region (Parker 2007).

The trunk-caudal transition for *Scutarx deltatylylus* is best preserved in PEFO 34919 in which the dorsal eminences show a marked increase in height from 16.35 mm in the mid-trunk region to 40.07 mm in the anterior dorsal caudal region. Width/length ratios across this same transition are 2.54 to 2.16, showing the corresponding decrease. The dorsal eminence is a tall
pyramid, with a posterior vertical keel (Figure 25). In all other respects the anterior caudal osteoderms are similar to those of the trunk region.

Dorsal mid-caudal paramedians are relatively equal in width and length (w/l ratio = 1.08). Those osteoderms still possess the pronounced dorsal eminence (Figures 26a-j), as well as the anteromedial and anterolateral projections of the anterior bar. In PEFO 34045 these osteoderms are extremely thickened (Figures 26a-b, e-f).

The posterior dorsal caudal paramedians (Figures 26k-n) become longer than wide (w/l ratios of 0.73 and 0.66), and the dorsal eminence is reduced to a raised, anteroposteriorly elongate keel with a posterior projection that extends beyond the posterior margin of the osteoderm. Presumably these continue until they become elongate strips of bone as in *Aetosaurus ferratus* (Schoch 2007) and *Typothorax coccinarum* (NMMNH P56299; Heckert et al. 2010).

**Lateral osteoderms**

The best guide for the distribution of the lateral osteoderms is UMMP 13950, the holotype of *Calyptosuchus wellesi*, which preserves the posterior dorsal armor and much of the caudal lateral armor in articulation (Case 1932). *Scutarx deltatylus* possesses lateral plates that are identical in shape to those of *Calyptosuchus wellesi*, allowing for determination of caudal and posterior dorsal osteoderms. Therefore, any lateral osteoderms falling outside of those morphotypes probably are from more anterior regions. Anterior dorsal lateral osteoderms are preserved in the articulated holotype of *Aetosauroides scagliai* (PFV 2073), which can be used to help assign isolated osteoderms.

Lateral osteoderms can be distinguished from paramedian osteoderms primarily by the lack of the prominent anterolateral projection. Furthermore, the anteromedial corner of the osteoderm is ‘cut-off’ and beveled for reception of the anterolateral projection of the associated adjacent paramedian osteoderm (poa; Figure 27).
Cervical

There are no lateral osteoderms in the material present that can unequivocally be assigned to the cervical region.

Trunk

Anterior lateral trunk osteoderms are not preserved in the holotype of *Calyptosuchus wellesi*, but they are preserved in *Aetosaurus ferratus* (Schoch 2007). In *Aetosaurus* those osteoderms are strongly asymmetrical with the dorsal flanges roughly half the dimensions of the lateral flanges. Furthermore, the dorsal flanges are triangular or trapezoidal in dorsal view rather than rectangular, with a slight, medially projecting posterior tongue.

Two osteoderms from the left side in PEFO 34616 and a third from the right side in PEFO 34045 match this anatomy and are probably from the anterior portion of the carapace (Figures 27a-d). In addition to the features just mentioned, those osteoderms possess a distinct anterior bar. The anteromedial corner of the anterior bar is beveled for articulation with the anterolateral process of the paramedian osteoderm. The dorsal eminence of the lateral osteoderm is a prominent pyramidal boss that contacts the posterior plate margin and extends anteriorly, covering two-thirds of the osteoderm length. Surface ornamentation consists of elongate grooves and ridges radiating from the dorsal eminence. In posterior view, the osteoderms are only slightly angulated, with the angle between flanges strongly obtuse (Figures 27b, d). Similarly shaped osteoderms are found in the anterior lateral trunk region of *Aetosauroides scagliai* (PVL 2073).

Posterior-mid trunk osteoderms (from roughly the ninth through 12th positions) are sub-rectangular with a distinct, posteromedially sloping lateral edge (Figures 27e-h; Case 1932). The dorsal flange is sub-rectangular in dorsal view. The medial edge of the dorsal flange is beveled and slightly sigmoidal with a ‘cut-off’ anterior corner for the anterolateral projection of the paramedian plate. The osteoderm is moderately flexed with the lateral flange extending at about 45 degrees relative to the dorsal flange (Figures 27f, h). Both flanges are roughly the same size, although the sloping lateral edge produces a small anteromedial ‘wing’ that extends that edge a bit farther laterally and provides a trapezoidal shape for the lateral flange (alw; Figures 27e, g).
The dorsal eminence is pyramidal, and the degree of its development differs between specimens, from a low mound in PEFO 34045 to a distinct tall, triangular boss in PEFO 34919. On the dorsal surface a distinct anterior bar is present and the surface ornamentation consists of small pits and elongate grooves radiating from the dorsal eminence. Ventrally the osteoderms are smooth, except for longitudinal striations along the posterior margin where this margin would overlap the anterior bar of the preceding lateral osteoderm.

The posteriormost lateral trunk osteoderms (15th and 16th positions) are similar to the posterior mid-trunk osteoderms but lack the anterolateral ‘wing’ and are much more strongly flexed, enclosing an angle of approximately 90 degrees in posterior view (Figures 27i-j). They are similar to the posterior lateral trunk osteoderms in *Calyptosuchus wellesi* (Case 1932).

**Caudal**

Caudal lateral osteoderms are more equal in dimension, and bear rectangular dorsal flanges (Figures 27k-p). The angle enclosed between the dorsal and lateral flanges is about 45-50 degrees (Figures 27l, n, p). Overall these osteoderms possess some of the same surficial features as the other osteoderms, such as an anterior bar, radial ornamentation, and a posteriorly placed dorsal eminence. However, the anterior caudal osteoderms in some specimens (e.g., PEFO 34919) possess some of the tallest dorsal eminences in the carapace (Figures 25; 27n). The caudal lateral osteoderms also decrease in width posteriorly (Figure 27m-n). The height of the dorsal eminence is gradually reduced and becomes an elongate sharp ridge.

**Ventral trunk osteoderms**

Ventral trunk osteoderms are preserved in all of the PEFO specimens, including an articulated, but badly preserved, set in PEFO 31217. They consist mainly of square to rectangular osteoderms, with reduced anterior bars, no dorsal eminence and a surface ornamentation of pits and elongated pits in a radial pattern emanating from the center of the osteoderm (Figures 28a-f). Because no complete set is preserved the exact numbers of rows and column cannot be
determined; however, they would have been overlapping as in *Stagonolepis robertsoni* (Walker, 1961) and *Typothorax coccinarum* (Heckert et al., 2010).

**Appendicular osteoderms**

A few irregular, small, rounded osteoderms most likely represent appendicular osteoderms. There are two types: one featureless except for a distinct raised keel (Figure 28g), and the other with a surface ornamentation of radial pits (Figure 28g i). A triangular osteoderm (Figure 28h) from PEFO 34616 could represent a different type of appendicular osteoderm, or it could also be an irregularly shaped osteoderm from the ventral carapace possibly from the vicinity of the cloaca (A. Heckert, pers. comm., 2016).

**Broken osteoderms**

An interesting aspect of PEFO 34045 is the presence of many irregularly shaped osteoderms recovered with the specimen (Figure 29). All of the edges on these osteoderms are compact bone and do not represent recent breaks. Close examination shows that these specimens are the lateral ends of dorsal paramedian osteoderms because they possess anterior bars with strong anterolateral projections and sigmoidal edges (Figures 29a-d). It is unclear why these osteoderms are incomplete but two possibilities exist. The first possibility is that these osteoderms were incompletely ossified. Alternatively, they were broken and then the edges healed during the life of the animal. However, there is no visible sign of pathology because the edges are smooth and the dorsoventral thickness of the osteoderms remains constant. The osteoderms are also from opposite sides of the body precluding a cause from a single injury if they are pathologic in nature. Histological examination could help determine the ontogeny of these elements. If growth rings are uniform throughout the specimen, it would demonstrate that either damage occurred at a young age or that the remainder of the element did not ossify. If the
DISCUSSION

Scutarx deltatylus exemplifies the importance of utilizing a detailed apomorphy-based approach to differentiate Late Triassic archosauromorph taxa (e.g., Nesbitt, Irmis & Parker 2007; Nesbitt & Stocker 2008; Stocker 2010). The material here referred to Scutarx deltatylus was originally assigned to Calyptosuchus wellesi (Long & Murry 1995; Parker & Irmis 2005; Martz et al. 2013), which was differentiated from Stagonolepis robertsoni by the presence of the triangular protuberance on the paramedian osteoderms (Martz et al. 2013). However, reexamination of the holotype of Calyptosuchus wellesi (UMMP 13950) as well as referred material from the Placerias Quarry of Arizona shows that material of Calyptosuchus wellesi actually lacks the triangular protuberance. Moreover, the skull of Scutarx deltatylus possesses characters of the braincase (e.g., foreshortened parabasisphenoid) that are more similar to Desmatosuchus than to other aetosaurians that are similar to Stagonolepis. Unfortunately, the skull of Calyptosuchus wellesi is still mostly unknown. The Placerias Quarry contains a number of isolated aetosaurian skull bones (most notably basicrania), with differing anatomical characteristics, but none of these can be referred with certainty to Calyptosuchus wellesi (Parker 2014). Nonetheless, prior to the discovery of the skull of Scutarx deltatylus, Calyptosuchus wellesi was assumed to have a skull more like that of Stagonolepis robertsoni and Aetosauroides scagliai (i.e. with an elongate parabasisphenoid). That assumption can no longer be maintained. A phylogenetic analysis (Parker, 2016) recovers Scutarx deltatylus as the sister taxon to Adamanasuchus eisenhardtae and forming a clade with Calyptosuchus wellesi. The unnamed clade formed by these three taxa is the sister taxon of Desmatosuchini (Parker, 2016) within Desmatosuchinae (Figure 30). The presence of a aetosaurian with armor similar to Stagonolepis robertsoni (sensu Heckert and Lucas, 2000), but with a skull more like that of desmatosuchins...
provides further support that certain characteristic of the armor that were once used to unite taxa, such as paramedian osteoderm ornamentation (Heckert & Lucas 2000; Long & Ballew 1985; Long & Murry 1995), may have wider distributions across Aetosauria than previously recognized (Parker 2008b; Desojo & Ezcurra, 2011; Small & Martz, 2013; Heckert et al. 2015).

Implications for Late Triassic Vertebrate Biochronology

The holotype and all of the referred specimens of *Scutarx deltatylus* were originally assigned to *Calyptosuchus wellesi* (Long & Murry 1995; Martz et al. 2013; Parker & Irmis 2005; Parker & Martz 2011), a proposed index taxon of the Adamanian biozone (Parker & Martz 2011), which is earliest Norian in age (Irmis et al. 2011). However, all of the recognized specimens of *Scutarx deltatylus* originate only from the Adamanian portion of the Sonsela Member of the Chinle Formation and the middle part of the Cooper Canyon Formation of Texas (Martz et al. 2013; Parker & Martz 2011). The reassignment of this material restricts the stratigraphic range of *Calyptosuchus wellesi* to the Bluewater Creek and Blue Mesa members of the Chinle Formation as well as the Tecovas Formation of Texas (Heckert 1997; Long & Murry 1995), which are stratigraphically lower than the Sonsela Member and middle part of the Cooper Canyon (Martz et al. 2013).

It has been suggested that the Adamanian biozone (*sensu* Parker & Martz 2011) could possibly be subdivided into sub-zones (Martz et al. 2013). That hypothesis was supported by a list of Adamanian taxa of the Chinle Formation that noted which are known solely from the Blue Mesa Member and which are known only from the lower part of the Sonsela Member. The list of taxa shared by both units is small and consists of *Placerias hesternus* (a dicynodont synapsid),
the archosauromorph *Trilophosaurus dornorum*, the poposaurid *Poposaurus gracilis*, a paratypothoracin aetosaur similar to *Tecovasuchus chatterjeei*, and *Calyptosuchus wellesi* (Martz et al. 2013). The reassignment of the Sonsela material previously placed in *Calyptosuchus wellesi* to *Scutarx deltatlus* further reduces that list. *Scutarx deltatlus* also occurs in the upper Adamanian Post Quarry of Texas, which contains taxa elsewhere only found in the lower part of the Sonsela Member (e.g., *Desmatosuchus smalli, Trilophosaurus dornorum, Typothorax coccinarum, Paratypothorax* sp.; Martz et al. 2013). Thus, *Scutarx deltatlus* can presently be considered an index taxon of the upper part of the Adamanian biozone, which is presently considered to be middle Norian in age (Figure 30; Irmis et al., 2011).

Hunt et al. (2005) previously divided the Adamanian biozone into older and younger parts, respectively called the St. Johnsian and Lamyan sub-biuchrons. Index taxa of the Lamyan are the aetosaur *Typothorax antiquus (=Typothorax coccinarum)* and the pseudopalatine phytosaur *Machaeroprosopus* (Hunt et al., 2005). However, the lowest known occurrence of *Machaeroprosopus* would represent the base of the Revueltian biozone (Martz & Parker, in press), thus the Lamyan would be Revueltian in age and not represent a subdivision of the Adamanian (Heckert, 2006; Parker, 2006). Accordingly I leave any proposed subdivisions presently unnamed.

**CONCLUSIONS**

*Scutarx deltatlus* is a new taxon of aetosaurian from the middle Norian (late Adamanian) of the American Southwest, based on material that was originally assigned to *Calyptosuchus wellesi*. This taxon is known from several carapaces and includes rare skull material from western North America. *Scutarx deltatlus* differs from all other aetosaurs in the presence of a raised
triangular boss in the posteromedial corner of the presacral paramedian osteoderms, a
dorsoventrally thickened skull roof, and an anteroposteriorly shortened parabasisphenoid. A
phylogenetic analysis places it as the sister taxon of *Adamanasuchus eisenhardtae* near the base
of Desmatosuchinae (Parker, 2016). *Scutarx deltatylus* appears to have utility as an index taxon
for the late Adamanian biozone.

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FIGURE CAPTIONS
Figure 1. Map of Petrified Forest National Park showing relevant vertebrate fossil localities. Modified from Parker & Irmis (2005).

Figure 2. Regional stratigraphy of the Petrified Forest area showing the stratigraphic position of the localities discussed in the text. All occurrences are in the lower part of the Sonsela Member of the Chinle Formation and are within the Adamanian biozone. Stratigraphy from Martz & Parker, 2010. Biozones from Parker & Martz (2011) and Reichgelt et al. (2013). Ages from Ramezani et al. (2011) and Atchley et al. (2013).

Figure 3. Differentiation and terminology for aetosaurian osteoderms, based on Stagonolepis robertsoni. Reconstruction courtesy of Jeffrey Martz.

Figure 4. Photos and interpretive sketches of the left nasal (PEFO 34616) in dorsal (A) and ventral (B) views. Arrows point anteriorly and scale bars equal 1 cm. Abbreviations: en, external nares; fr, frontal; la, lacrimal; mx, maxilla; s., suture with listed element.

Figure 5. Photo and interpretive sketch of posterodorsal portion of the skull of Scutarx deltatylus (PEFO 34616) in dorsal view. Scale bar equals 1 cm. Abbreviations: bo, basisioccipital; gr, groove; ex, exoccipital; lfr, left frontal; ls, laterosphenoid; na, nasal; orb, orbit; pa, parietal; par, paroccipital process of the opisthotic; plpr, palpebral; po, postorbital; pof, postfrontal; pr, prootic; prf, prefrontal; rfr, right frontal; s., suture with listed element; so, supraoccipital; sq, squamosal; stf, supratemporal fenestra.

Figure 6. Partial skull of Scutarx deltatylus (PEFO 34616) in right lateral view. Scale bar equals 1 cm. Abbreviations: bo, basisioccipital; bpt, basipterygoid processes; bsr, basisphenoid recess; bt, basal tubera; cp, cultriform process; fr, frontal; ls, laterosphenoid; na, nasal; of, orbital fossa; orb, orbit; pa, parietal; palp, palpebral; po, postorbital; pof, postfrontal; pr, prootic; prf, prefrontal; qj, quadratojugal; qu, quadrate; sq, squamosal; stf, supratemporal fenestra; uc, unossified cleft of the basal tubera.

Figure 7. Partial skull of Scutarx deltatylus (PEFO 34616) in ventral view. Scale bar equals 1 cm. Abbreviations: bo, basisioccipital; btp, basipterygoid processes; bsr, basisphenoid recess; bt, basal tubera; cp, cultriform process; f., fossa for specified element; lfr, left frontal; ls, laterosphenoid; mf, metotic fissure; na, nasal; of, orbital fossa; orb, orbit; pa, parietal; palp, palpebral; par, paroccipital process of the opisthotic; po, postorbital; pof, postfrontal; pr, prootic; prf, prefrontal; qj, quadratojugal; qu, quadrate; sq, squamosal; stf, supratemporal fenestra; uc, unossified cleft of the basal tubera.

Figure 8. Partial skull of Scutarx deltatylus (PEFO 34616) in posterior view. Scale bar equals 1 cm. Abbreviations: bo, basisioccipital; btp, basipterygoid processes; bs, basisphenoid; ex, exoccipital; ex.pr; exoccipital prong; fm, foramen magnum; lfr, left frontal; pa, parietal; par.op, paroccipital process of the opisthotic; po, postorbital; rfr, right frontal; sq, squamosal.
**Figure 9.** Braincase of *Scutax deltatlus* (PEFO 34616) in ventrolateral view. Scale bar equals 1 cm. Abbreviations: **bpt**, basiptyergoid processes; **bsr**, basisphenoid recess; **bt**, basal tubera; **cc**, cotylar crest; **clp**, clinoid process; **cp**, cultriform process; **crp**, crista prootica; **fo**, foramen ovale; **hypf**, hypophyseal fossa; **ic**, exit area of the internal carotid artery; **lfr**, left frontal; **lr**, lateral ridge; **ls**, laterosphenoid; **mf**, metotic foramen; **na**, nasal; **oc**, occipital condyle; **orb**, orbit; **pa**, parietal; **par**, paroccipital process of the opisthotic; **po**, postorbital; **pr**, prootic; **prf**, prefrontal; **psr**, parasphenoid recess; **rfr**, right frontal; **s**, suture with designated element; **sq**, squamosal; **uc**, unossified cleft of the basal tubera; **V**, passageway for the Trigeminal nerve.

**Figure 10.** Parabasisphenoid of *Scutax deltatlus* (PEFO 34616) in ventral view. Scale bar equals 1 cm. Abbreviations: **bpt**, basiptyergoid 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; **pr**, prootic; **prf**, prefrontal; **psr**, parasphenoid recess; **rfr**, right frontal; **sq**, squamosal; **ssr**, subsellar recess; **stf**, supratemporal fenestra; **uc**, unossified cleft of the basal tubera.

**Figure 11.** Articulated anterior post-axial vertebrae of *Scutax deltatlus* (PEFO 31217) in posterolateral (A), posterior (B), anterior (C), and ventral (D) views. Scale bar equals 1 cm. Abbreviations: **diap**, diaphysis; **k**, keel; **nc**, neural canal; **ns**, neural spine; **parp**, parapophysis; **pocdf**, postzygapophyseal centrodiapophyseal fossa; **posz**, postzygapophysis; **prez**, prezygapophysis; **spof**, spinopostzygapophyseal fossa; **spol**, spinopostzygapophyseal lamina; **tpol**, intrapostzygapophyseal lamina.

**Figure 12.** Trunk vertebrae of *Scutax deltatlus*. A-C, PEFO 34045/FF-51, mid-trunk vertebra in posterior (A), anterior (B), and lateral (C) views. Scale bar equals 1 cm. Abbreviations: **b.**, broken designated element; **cpof**, centropostzygapophyseal fossa; **crp**, centroprezygapophyseal fossa; **diap**, diaphysis; **nst**, neural spine table; **parp**, parapophysis; **podl**, postzygadiapophyseal lamina; **posz**, postzygapophysis; **prez**, prezygapophysis; **pro**, projection; **sprf**, spinoprezygapophyseal fossa; **spol**, spinopostzygapophyseal lamina.

**Figure 13.** Trunk vertebrae of *Scutax deltatlus*. A-C, PEFO 34045/19, Anterior trunk vertebra in anterior (A), posterior (B), and lateral (C) views. D-E, PEFO 34045/22, Posterior trunk vertebra in anterior (D) and lateral (E) views. Scale bar equals 1 cm. Abbreviations: **b.**, broken designated element; **bf**, bone fragment; **cpof**, centropostzygapophyseal fossa; **k**, keel; **nst**, neural spine table; **parp**, parapophysis; **podl**, postzygadiapophyseal lamina; **posdf**, postzygapophyseal spinodiapophyseal fossa; **posz**, postzygapophysis; **prez**, prezygapophysis; **pro**, projection; **sprf**, spinoprezygapophyseal fossa; **tp**, transverse process; **vb**, ventral bar.

**Figure 14.** Posterior trunk vertebrae of *Scutax deltatlus*. A-B, PEFO 34045 in anterior (A) and dorsal (B) view. C, PEFO 31217 in anterior view. Scale bar equals 1 cm. Abbreviations: **cp**, capitulum; **crp**, centroprezygapophyseal fossa; **diap**, diaphysis; **ns**, neural spine; **nst**, neural spine table; **parp**, parapophysis; **prdl**, prezygadiapophyseal lamina; **posdf**, postzygapophyseal spinodiapophyseal fossa; **posz**, postzygapophysis; **prez**, prezygapophysis; **pro**, projection; **sprf**, spinoprezygapophyseal fossa; **tp**, transverse process; **vb**, ventral bar.
spinodiapophyseal fossa; posz, postzygapophysis; prez, prezygapophysis; sprf, spinoprezygapophyseal fossa; tb, tuberculum; tp, transverse process; vb, ventral bar.

**Figure 15.** Photo and interpretive sketch of a partially articulated sacrum and anterior portion of the tail of *Scutarx deltatylus* (PEFO 31217). Scale bar equals 10 cm. Abbreviations: ac, acetabulum, apib, anterior process of the iliac blade; cdv, caudal vertebra; dv, trunk vertebra; f, foramen; isc, ischia; lil, left ilium; lpu, left pubis; lo, lateral osteoderm; os, osteoderm; pos, paramedian osteoderm; ril, right ilium; rpu, right pubis; scv, sacral vertebra.

**Figure 16.** Anterior caudal vertebrae of *Scutarx deltatylus* (PEFO 34045). A-D, anterior caudal in posterior (A), anterior (B), lateral (C), and ventral (D). E-F, Anterior caudal vertebra in ventral (E) and lateral (F). Scale bar equals 1 cm. Abbreviations: b., broken designated element; cf, chevron facet; cr, caudal rib; gr, ventral groove; posz, postzygapophysis; prez, prezygapophysis; spof, spinopostzygapophyseal fossa; sprf, spinoprezygapophyseal fossa.

**Figure 17.** Mid-caudal vertebrae of *Scutarx deltatylus*. A-C, anterior mid-caudal vertebra (PEFO 34919) in lateral (A), anterior (B), and posterior (C) views. D, posterior mid-caudal vertebra (PEFO 34045) in lateral view. Scale bar = 1 cm. Abbreviations: cf, chevron facet; cr, caudal rib; ns, neural spine; prez, prezygapophysis; posz, postzygapophysis.

**Figure 18.** Chevrons and ribs of *Scutarx deltatylus*. A-B, partial anterior chevrons from PEFO 34045 in posterior view; C-D, left trunk rib from PEFO 34045 in posterior (C) and anterior (D) views. E, close-up view of head of trunk rib from PEFO 34045. F, paired gastral ribs from PEFO 34616. Scale bars equal 1 cm. Abbreviations: cp, capitulum; fo, fossa; gr, groove; tb, tuberculum.

**Figure 19.** Left scapulocoracoid of *Scutarx deltatylus*. of PEFO 31217 in lateral view. Scale bar equals 10 cm. Abbreviations: ap, acromion process; cor, coracoid; fm, foramen; ost, osteoderms; sgb, supraglenoid buttress; tt, triceps tubercle.

**Figure 20.** Close-up of pelvis of *Scutarx deltatylus* (PEFO 31217). Scale bar equals 5 cm. Abbreviations: ac, acetabulum, apib, anterior process of the iliac blade; f, foramen; isc, ischia; lil, left ilium; lpu, left pubis; ril, right ilium; rpu, right pubis.

**Figure 21.** A-B, right ilium of PEFO 34919 in ‘lateral’ and ‘medial’ views (see text for discussion regarding anatomical direction of the ilium). Scale bar equals 1 cm. Abbreviations: ac, acetabulum; apib, anterior process of the iliac blade; fm, foramen; ip, ischiadic peduncle; pp, pubic peduncle; ppib, posterior process of the iliac blade; re, recess; sac, supraacetabular crest; sh, shelf; sras, sacral rib attachment surfaces.

**Figure 22.** Cervical and dorsal trunk paramedian osteoderms of *Scutarx deltatylus* from PEFO 34045. A-B, left mid-cervical osteoderm in dorsal (A) and posterior (B) views. C-D, right mid-cervical osteoderm in dorsal (C) and posterior (D). E-F, left (E) and right (F) dorsal trunk osteoderms in dorsal view. G-I, left (G, H) and right (I) dorsal trunk osteoderms in dorsal (G, I) and posterior (H) views. J-K, left (J) and right (K) dorsal trunk osteoderms in dorsal view. L-M,
posterior dorsal trunk osteoderm in dorsal (L) and posterior (M) views. Scale bar = 1 cm. Abbreviations: ab, anterior bar; alp, anterolateral process; amp, anteromedial process; anp, anterior process; de, dorsal eminence; trp, triangular protuberance.

**Figure 23.** Holotype paramedian osteoderms of *Scutarx deltatylistus* 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 24.** Comparison of dorsal trunk paramedian osteoderms of *Calyptosuchus wellesi* (A) and *Scutarx deltatylistus* (B-D) in dorsal view. A, MNA 2930, left osteoderm of *Calyptosuchus wellesi* lacking the triangular protuberance (trp). B, UCMP 36656, right osteoderms of *Scutarx deltatylistus* showing the triangular protuberance. C, UCMP 126844, medial portion of left osteoderm of *Scutarx deltatylistus* showing the triangular protuberance. D, UCMP 35738, medial half of left osteoderm of *Scutarx deltatylistus* showing the triangular protuberance. Scale bar equals 5 cm. Abbreviations: ab, anterior bar; alp, anterolateral process; amp, anteromedial process; de, dorsal eminence; trp, triangular protuberance.

**Figure 25.** Fused semi-articulated anterior dorsal caudal paramedian and dorsal caudal lateral osteoderms of *Scutarx deltatylistus* (PEFO 34919) in a lateral view showing extreme development of the dorsal eminences. Scale bar equals 1 cm. Abbreviations: lo, lateral osteoderm; po, paramedian osteoderm.

**Figure 26.** Dorsal caudal paramedian osteoderms of *Scutarx deltatylistus*. A-B, left anterior mid-caudal osteoderm (PEFO 34045) in dorsal (A) and posterior (B) views. C-D, right anterior mid-caudal osteoderm (PEFO 34919) in dorsal (C) and posterior (D) views; E-F, left mid-caudal osteoderm (PEFO 34045) in dorsal (E) and posterior (F) views. G-H, right mid-caudal osteoderm (PEFO 34919) in dorsal (G) and posterior (H) views. I-J, left mid-caudal osteoderm (PEFO 34919) in dorsal (I) and posterior (J) views. K-L, right posterior caudal osteoderm (PEFO 34045) in dorsal (K) and posterior (L) views. M-N, left posterior caudal osteoderm (PEFO 34045) in dorsal (M) and posterior (N) views. Scale bar equals 1 cm. Abbreviations: ab, anterior bar; alp, anterolateral process; amp, anteromedial process; de, dorsal eminence; me, medial edge.

**Figure 27.** Lateral osteoderms of *Scutarx deltatylistus*. A-B, left anterior trunk osteoderm (PEFO 34616) in dorsal (A) and posterior (B) views; C-D, right anterior trunk osteoderm (PEFO 34045) in dorsal (C) and posterior (D) views; E-F, right posterior mid-trunk osteoderm (PEFO 34045) in dorsal (E) and posterior (F) views; G-H, left posterior mid-trunk osteoderm (PEFO 34045) in dorsal (G) and posterior (H) views; I-J, right posterior trunk osteoderm (PEFO 34045) in dorsal (I) and posterior (J) views; K-L, right anterior dorsal caudal osteoderm (PEFO 34045) in dorsal (K) and posterior (L) views; right posterior dorsal mid-caudal osteoderm (PEFO 34919) in dorsal (M) and posterior (N) views; O-P, left dorsal mid-caudal osteoderm (PEFO 34166) in dorsal (O) and posterior (P) views. Scale bar equals 1 cm. Abbreviations: ab, anterior bar; alw, anterolateral
wing; de, dorsal eminence; df, dorsal flange; mf, medial flange; poa, paramedian osteoderm articular surface.

Figure 28. Ventral trunk and appendicular osteoderms of *Scutax deltatylus* from PEFO 34616. A-F, square ventral osteoderms. G, round, keeled appendicular osteoderm. H, triangular ventral (cloacal?) osteoderm. I, round, ornamented appendicular osteoderm. Scale bar equals 1 cm. Abbreviations: ab, anterior bar; k, keel.

Figure 29. Incompletely formed trunk paramedian osteoderms from PEFO 34045. A-B, right osteoderms in dorsal view; C, left osteoderm in dorsal view; D, right osteoderm in dorsal view. Scale bar equals 1 cm. Abbreviations: ab, anterior bar; alp, anterolateral process.

Figure 30. Time-calibrated phylogeny of the Aetosauria showing estimated ranges of taxa in the Triassic stages and associated vertebrate biozones. The Adamanian biozone is highlighted in blue.
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