

Memoir

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Cranial anatomy, intraspecific variation, and positional variation within *Calyptosuchus wellesi* (Pseudosuchia: Aetosauria) based on new specimens from the Upper Triassic Chinle Formation (Adamanian, early middle Norian) of Petrified Forest National Park, Arizona, USA

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Abstract

Calyptosuchus wellesi is an aetosaur known from the upper Blue Mesa Member and lowermost Sonsela Member of the Chinle Formation in Arizona, and the Tecovas Formation of the Dockum Group of Texas. The taxon is considered biostratigraphically informative and aids in correlating Upper Triassic strata across the southwestern United States. Our anatomical understanding of *Calyptosuchus* was primarily based on the holotype specimen from Texas and referred specimens, including several disarticulated elements from the *Placerias* Quarry in northern Arizona. We provide a re-interpretation of the holotype specimen and describe two new specimens referable to *Calyptosuchus* from northern Arizona. Together these specimens provide new information on the cranial anatomy, including dentition, and the positional and intraspecific variation within the carapace and vertebral column of the taxon. This new evidence suggests that the skull anatomy of *Calyptosuchus* is more similar to that of *Neoetosauroides* and *Stagonolepis* than to other aetosaurs. The dentition of *Calyptosuchus* supports recent hypotheses suggesting that aetosaurs were more omnivorous/faunivorous. The associated carapace expands our anatomical understanding of characters that vary among trunk paramedian osteoderms. We identify variation in the vertebral column within the trunk region, including the prominence of the centrodiapophyseal lamina and anatomy of the neural spine. Additionally, we report the first documentation of co-ossified sacral vertebrae within *Calyptosuchus*, which is also the first observation of this state within the Aetosauria outside of the Desmatosuchini. This suggests that co-ossification of the sacral vertebrae may be more prevalent within the Aetosauria than previously recognized.

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Non-technical Summary

Calyptosuchus wellesi is an aetosaur known exclusively from the southwestern United States. This species is collected from specific rock layers in northwestern Texas and northern Arizona that are approximately 223–218 million years old. Aetosaurs are characterized by their armor-covered bodies, similar to armadillos. This armor is formed by individual bony plates called osteoderms, which are the main way we identify a species of aetosaur. *Calyptosuchus* is an index fossil that allows us to understand the relationship of the rocks across a wider geographic area, including their ages. Because *Calyptosuchus* is an index taxon, it is important that we understand its anatomy to the best of our abilities so that way we can identify the species based on limited material.

Prior to our work, the skull anatomy of *Calyptosuchus* was based on a fragmentary dentary. Here we present new fossils that provide clarity on the skull of this animal, including new details on its teeth, which suggests that *Calyptosuchus* was likely an omnivorous animal. We present another individual that provides clarity on the variation of the osteoderms across the various divisions of the body, which allows us to identify isolated osteoderms of *Calyptosuchus* with a higher level of accuracy. This specimen preserves several complete vertebrae spanning most of the mid-section of the body, including the pelvis. This provides a better understanding of the variation in the vertebral column, which was previously not understood. Lastly, this new specimen also preserves a complete pelvic girdle. These new data resulted in the identification of a new pattern in the shape of the ilium and allowed us to reconstruct the pelvis of *Calyptosuchus*. Together, the two new specimens provide a better understanding of the anatomy of *Calyptosuchus*.

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Introduction

Aetosaurs are a group of pseudosuchian archosaurs that were prevalent across terrestrial ecosystems during the Late Triassic epoch (Carnian–Rhaetian, ~237–201 Ma) (Desojo et al., 2013). They are characterized by their osteoderm-covered bodies (Desojo et al., 2013), similar to ankylosaurian dinosaurs (Burns and Currie, 2014), extant armadillos (Hill, 2006), and some extant squamates (e.g., cordylids, skinks, anguids; Williams et al., 2022). Aetosaurs are documented from Upper Triassic strata within the United States, Argentina, Brazil, Greenland, western Europe, India, and northern Africa (Desojo et al., 2013). Out of the 29 currently described species (Reyes et al., 2024; Halder et al., 2025), 21 taxa are documented exclusively from Upper Triassic strata of North America, particularly from the Chinle Formation and Dockum Group in the southwestern United States (Desojo et al., 2013; Parker, 2016a; Reyes et al., 2024). There, the occurrence of aetosaurs provides a means to temporally constrain Upper Triassic strata through biostratigraphic and thus biochronologic correlation (e.g., Long and Murry, 1995; Heckert and Lucas, 2000; Parker and Martz, 2011; Parker, 2016a; Martz and Parker, 2017; Reyes et al., 2023).

Aetosaurs are often documented based on their isolated dorsal osteoderms, which can be referred to a taxon based on the unique combination of character states that they exhibit (Long and Ballew, 1985; Desojo et al., 2013; Parker, 2016a; Reyes et al., 2023). However, it is becoming more apparent that dorsal osteoderms can exhibit a degree of convergence between distantly related taxa within the clade (Parker, 2008b, 2016a; Parker and Halder, 2024; Reyes et al., 2024). Aetosaurs exhibit an array of tooth morphotypes that can be generalized into either constricted at the base and apically bulbous (e.g., *Desmatosuchus smalli* Parker, 2005; Small, 2002), or slightly labiolingually compressed, basally broad, and apically straight (e.g., *Aetosaurus ferratus* Fraas, 1877; Schoch, 2007) or recurved (e.g., *Aetosauroides scagliai* Casamiquela, 1960; Paes Neto et al., 2021b). Thus, it is hypothesized that aetosaurs exhibited various feeding ecologies including herbivory, omnivory, and carnivory (Long and Murry, 1995; Desojo and Ezcurra, 2011; von Baczko et al., 2018, 2021; Reyes et al., 2020; Paes Neto et al., 2021b). This may in part relate to the high species diversity, spatial distribution, and temporal longevity of the Aetosauria during the Late Triassic.

Partially or relatively complete aetosaur skeletons have been described or redescribed, thus allowing for a more holistic assessment of the interspecific relationships within the clade. Although these new data have become available, our understanding of the intraspecific variation within the clade remains limited. Historically, histological analyses of dorsal osteoderms have provided insight into intraspecific variation with relation to ontogeny and sexual maturity within aetosaurs (de Ricqlès et al., 2003; Parker et al., 2008; Werning, 2013; Scheyer et al., 2014; Taborda et al., 2015; Cerda et al., 2018; Hoffman et al., 2019; Ponce et al., 2023; Teschner et al., 2023). Recent studies on the vertebral anatomy of *Aetosauroides scagliai* by Paes-Neto et al. (2021a) resulted in the identification of ontogenetically variable character states that are often used to identify and diagnose taxa within the clade. This new understanding resulted in a taxonomic reassessment of *Polesinosuchus aurelioi* (Roberto-Da-Silva et al., 2014) and indicated that our lack of understanding of intraspecific variation within aetosaurs is influencing our assessments of species diversity within the clade.

Aetosaur skeletons that preserve significant portions of their respective carapaces not only indicate that osteoderms are osteologically variable between species, but that there is also positional

and osteological variation of the dorsal osteoderms across the various regions of the body within a single individual (Fig. 1; i.e., cervical, trunk, sacral, caudal; Parker and Martz, 2010). Because of this, it is important that we understand the osteology and variation of osteoderms because they are fundamental in our assessments of interspecific relationships within the Aetosauria (Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 1999; Parker, 2016a) and directly influence our ability to use aetosaurs for temporally constraining strata across the southwestern United States through biostratigraphic correlation (Fig. 2; Lucas and Hunt, 1993; Heckert and Lucas, 2000; Parker and Martz, 2011; Martz and Parker, 2017).

Calyptosuchus wellsi Long and Ballew, 1985, is a stagonolepidoid aetosaur known from both the Dockum Group and the Chinle Formation in Texas and Arizona (Fig. 2; Case, 1932; Long and Murry, 1995; Parker, 2016a). The paramedian, lateral, ventral, and appendicular osteoderms from the trunk through caudal region of *Calyptosuchus wellsi* have been described (Long and Ballew, 1985; Parker, 2018a) and are primarily based on the articulated carapace of the holotype specimen (UMMP 13950; Case, 1932), the referred individual UMMP 7470, and several disarticulated elements from UCMP A269 (the Placerias Quarry, Camp and Welles, 1956; Long and Murry, 1995; Parker, 2018a). However, documentation of the anatomical variation across the dorsal carapace was limited because of how the holotype bones were set in plaster for display and the loss of original association and/or non-documentation of the referred elements from UCMP A269 (Parker, 2018a). Close re-examination of the holotype specimen of *Calyptosuchus wellsi* (UMMP 13950), now possible after its removal from exhibit, resulted in a new understanding of the postcrania, including the positional variation within the dorsal carapace and intraspecific variation of the vertebral column. Thus, a revision of the previous anatomical interpretations of the specimen (i.e., Case, 1932; Long and Murry, 1995; Parker, 2018a) is merited.

We present our re-interpretations of the holotype specimen of *Calyptosuchus wellsi* (UMMP 13950), as well as two new specimens referable to *C. wellsi* (PEFO 49321, PEFO 46222) collected from the Chinle Formation of northern Arizona (Fig. 1). PEFO 49321 preserves several skull elements and provides new data about the interspecific variation of the skull in aetosaurs. Furthermore, PEFO 46222 preserves anatomy that is otherwise obscured, poorly preserved, or missing in UMMP 13950 and provides new anatomical understanding of the postcrania of *Calyptosuchus wellsi*, including portions of the skeleton subject to both positional and intraspecific variation. Understanding the degree of variation in *Calyptosuchus wellsi* is important because this taxon represents an index taxon of the Adamanian Land Vertebrate Estimated Holochronozone (~224–215 Ma; Parker and Martz, 2011; Martz and Parker, 2017).

Geological setting

Stratigraphic occurrence

Currently, *Calyptosuchus wellsi* has only been reported from the upper Blue Mesa Member and lower Sonsela Member of the Chinle Formation in northern Arizona (Fig. 2; Long and Murry, 1995; Parker and Martz, 2011), and from the Tecovas Formation of the Dockum Group in northwestern Texas (Fig. 2; Martz, 2008; Parker, 2016a). Previously, a pair of paramedian osteoderms (TTU-P 9420) from the Post Quarry (MOTT 3624), which is located within the lower Tecovas Formation-equivalent part of the Cooper Canyon Formation, Dockum Group, Texas, were referred to *Calyptosuchus*

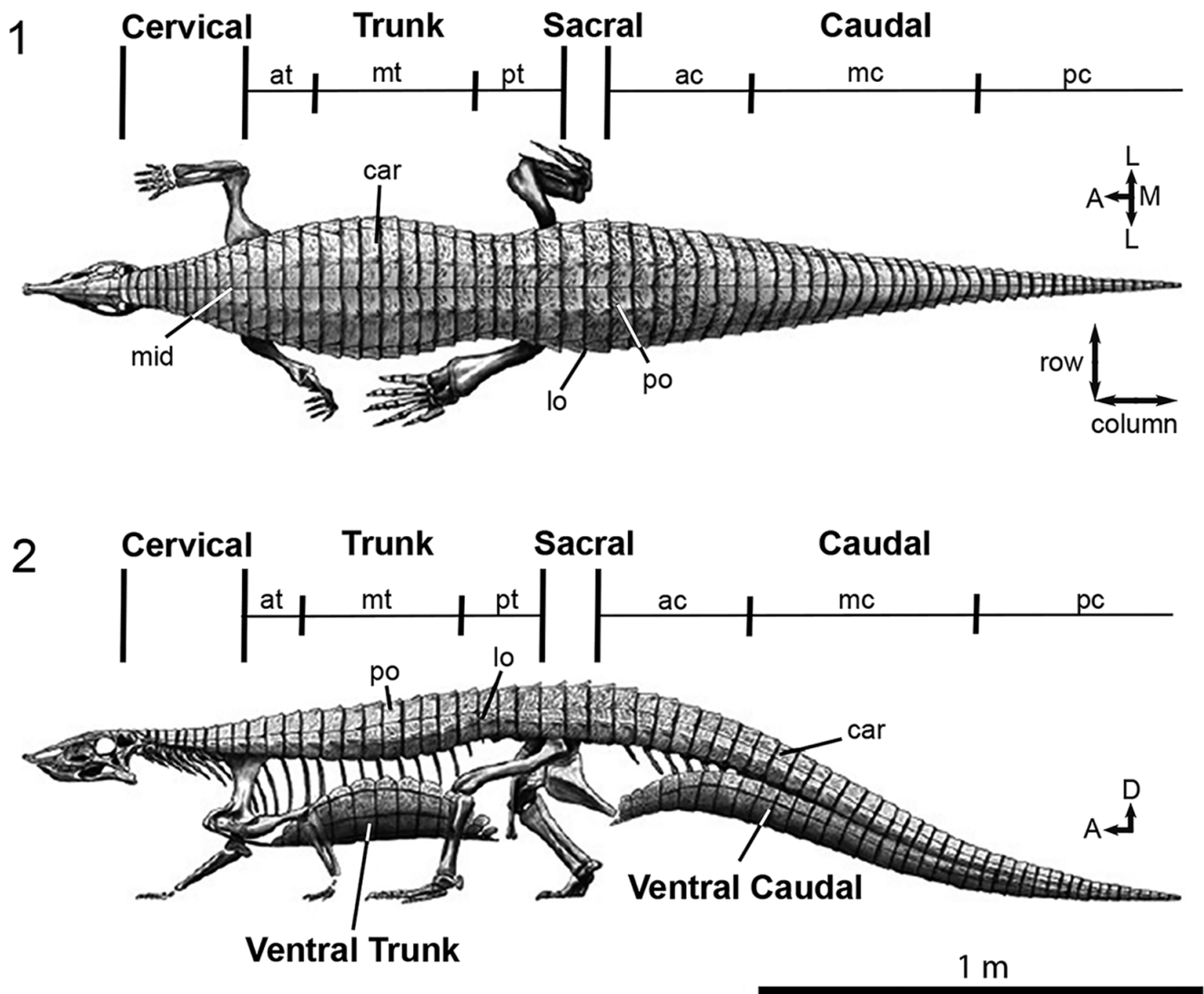


Figure 1. (1, 2) Generalized aetosaur body plan and osteoderm differentiation exemplified by *Stagonolepis robertsoni* in (1) dorsal, and (2) lateral views. Figure modified from Parker (2016b) and illustration by Jeffrey Martz. A = anterior; ac = anterior caudal region; at = anterior trunk region; car = carapace; D = dorsal; L = lateral; lo = lateral osteoderm; M = medial; mc = mid-caudal region; mid = midline; mt = mid-trunk region; pc = posterior-caudal region; po = paramedian osteoderm; pt = posterior trunk region. Arrows indicate anatomical direction.

wellesi (Martz, 2008; Parker and Martz, 2011; Martz et al., 2013), however revision of these osteoderms indicate that they are actually referable to *Scutarx deltatylus* Parker, 2016a, based on the presence of a thick dorsal protuberance on the posteromedial corner of the dorsal surface (Parker, 2016a, b, 2018a). UMMP 13950 (Case, 1932) and UMMP 7470 (Case, 1922, 1929) were recovered from the Tecovas Formation of the Dockum Group near Sierrita de la Cruz Creek, Oldham County, Amarillo, Texas, and Holmes Creek (sometimes referred to as 'Home[s] Creek', Gregory, 1972), Crosby County, Texas, respectively (Fig. 2.1; Parker, 2016a). UCMP 27225, UCMP 25941, and UCMP 32148 were collected from the Chinle Formation near St. Johns in northern Arizona (Fig. 2.1; Long and Murry, 1995); UCMP 27225 from locality UCMP V7308 (the Blue Hills, Parker, 2018a), and UCMP 25941 and UCMP 32148 were collected from locality UCMP A269/MNA locality 207 (the *Placerias* Quarry, Camp and Welles, 1956) in Apache County, which is equivalent to the uppermost Blue Mesa Member or the lowermost Sonsela Member (Fig. 2.2; Parker, 2018a).

PEFO 46222 was collected from PFV 456 (Thunderstorm Ridge), and PEFO 49321 was collected from PFV 467 (Metoposaurus Genesis Supreme). Both localities are located in the upper Blue Mesa Member of the Chinle Formation (sensu Woody, 2006), near Blue Tank and Billings Gap, respectively, at Petrified Forest National Park, Arizona (Fig. 2.2). The Blue Mesa Member of the Chinle Formation within PEFO is divided into an upper and lower portion by the lithologically complex Newspaper Rock beds (Martz et al., 2012). The strata of the upper Blue Mesa Member exhibit a pastel gray and blue color, and are composed primarily of mudstones, siltstones, and sandstones (Martz et al., 2012). The mudstones and siltstones of the Blue Mesa Member were deposited by a large northwest-trending fluvial system on the western margin of Pangea at an equatorial paleolatitude of 5–15°N (Dubiel et al., 1991; Kent and Irving, 2010; Martz et al., 2012). Sedimentological evidence indicates deposition in a humid climatic regime with intense monsoonal influence (Nordt et al., 2015).

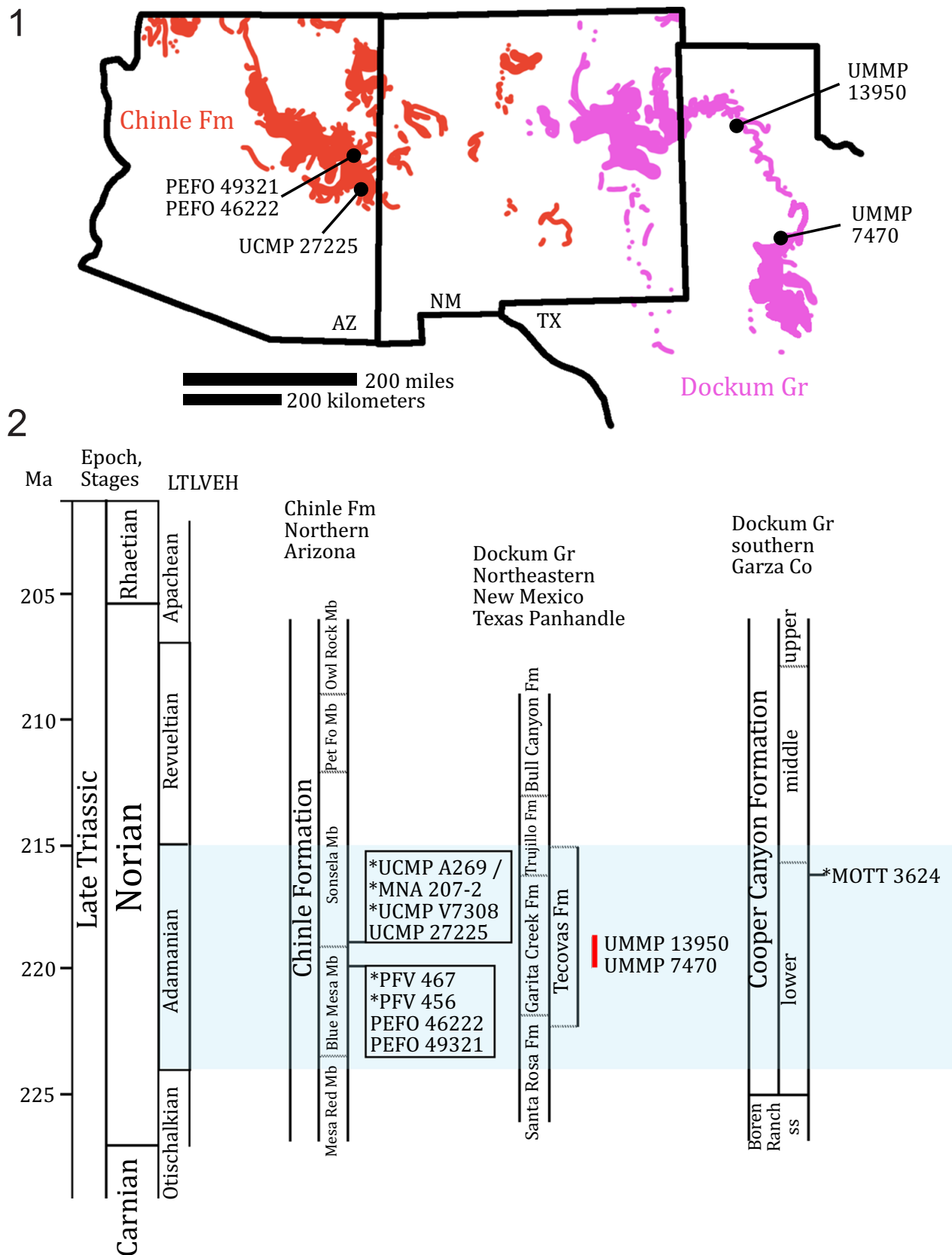


Figure 2. (1) Geographic and (2) stratigraphic occurrences of relevant specimens of *Calyptosuchus welllesi* and relevant localities (marked with *) across the Chinle Formation and Dockum Group in the southwestern United States. MOTT 3624 (the Post Quarry) is included because it is a fossil locality that provides important biostratigraphic context in the region. Red line marks hypothetical stratigraphical occurrence of UMP 13950 and UMP 7470 within the Tecovas Formation based on biostratigraphic range of *Calyptosuchus welllesi* within the Chinle Formation. Figure modified from Martz and Parker (2017), Lessner et al. (2018), Nesbitt et al. (2021), and Reyes et al. (2023, 2024). AZ = Arizona; Co = County; Fm = Formation; Gr = Group; LTLVEH = Late Triassic Land Vertebrate Estimated Holochronozones; Ma = millions of years; Mb = Member; MOTT = Museum of Texas Tech University vertebrate fossil locality; ss = sandstone; NM = New Mexico; Pet Fo = Petrified Forest; TX = Texas.

PEFO 46222 was collected at PFV 456 from a medium light gray siltstone with a thickness of 60 cm characterized by large-scale slickensides. Additionally, a few elements of PEFO 46222 graded into the underlying unit, which is a 15-cm thick, highly fossiliferous, poorly sorted siltstone horizon characterized by coprolites and microvertebrate remains (Kligman et al., 2020, 2023).

The stratigraphy of PFV 456 suggests that most of the vertebrate remains preserved at the site were initially deposited in a marginal lacustrine setting, likely a pond or lake bottom (Kligman, 2023). A subsequent episode of transport, likely a short-lived channel avulsion event, resulted in both the complete disarticulation and disassociation of these vertebrate remains and their redeposition at PFV 456 (Kligman, 2023). This is further supported by the well-preserved state of the delicate microvertebrate remains (Jenkins et al., 2020; Kligman et al., 2020, 2023; Marsh et al., 2020) that would otherwise not survive extensive fluvial transport. Additionally, this same episode of transport likely also incorporated the associated skeleton of PEFO 46222 and re-deposited it at PFV 456 (Kligman, 2023), explaining why some of the skeletal elements of PEFO 46222 were also recovered from the underlying fossiliferous unit.

Preservation of the bones varies at the PFV 467 locality. Some are coated with a thick red layer of iron-rich mineralization making the bones dense, while this is not the case for other fossilized material occurring immediately adjacent. This variation in preservation is exemplified by PEFO 49321, in which the elements were found in close association, yet only some are coated with the iron-rich mineralization.

Age

Six localities are considered here: UCMP A269 (the *Placerias* Quarry), UCMP V7308 (the Blue Hills), PFV 456 (Thunderstorm Ridge), and PFV 467 (Metoposaurus Genesis Supreme) within the Chinle Formation, and Sierrita de la Cruz Creek and Holmes (=Home[s], Gregory, 1972) Creek within the Dockum Group. U–Pb detrital zircon geochronology suggests an early-middle Norian (ca. 227–205 Ma; Kent et al., 2019) maximum depositional age (MDA) of ca. 219.39 ± 0.16 Ma for UCMP A269 (Fig. 2.2; Ramezani et al., 2014), and by proxy UCMP V7308 because it occurs in a stratigraphically similar horizon. Chronostratigraphic correlation to the better age-calibrated Chinle Formation within PEFO suggests that UCMP A269 (the *Placerias* Quarry; Camp and Welles, 1956) is potentially contemporaneous with the upper Blue Mesa Member or lower Sonsela Member (Fig. 2.2; Martz et al., 2012; Rasmussen et al., 2020). This is based on the current geochronological understanding of the lower Chinle Formation within PEFO, where the upper Blue Mesa Member exhibits a maximum age of deposition (MDA) of ca. 223–218 Ma (Atchley et al., 2013; Rasmussen et al., 2020) and the lower Sonsela Member exhibits an MDA of ca. 219 Ma in the Lot's Wife Beds (Parker, 2018a; Marsh et al., 2019). Additionally, recent hypotheses by Irmis et al. (2011) and Marsh et al. (2019) suggest that the fine-grained 'upper Blue Mesa Member' facies that characterize the *Placerias* Quarry in St. Johns, Arizona, are regionally diachronous with the course-grained lower Sonsela Member facies in PEFO (= Lot's Wife Beds), as a result of the northeastward progradation of a massive fluvial fan (distributive fluvial system) that deposited the Blue Mesa Member and Sonsela Member in northern Arizona (Trendell et al., 2013).

Currently, there are no U–Pb maximum depositional ages for the Dockum Group (Riggs et al., 1996). Rb–Sr ages bound the lower and most of the middle units of the Cooper Canyon Formation in

Garza County, Texas, with an estimated age interval of ca. 225–211 Ma (Long and Lehman, 1993, 1994; Long, 2009; Marsh and Parker, 2020; Nesbitt et al., 2021). The Tecovas Formation of the Dockum Group in eastern New Mexico and the Texas Panhandle is stratigraphically equivalent to the lower Cooper Canyon Formation in Garza County (Fig. 2.2; Martz, 2008; Martz and Parker, 2017, fig. 14; Martz et al., 2013). Biochronological correlation of the Dockum Group to the better age-calibrated Chinle Formation exposed within PEFO places most of the Tecovas Formation and most of the lower Cooper Canyon Formation within the Adamanian Land Vertebrate Estimated Holochronozone, which currently has a temporal range of ca. 221–215 Ma (Fig. 2.2; Lucas and Hunt, 1993; Ramezani et al., 2011, 2014; Martz and Parker, 2017, fig. 14; Nesbitt et al., 2021, fig. 11).

PFV 456 and PFV 467 are stratigraphically located within the upper Blue Mesa Member (Fig. 2.2; Jenkins et al., 2020; Kligman et al., 2020, 2023; Marsh et al., 2020; Reyes et al., 2023), which currently exhibits temporal bounds of ca. 223–218 Ma (discussed above; Atchley et al., 2013; Rasmussen et al., 2020), placing the localities within the Adamanian Land Vertebrate Estimated Holochronozone (Fig. 2.2; Martz and Parker, 2017). These refined temporal constraints suggest a temporal range of ca. 223–218 Ma for *Calyptosuchus wellsi* (Parker and Martz, 2011; Rasmussen et al., 2020).

Materials and methods

Collection of new referred specimens

PEFO 46222 was collected from PFV 456 across a 5×4 m area (Fig. S1). We employed a 1-m^2 grid system to document element type, orientation, and collection numbers. A significant portion of the trunk and sacral region was collected from a single 1-m^2 quadrant; those elements were semi-articulated and closely associated, so they were collected in a field jacket made with single-sheeted polyester air filter medium (MSC Industrial Supply) and Hydrocal plaster (United States Gypsum Co.). The remaining associated elements found across the larger area were collected using Gypsona plaster bandages (BSN Medical) or with aluminum foil. A combination of Butvar B-72 (Rhom and Hass) and Paraloid B-76 (Eastman Chemical Company) were used to stabilize the bones in the field and lab. A combination of water and toothbrush, pin vices with carbide steel needles, dental tools, acetone, and air scribes were used to remove the matrix from the bone under dissecting microscope magnification. The elements were individually prepared and separated, although a few elements were diagenetically cemented, which impeded separation.

PEFO 49321 was collected from PFV 467 using Gypsona plaster bandages (BSN Medical) and aluminum foil. The elements were found in close association in the field with some being discovered during preparation because they were overlapped by other elements. Both Butvar B-72 (Rhom and Hass) and Paraloid B-76 (Eastman Chemical Company) was used to stabilize the bones in the field and lab. Several of the elements of PEFO 49321 preserve a thick iron-rich mineral crust (Fig. S2), so preparators chose not to mechanically remove this coating because the anatomy is still discernable or better represented in other elements that lack this mineralization.

PEFO 46222 and PEFO 49321 are catalogued, stored in cushioned drawers, and reposit in the museum collections at Petrified Forest National Park and are available to future researchers. Most of the skeletal elements of PEFO 46222 were scanned with an Artec Space Spider high-resolution laser/optical scanner and 3D models

were made from those data using Artec Studio 16 Professional (16.0.5.114). Surface meshes of PEFO 46222 are hosted on MorphoSource Project 609256 (<https://www.morphosource.org/projects/000609256>). High-resolution 3D surface scans of the pelvic girdles of UMMP 13950 and UMMP 7470 are available within the online repository of fossils of the UMMP at: <https://umorf.ummp.lsa.umich.edu/wp/class-reptilia/>.

Phylogenetic analyses

Our phylogenetic analyses build on those of Parker (2016a), Reyes et al. (2020, 2024), Paes Neto et al. (2021c), and Haldar et al. (2023). We modified the definitions of characters 69 and 76 (Parker, 2016a) to focus on the middle trunk region rather than the entire trunk region (see [Supplemental Material](#)). Additionally, we modified the scoring for *Stagonolepis olenkae* Sulej, 2010 (see [Supplemental Material](#)). We expanded a recent matrix of the Aetosauria by Reyes et al. (2024) by incorporating four new anatomical characters: [105] number of alveoli on the posterior process of the maxilla, starting ventral to the anteriormost margin of the antorbital fenestra; [106] presence of a pneumatic accessory cavity on the medial shelf of the maxilla; [107] co-ossification of the sacral vertebrae; and [108] position of anterior tip of preacetabular process in lateral view relative to the position of the pubic peduncle. We omitted the operational taxonomic unit (OTU) *Aetobarkinoides brasiliensis* Desojo, Ezcurra, and Kischlat, 2012, because it currently acts as a wildcard taxon (sensu Nixon and Wheeler, 1992; Kearney, 2002; Kearney and Clark, 2003) as determined by Heckert et al. (2015) and Parker (2016a). Additionally, we excluded *Kryphioparma caerulea* Reyes, Parker, and Heckert, 2023, following the discussion by Parker and Haldar (2024), suggesting that the taxon should be omitted from future phylogenetic analyses as it is likely acting as a wildcard because of the lack of scorable characters (Nixon and Wheeler, 1992; Kearney, 2002; Kearney and Clark, 2003). A recent study proposed that *Polesinesuchus aurelioi* Roberto-Da-Silva et al., 2014, is a junior synonym of *Aetosauroides scagliai* based on the documentation of diagnostic characters being subjected to intraspecific variation due to ontogeny (Paes-Neto et al., 2021a). Accordingly, we omitted *Polesinesuchus aurelioi* Roberto-Da-Silva et al., 2014, from our analysis. Additionally, we excluded *Garzapelta muelleri* Reyes, Martz, and Small, 2024, from the analyses because our study does not include new character information associated to the osteoderms that could assist in assessing the convergence exhibited by the trunk lateral osteoderms of this taxon (see discussion in Reyes et al., 2024).

The modified matrix comprises 108 anatomical characters (49 cranial, 59 postcranial; see [Supplemental Material](#)). Two versions of the matrix (i.e., Run 1, Run 2) were each analyzed using both maximum parsimony and Bayesian inference in order to explore evolutionary hypotheses under two different models. Run 1 included 33 taxa with an ingroup composed of 31 aetosaur taxa, including the holotype specimen of *Calypotosuchus wellsi* and four referred specimens. We scored the holotype specimen of *Calypotosuchus wellsi* (UMMP 13950, Case, 1932) independently from other referred material with the goal of assessing the referral of UMMP 7470, UCMP 27225, PEFO 46222, and PEFO 49321 to *C. wellsi* through a phylogenetic analysis. The array of isolated specimens from UCMP A269, including braincases referred to *Calypotosuchus wellsi* (Paes Neto et al., 2021c), were omitted because of both our inability to unambiguously refer them to a particular individual, and the ambiguity surrounding some of their taxonomic affinities (discussed below). Run 2 included 28 taxa with an ingroup composed of 26 aetosaur taxa. We coded all of the referred individuals listed above into a composite OTU of *Calypotosuchus wellsi*

to assess its phylogenetic relationships within Aetosauria. The non-aetosaur aetosauriform *Revueltosaurus callenderi* Hunt, 1989, and rauisuchid *Postosuchus kirkpatricki* Chatterjee, 1985, served as the outgroup for all analyses (following Parker, 2016a). The new and revised character scorings within this study were based on specimens that were studied firsthand, from figures and descriptions in the literature, personal communications, and/or shared photographs and 3D models. The supplemental material includes a detailed list of the taxa, specimens, and main references from which the new characters were scored.

Maximum parsimony. The matrix was analyzed via parsimony using the phylogenetic analysis software package TNT v1.5 (Goloboff et al., 2008). The analysis was performed using the traditional search option with 1,000 replications and tree bisection reconnection swapping while keeping 10 trees per replication and condensing zero-length branches (see Parker, 2016a; Reyes et al., 2020; Paes Neto et al., 2021c). Fourteen characters (3, 4, 14, 20, 22, 23, 24, 28, 64, 70, 73, 76, 79, 83) were ordered. Our analysis resulted in 424 most-parsimonious trees (MPTs) with a length of 282 steps for Run 1 and 18 MPTs with a length of 281 steps for Run 2, a Consistency Index (C.I.) of 0.546 for Run 1 and 0.548 for Run 2, and a Retention Index (R.I.) of 0.721 for Run 1 and 0.723 for Run 2 (see [Supplemental Material](#)). The strict consensus of the MPTs for both runs is discussed below.

Bayesian inference. In addition to maximum parsimony, the matrix was analyzed via Bayesian inference to explore alternative hypotheses and methodologies. This was performed using the phylogenetic analysis software MrBayes v3.2.6 (Huelsenbeck and Ronquist, 2001) with the Mkv model and gamma rate variation under the following parameters: two runs with four Markov chain Monte Carlo (MCMC) chains each, sampled every 1000 generations, for five-million generations with a relative burn-in frequency of 0.25. Convergence of independent runs was assessed using Tracer v1.7.1 (<http://beast.bio.ed.ac.uk/Tracer>). For consistency we ordered the same 14 characters listed above. The consensus cladogram and associated matrix for Run 2 were imported into PAUP*4.0 (Swofford, 2003) to extrapolate the synapomorphies of the consensus cladogram (see [Supplemental Information](#)).

Repositories and institutional abbreviations

AMNH, American Museum of Natural History, New York, New York, USA; DMNH V., Denver Museum of Nature and Science, Denver, Colorado, USA; ISI, Indian Statistical Institute, Kolkata, India; MCN, Museu de Ciências Naturais, Secretaria Estadual do Meio Ambiente e Infraestrutura, Porto Alegre, Brazil; MCP, Museu de Ciências e Tecnologia de Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; MCZD, Marischal College, Zoology Department, University of Aberdeen, Scotland; MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; MOTT, refers to a fossil locality of TTU; NCSM, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA; NHMUK, Natural History Museum, London, England, United Kingdom; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; PEFO, Petrified Forest National Park, Arizona, USA; PFV, refers to a vertebrate locality number from PEFO; PULR, Paleontología Museo de Ciencias Naturales, Universidad de La Rioja, La Rioja, Argentina; PVL, Instituto Miguel Lillo, Paleontología de Vertebrados, Tucumán, Argentina; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TMM, Texas Vertebrate Paleontology Collections, University of Texas at Austin, Austin, Texas, USA; TTU-P, Museum of

Texas Tech University, Lubbock, Texas, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; ULBRA PVT, Universidade Luterana do Brasil, Coleção de Paleovertebrados, Canoas, Rio Grande do Sul, Brazil; UFSM, Laboratório de Estratigrafia e Paleobiologia of Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brazil; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA; UOPB, University of Opole, Palaeobiology Department, Opole, Poland; YPM, Yale Peabody Museum, New Haven Connecticut, USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Systematic paleontology

Archosauria Cope, 1869, sensu Gauthier and Padian, 1985
Pseudosuchia Zittel, 1887–1890, sensu Gauthier and Padian, 1985
Aetosauria Marsh, 1884, sensu Parker, 2007
Stagonolepididae Lydekker, 1887, sensu Heckert and Lucas, 2000
Stagonolepidoidea Parker, 2018a
Calyptosuchini new clade

Definition

The least inclusive clade containing *Calyptosuchus wellsi*, *Scutarx deltatylus*, and *Adamanasuchus eisenhardtae* Lucas et al., 2007a.

Unambiguous synapomorphy

Pubis exhibits two obturator foramina (character 50-1; convergent in *Stagonolepis robertsoni* Agassiz, 1844, unknown in *Adamanasuchus eisenhardtae*).

Other possible synapomorphies. ACCTRAN: The basal tubera and basipterygoid processes are closely situated to each other (character 25-1); maxillary teeth are ovate, but not strongly medio-laterally compressed in occlusal view (character 34-1); maxillary teeth crown is bulbous and partly recurved, has a concave anterior edge, and straight posterior edge (character 35-1); co-ossified sacral vertebrae (character 106-1). DELTRAN: none.

Calyptosuchus Long and Ballew, 1985

Type species

Calyptosuchus wellsi Long and Ballew, 1985, by monotypy.

Diagnosis

As the monotypic species.

Occurrence

As the monotypic species.

Calyptosuchus wellsi Long and Ballew, 1985
 Figures 3–13

Holotype

UMMP 13950, a partially articulated skeleton that preserves the dorsal carapace from the mid-trunk through mid-caudal region with the associated vertebral column and pelvic girdle (Case, 1932).

Revised diagnosis

Calyptosuchus wellsi is a medium-sized aetosaur that currently lacks autapomorphies. It is differentiated from all other aetosaurs based on a unique combination of characters including a maxilla

that lacks a pneumatic accessory cavity, unlike *Desmatosuchus* (Case, 1920; Small, 2002), *Stagonolepis* (Walker, 1961; Sulej, 2010; Parker, 2018b), *Longosuchus meadei* (Sawin, 1947) (Parrish, 1994), and *Stenomylis huangae* Small and Martz, 2013; a preacetabular process of the ilium that is positioned dorsal to the pubic peduncle, a condition shared with most aetosaurs that preserve an ilium except for *Neoaetosauroides engaeus* Bonaparte, 1969, where the preacetabular process is positioned far anteriorly of the pubic peduncle (Desojo and Báez, 2005); a pubic apron that is perforated by two foramina as observed in *Scutarx deltatylus* (Parker, 2016b) and *Stagonolepis robertsoni* (Walker, 1961); and a posterior centrodiapophyseal lamina that becomes more discernable in the vertebrae from the middle trunk into the posterior-trunk region. Furthermore, *Calyptosuchus wellsi* exhibits two characters subject to intraspecific variation. These are the presence/absence of zyga-diapophyseal laminae in the trunk vertebrae and co-ossification, or lack thereof, between the centra of sacral vertebrae #1–2.

Occurrence

Late Triassic, early-middle Norian, ca. 223–218 Ma, Adamanian Late Triassic Land Vertebrate Estimated Holochronozone (Atchley et al., 2013; Martz and Parker, 2017; Marsh et al., 2019; Rasmussen et al., 2020). Upper part of the Blue Mesa Member and lower part of the Sonsela Member (sensu Parker and Martz, 2011), Chinle Formation, Arizona (Long and Murry, 1995; Parker, 2018a); Tecovas Formation, Dockum Group, Texas (Case, 1932; Long and Ballew, 1985).

Cranial description

PEFO 49321 preserves elements of the cranium and mandible, including the first dentition and unambiguous braincase elements referable to *Calyptosuchus wellsi* (Fig. 3). A dentary from another associated individual (UCMP 27225; Parker, 2018a) represents the only other unambiguous skull material referable to this taxon. There are several braincases from UCMP A269 (the *Placerias* Quarry) that may be referable to *Calyptosuchus wellsi* (Paes Neto et al., 2021c), but their referral remains ambiguous due to the disarticulated nature and loss of original association of the elements collected from the site (Parker, 2018a). The elements of PEFO 49321 are moderately well preserved with those associated with the left side of the skull being coated with an iron-rich mineralization. No elements from the skull roof or palate are preserved.

Maxilla. PEFO 49321 preserves both maxillae, but the anatomy of the maxilla is best observed on the right element (Fig. 3.1, 3.2). The right maxilla is well preserved, nearly complete, and not coated with the iron mineralization. The maxilla is triradiate in shape with a main body and three processes (Desojo et al., 2013). In lateral view, the anterior process is dorsoventrally tall, and its dorsal margin forms the posterior half of the ventral margin of the external naris (Fig. 3.1). Anteriorly, the dorsolateral margin is crushed. It is evident that the anterior margin is not fully preserved in the maxillae (Figs. 3.1, S2), so it is likely that the anterior process tapers farther anteriorly, underlapping the lateral process of the premaxilla as typically observed in aetosaurs (e.g., Czepiński et al., 2021, fig. 6). The anteroventral margin of the dorsal process bears a posterodorsally inclined embayment in lateral view (Fig. 3.1, 3.2) at the junction between the anterior and dorsal processes. This embayment marks the lateral insertion point of the ventral process of the nasal, which comprises the posterior margin of the external naris as observed in most aetosaur taxa that preserve these elements (except *Desmatosuchus smalli*, TTU-P 9024, Small, 2002).

The dorsal process is acutely inclined posteriorly in relation to the main body of the element (Fig. 3.1, 3.2), but more so than the

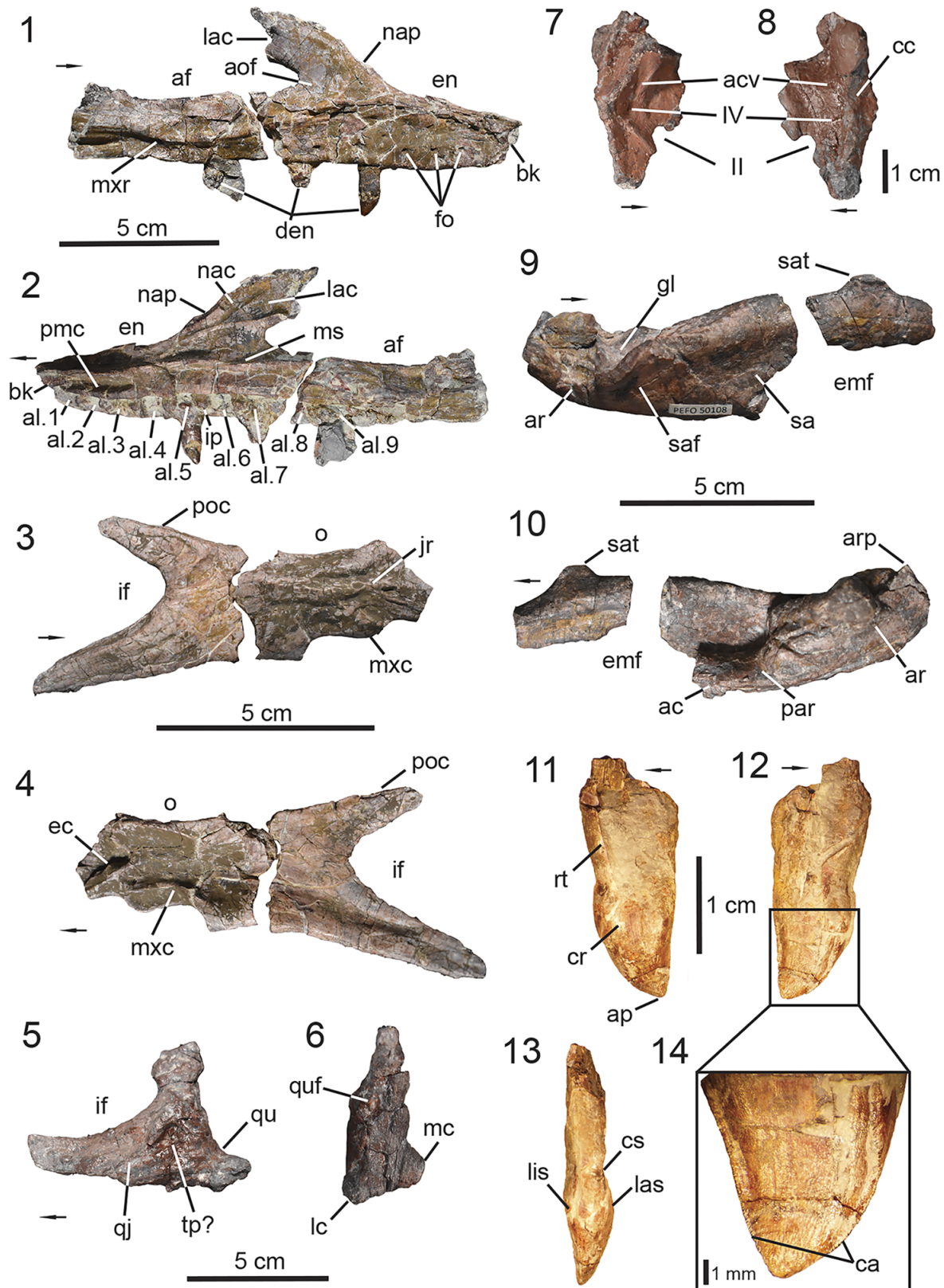


Figure 3. PEFO 49321, skull anatomy. (1, 2) Right maxilla; (3, 4) right jugal; (5, 6) left quadratojugal and quadrate; (7, 8) left laterosphenoid; (9, 10) right surangular, prearticular, and articular; (11–14) maxillary teeth. (1, 3, 5, 8, 9) Lateral views, (2, 4, 7, 10) medial views, (6) posterior view, (11) labial view, (12, 14) lingual view, (13) mesial view. ac = angular contact; acv = anterior cerebral vein; af = antorbital fenestra; al = alveoli; aof = antorbital fossa; ap = apex; ar = articular; arp = articular process; bk = break; ca = carinae; cc = cotylar crest; cr = crown; cs = constriction; den = dentition; ec = ectopterygoid contact; emf = external mandibular fenestra; en = external naris; fo = foramina; gl = glenoid; if = infraorbital foramen; ip = intradental plates; jr = jugal ridge; lac = lacrimal contact; las = labial surface; lc = lateral condyle; lis = lingual surface; mc = medial condyle; ms = medial shelf; mxc = maxilla contact; mxr = maxillary ridge; nac = nasal contact; nap = nasal process; o = orbit; poc = postorbital contact; par = prearticular; pmc = premaxilla contact; qj = quadratojugal; qu = quadrate; quf = quadrate foramen; rt = root; sa = surangular; saf = surangular foramen; sat = surangular tuber; tp = taphonomic pit; IV = foramen or canal for trochlear nerve. Arrows indicate anterior or distal direction (dentition).

condition observed in *Paratypothorax andressorum* Long and Bal-
lew, 1985 (SMNS 19003, Schoch and Desojo, 2016) where the
orientation is more of a right angle. Overall, it resembles the
condition observed in *Stagonolepis* spp. (*S. robertsoni*, NHMUK
PV R 4787, Walker, 1961; *S. olenkae*, ZPAL AbIII/1995, Sulej, 2010)
and *Aetosauroides scagliai* (MCN-PV 2347, Paes Neto et al., 2021b).
Posterolaterally, the dorsal process is dorsoventrally tall and tapers
into a posteriorly oriented triangular process near its dorsal border
that wedges itself between the lacrimal and nasal in lateral view,
resembling the condition in *Stagonolepis robertsoni* (Walker, 1961)
and *Aetosauros ferratus* (SMNS 5770, Schoch, 2007). Additionally,
the posteroventral margin of the dorsal process forms the ante-
rodorsal border of the antorbital fenestra. The posterior process of
the maxilla is nearly half the anteroposterior length of the entire
element with a dorsal margin that is anteroposteriorly straight in
lateral view and forms the ventral border of the antorbital fenestra.
The anterior portion of the fenestra between the dorsal and poste-
rior processes is not dorsoventrally tall (Fig. 3.1, 3.2), suggesting
that the antorbital fenestra of *Calyptosuchus wellsi* is subtriangular
in shape rather than semicircular or elliptical, resembling that of
Aetosauroides scagliai (UFSM 11505, Biacchi Brust et al., 2018;
MCN-PV 2347, Paes Neto et al., 2021b) and *Typothorax coccin-
arum* Cope, 1875 (NMMNH P-12964, Heckert et al., 2010; PEFO
38001/YPM VP.58121, Reyes et al., 2020). The posterior extent of
the maxilla is not preserved. Thus, the posterior process does not
provide information regarding the contact between the maxilla,
lacrimal, and jugal.

The ventral margin of the maxilla is anteroposteriorly straight in
lateral view (Fig. 3.1, 3.2), resembling that of *Coahomasuchus
kahleorum* Heckert and Lucas, 1999 (TMM 31100-437) and *Kocur-
ypelta silvestris* Czepiński et al., 2021 (ZPAL V.66/4). The antorbital
fossa is deep and well demarcated on the lateral surface of the
maxilla (Fig. 3.1). On the dorsal process the fossa expands onto
most of the lateral surface of the maxilla, but it is evident that it does
not continue onto the lateral extent of the nasal; instead, it con-
tinues posteriorly onto the lacrimal. On the posterior process, the
fossa is restricted to the dorsal two-thirds of the lateral surface and
is ventrally bordered by a well-developed transverse ridge (Fig. 3.1);
a condition also described in the two maxillary fragments UCMP
195193 and UCMP 195194 referred to *Calyptosuchus wellsi* from
UCMP A269 (the Placerias Quarry, Parker, 2018a). In most aeto-
saurs with described maxillae this ridge is prominent except in both
species of *Desmotosuchus* (*D. spurensis* Case, 1920, UMMP 7476,
Case, 1922; *D. smalli*, Small, 2002), *Longosuchus meadei* (TMM
31185-98, Sawin, 1947; Parrish, 1994), *Typothorax coccinarum*
(Heckert et al., 2010; Reyes et al., 2020), and *Kocurypelta sylvestris*
Czepiński et al., 2021, in which the ridge is poorly developed or
absent. Additionally, the transverse ridge in PEFO 49321 continues
anterodorsally, confining the antorbital fossa, and fades distally on
the lateral surface of the dorsal process (Fig. 3.1) similar to the
condition observed in *Aetosauroides scagliai* (Biacchi Brust et al.,
2018; Paes Neto et al., 2021b), *Paratypothorax andressorum*
(Schoch and Desojo, 2016), *Aetosauros ferratus* (Schoch, 2007),
and *Stenomyti huangae* Small and Martz, 2013.

A row of five foramina is present on the ventrolateral surface of
the maxilla that extends parallel to the ventral margin, just dorsal of
the alveolar row (Fig. 3.1). This row of foramina begins 1 cm
posterior of the anterior margin of the anterior process and termi-
nates just posteroventral to the anterior margin of the antorbital
fenestra, indicating that there is not a one-to-one correlation with
the alveoli. In life, these foramina likely transmitted fibers of the
superior alveolar nerve, an extension of the maxillary branch of the

trigeminal nerve (CN V₂) that innervates the alveoli and soft tissues
surrounding the maxilla (George and Holliday, 2013; Lessner and
Holliday, 2020, fig. 10). As in *Stenomyti huangae* (DMNH V.34565;
Small and Martz, 2013), the alveolar row of the maxilla of PEFO
49321 contains nine alveoli with three teeth still in situ (Fig. 3.1, 3.2;
described below). Based on current understanding, only *Neoaeto-
sauroides engaeus* (PVL 4363, Desojo and Baez, 2007; Taborda
et al., 2021), *Aetosauros ferratus* (Schoch, 2007), *Typothorax coccin-
arum* (Reyes et al., 2020), and *Calyptosuchus wellsi* (based on
PEFO 49321) exhibit fewer than 10 tooth positions in their max-
illae. The alveolar row extends far posteriorly onto the posterior
process terminating at the midline of the antorbital fenestra, unlike
Neoaetosauroides engaeus (Desojo and Baez, 2007) and *Kocurypelta
silvestris* (Czepiński et al., 2021), where the alveolar row terminates
more anterior to it.

In medial view, the maxilla bears a medial shelf that runs the
length of the element parallel to and dorsal to the alveolar row
(Fig. 3.2). Anteriorly, on the anterior process, the shelf is bifurcated
by a deep longitudinal groove that terminates dorsal to the third
alveolus (from anterior to posterior). That groove marks the
articulation point for the posteromedial process of the premaxilla
(Fig. 3.2) as observed in *Desmotosuchus smalli* (Small, 2002) and
Stagonolepis olenkae (Sulej, 2010). Dorsally, the medial ridge
exhibits a shallow choanal recess (Witmer, 1997) at the junction
of the anterior and dorsal processes. The medial surface of the
dorsal process exhibits a triangular-shaped articular surface for
its contact with the nasal and lacrimal dorsal to the choanal
recess (Fig. 3.2). The anterior process of the lacrimal fits ante-
roventrally into a slot while the nasal truncates this process
dorsally; this articulation is best observed in *Longosuchus meadei*
(TMM 31185-97, Parrish, 1994, fig. 3). On the posterior process,
the medial shelf is concave ventrally and expands mediolaterally
just posterior to the last alveolus for the contact between the
maxilla and palate.

PEFO 49321 shows no evidence of a pneumatic accessory cavity
at the junction of the dorsal and posterior processes of the maxilla,
posterior to the choanal recess (Fig. 3.2) (Witmer, 1997), similar to
Aetosauroides scagliai (Paes Neto et al., 2021b). A pneumatic
accessory cavity is documented in *Stenomyti huangae* (Small and
Martz, 2013), *Stagonolepis* (Walker, 1961; Sulej, 2010; Parker,
2018b), *Longosuchus meadei* (Parrish, 1994), and *Desmotosuchus*
(Case, 1920; Small, 2002), suggesting that this character may be
phylogenetically informative, as originally proposed by Small
(2002). In medial view, the nine alveoli are equally spaced from
each other and are divided by ventrally directed, well-spaced, sub-
triangular interdental plates (Fig. 3.2), as also observed in *Aetosaur-
oides scagliai* (Paes Neto et al., 2021b). Additionally, the anterior
wall of the first alveolus is not preserved (Fig. 3.2), further indicat-
ing that the anterior extent of the maxilla is not fully preserved.

Jugal. The right jugal of PEFO 49321 is only missing portions of
the mid-body and its anterior margin (Fig. 3.3, 3.4). The element is
~60% the anteroposterior length of the maxilla, which is unlike
Aetosauros ferratus (Schoch, 2007) in which the jugal is shorter in
length, being ~40% of the length of the maxilla. However, we note
that the morphology of *Aetosauros ferratus* is based on an aggregate
of hatchling specimens (SMNS 5220; Teschner et al., 2023), sug-
gesting that proportion between the jugal and maxilla may be
influenced by its skeletal maturity. Anteriorly, the anterodorsal
margin of the jugal is not preserved. Thus, we are unable to
determine if the jugal separates the lacrimal and maxilla posteriorly
and participates in the posterior margin of the antorbital fenestra, a
variable character within the Aetosauria (Parker, 2016a). The

anteroventral margin of the jugal is partially preserved with a posteroventral incision (Fig. 3.3, 3.4). This indicates that the posterior process of the maxilla underlapped the jugal in lateral view as it would have tapered posteroventrally, exhibiting a sinuous, wedge-shaped contact with the jugal as described for *Paratyphothorax andressorum* (Schoch and Desojo, 2016). That condition differs from the prong-like bifurcating contact exhibited by the non-aetosaur aetosauriform *Revueltosaurus callenderi* (PEFO 34561, Parker et al., 2021) and the early-branching aetosaur *Aetosauroides scagliai* (Paes Neto et al., 2021b). Dorsally, the margin is concave and forms the ventral border of the orbit.

The main body of the jugal is anteroposteriorly oriented with a straight ventral margin (Fig. 3.3, 3.4), as observed in *Stenomyti huangae* (Small and Martz, 2013) and both species of *Coahomasuchus* (*C. chathamensis*, Heckert, Fraser, and Schneider, 2017, NCSM 23618; *C. kahleorum*, TMM 31100-437). That condition differs from the strongly downturned jugal observed in *Desmatosuchus* (Case, 1920; Small, 2002) and *Longosuchus meadei* (Parrish, 1994). Posteriorly, the jugal bifurcates into two triangular-shaped processes that participate in the margins of the infratemporal fenestra. The posterodorsal process exhibits an anteroposterior length that is ~50% that of the posteroventral process. The posterodorsal process does not participate in the margins of the orbit, but its inclination indicates that the ventral process of the postorbital tapered anteroventrally along the posterior margin of the orbit (Fig. 3.3, 3.4), a condition commonly observed in aetosaurs except in both species of *Desmatosuchus* (*D. spurensis*, Case, 1922; *D. smalli*, Small, 2002). However, we are unable to ascertain if the postorbital contributes to the margin of the infratemporal fenestra as observed in *Typothorax coccinarum* (Reyes et al., 2020), *Paratyphothorax andressorum* (Schoch and Desojo, 2016), and *Aetosaurus ferratus* (Schoch, 2007) but does not in *Aetosauroides scagliai* (Paes Neto et al., 2021b). The posteroventral process is inclined posteroventrally indicating that the jugal wedged and underlapped the anterior process of the quadratojugal in lateral view (Fig. 3.3–3.5).

The lateral surface of the jugal is ornamented by a continuation of the transverse ridge described in the maxilla (Fig. 3.3). This condition is observed in several aetosaur taxa but not in *Desmatosuchus smalli* (TTU-P 9024, Small, 2002), *Typothorax coccinarum* (PEFO 38001/YPM VP.58121, Reyes et al., 2020), or *Paratyphothorax andressorum* (SMNS 19003, Schoch and Desojo, 2016). The transverse ridge terminates just anterior to the posterior bifurcation of the jugal and does not extend onto the posteroventral process, in contrast to the condition observed in *Stenomyti huangae* (Small and Martz, 2013) and *Coahomasuchus chathamensis* (Heckert et al., 2017). Additionally, there is no evidence of pitting or foramina on the external surface. In medial view, the anterior end of the jugal exhibits a posteriorly oriented, narrow, triangular surface for the medial reception of the ectopterygoid (Fig. 3.4). Ventral to the orbit, the surface is longitudinally depressed with well-delineated dorsal and ventral borders, as observed in *Erpetosuchus* (AMNH 29300, Foffa et al., 2021, fig. 5i), although there is no evidence of pneumatization (Fig. 3.4).

Quadratojugal. The left quadratojugal and quadrate of PEFO 49321 are still in articulation but are coated with an iron-rich mineralization, which inhibits our ability to fully differentiate the two elements and evaluate the nature of their articulation (Fig. 3.5, 3.6). The quadratojugal appears to exhibit an overall L-shape (Fig. 3.5), a condition that aetosaurs share with other pseudosuchians (Paes Neto et al., 2021b). Anteriorly, it is evident that the quadratojugal overlaps the posteroventral process of the jugal, as

observed in *Stenomyti huangae* (Small and Martz, 2013), but unlike that taxon the quadratojugal inhibits the jugal from framing the entire posteroventral margin of the cranium. Thus, the contact observed in PEFO 49321 resembles that of *Stagonolepis robertsoni* (Walker, 1961, fig. 2). As a result of the overlapping contact between the quadratojugal and jugal, the dorsal margin of the anterior process of the quadratojugal forms part of the ventral margin of the infratemporal fenestra, and the posterodorsal process of the jugal participates in the inclined anterior margin of the opening. Based on this information, the infratemporal fenestra most likely had an ovate shape in lateral view.

The lateral surface of the anterior process bears a shallow fossa around the margin of the infratemporal fenestra, which is separated from a deep pit by a ridge (Fig. 3.5). Because of the preservation of the element, it is difficult to ascertain whether the pit and ridge are true anatomical features or a result of taphonomic alteration. The dorsal process is dorsoventrally short, less than 50% of the anteroposterior length of the anterior process. The lateral surface is slightly depressed near the dorsal tip (Fig. 2.11, 2.12), marking the point of contact between the quadratojugal and ventral process of the squamosal. If this interpretation is accurate, then the squamosal would have participated in the margins of the infratemporal fenestra, a condition documented in most aetosaurs except *Aetosauroides scagliai* (Paes Neto et al., 2021b), *Coahomasuchus chathamensis* (Heckert et al., 2017), *Paratyphothorax andressorum* (Schoch and Desojo, 2016), and *Aetosaurus ferratus* (Schoch, 2007).

Quadrate. The left quadrate is articulated with the left quadratojugal. The element is only represented by its ventral half, so the head of the quadrate is not preserved (Fig. 3.6). The lateral wing (sensu Walker, 1961) is co-ossified to the medial surface of the quadratojugal, but the medial wing is not preserved. The quadrate crest, which divides both wings, is discernible but faint, unlike the well-developed strut in *Aetosauroides scagliai* (Paes Neto et al., 2021b, fig. 12). The crest is situated medially, dorsal to the medial condyle of the quadrate. Lateral to the quadrate crest, there is a shallow pit marking the perforation of the quadrate foramen. The margins of the foramen appear to be formed by both the quadratojugal and the lateral wing of the quadrate (Fig. 3.6), a condition observed in most aetosaurs (Parker, 2016a; Schoch and Desojo, 2016) except *Coahomasuchus kahleorum* (TMM 31100-437) and *Aetosaurus ferratus* (Schoch, 2007) in which the foramen is restricted to the lateral wing of the quadrate. However, there is no evidence of a fossa located on the external surface of the lateral wing just posterior to the quadrate foramen. Ventrally, the convex quadrate condyles are separated by an anteroposteriorly oriented groove. The lateral condyle is larger than the medial condyle and expanded anteromedially, similar to that of *Desmatosuchus smalli* (Small, 2002). In posterior view, the medial condyle is positioned more dorsally than the lateral condyle (Fig. 3.6).

Laterosphenoid. PEFO 49321 preserves the first unambiguous braincase element that is referred to *Calyptosuchus wellsi*. The left laterosphenoid is partially preserved, missing its anterior extent, and is coated in the same iron-rich mineralization present on some of the cranial bones of PEFO 49321 (Fig. 3.7, 3.8). Laterally, the surface is smooth but exhibits a distinct dorsoventrally oriented cotylar crest (Fig. 3.8) similar to *Stagonolepis olenkae* (ZPAL ABIII/466/17, Sulej, 2010). Two shallow foramina are present anterior to the cotylar crest (Fig. 3.8). The dorsal foramen marks the exit for the anterior cerebral vein (Walker, 1990; Sulej, 2010; = ophthalmic artery, Small, 2002; Clark et al., 2010; = transversotrigeminal vein, von Baczko et al., 2021), and the ventral foramen marks the exit of the trochlear nerve (CN IV). The ventral margin of

the laterosphenoid exhibits a well-incised notch for the exit of the optic nerve (CN II) anteroventral to the cotylar crest.

Medially, the laterosphenoid exhibits a rugose surface with shallow fossae that are separated by curved ridges (Fig. 3.7). This texture is reminiscent of the contact between the anterior wall of the braincase and the dural envelope, which encompasses the meninges, encephalon, associated nerves, blood vessels, and sinuses (Witmer et al., 2008). The medial foramina for the exits of the trochlear nerve (CN IV) and anterior cerebral vein are positioned within a dorsoventrally oriented fossa just dorsal of the notch for the optic nerve (CN II) (Fig. 3.7). Dorsally, the capitate process of the laterosphenoid, which contacts the parietal anteroventrally, is short and mediolaterally compressed. The anterior and posterior portions of the laterosphenoid are not preserved. Thus, we are unable to determine if the element participated in the margin of the foramen marking the external exit of the trigeminal nerve (CN V), a feature that is variable across the Aetosauria. The external exit of the trigeminal nerve can be enclosed by both the prootic and laterosphenoid, as observed in the early-branching aetosaur *Aetosauroides scagliai* (MCP-3450-PV; Paes Neto et al., 2021c) and *Desmatosuchus smalli* (TTU-P 9420, Small, 2002; UCMP 27410, von Baczko et al., 2021), a condition that is shared with the aetosauriforms *Parringtonia gracilis* von Huene, 1939 (NMT RB426, Nesbitt et al., 2017, figs. 4, 5) and, hypothetically, *Revueltosaurus callenderi* (PEFO 34561, Parker et al., 2021, fig. 6e). Alternatively, the foramen can be completely enclosed by the prootic as observed in *Scutarx deltatylos* (PEFO 34616, Parker, 2016b) and *Stagonolepis olenkae* (ZPAL AbIII/466/17, Sulej, 2010), a condition shared with the rauisuchids *Postosuchus kirkpatricki* (TTU-P 9002, Weinbaum, 2011, fig. 24).

Mandible description

Prior to the discovery of PEFO 49321, our understanding of the mandible of *Calyptosuchus wellsi* was based solely on one partially preserved dentary that was associated with an individual of *C. wellsi* (UCMP 27225, Parker, 2018a). PEFO 49321 preserves the posterior portion of the right mandible in articulation (Fig. 3.9, 3.10) and is not coated by the iron-rich mineralization that is present on several other elements from PFV 467, thus allowing the contacts of the elements to be differentiated.

Surangular. The surangular is missing a large portion of its anterodorsal process (Fig. 3.9, 3.10). As typically observed in aetosaurs (Desojo et al., 2013), the surangular arches posteriorly over the external mandibular fenestra and becomes dorsoventrally tall. The anterior process of the surangular is anteroposteriorly long, with a concave ventral margin that forms the dorsal border of the external mandibular fenestra. The process is mediolaterally compressed in contrast to the condition observed in *Revueltosaurus callenderi* (Parker et al., 2021) and erpetosuchids (Benton and Walker, 2002) in which it is expanded (= surangular shelf). A fragment of this process preserves a prominent anteroposteriorly broad tubercle on the dorsal margin of the element near the midline of the external mandibular fenestra (Fig. 3.9, 3.10), a feature documented in most taxa with a preserved surangular except *Aetosaurus ferratus* (SMNS 5770, Schoch, 2007), *Desmatosuchus smalli* (TTU-P 9024, Small, 2002), and *Coahomasuchus kahleorum* (TMM 31100-437, Parker, 2016a).

The lateral surface is smooth, unlike the ornamented surface observed in *Acaenasuchus geoffreyi* Long and Murry, 1995 (UCMP 293853, Marsh et al., 2020), and it lacks the surangular ridge that is present in *Revueltosaurus callenderi* (Parker et al., 2021) and

other archosauriforms (Ezcurra, 2016). As the surangular becomes dorsoventrally broad, a small process descends anteroventrally (Fig. 3.9). Although it is not fully preserved, it likely participated in forming the posteroventral margin of the external mandibular fenestra, as observed in *Stagonolepis* (Walker, 1961; Sulej, 2010). The angular is not preserved, however the surangular indicates that these two elements exhibited an anteroposteriorly long (Fig. 3.10), straight contact as the angular tapered posteriorly similar to that of *Longosuchus meadei* (TMM 31185-97, Parrish, 1994). Ventrally, the contact wraps medially on the surangular and terminates at the retroarticular process. The posterior portion of the surangular bears a posteroventrally inclined elliptical surangular foramen. This foramen likely transmitted fibers of the inferior alveolar nerve, a derivative of the mandibular branch of the trigeminal nerve (CN V₃) that innervates the lower jaw (Desojo and Báez, 2007; Lessner and Holliday, 2020). The surangular foramen exits ventromedially on the medial surangular shelf. Medially, that shelf is anteroposteriorly oriented, dorsoventrally broad, and laterally concave. Posteriorly, the surangular exhibits a dorsoventrally curved contact with the articular in lateral view (Fig. 3.9). The surangular only contributes slightly to the retroarticular process, as observed in *Typhothorax coccinarum* (Reyes et al., 2020).

Articular and prearticular. The right articular and posterior portion of the prearticular are co-ossified in PEFO 49321 (Fig. 3.9, 3.10). The articular is complete. The posterior portion comprises most of the retroarticular process and is anteroposteriorly longer than dorsoventrally tall, as observed in *Typhothorax coccinarum* (Reyes et al., 2020) and *Desmatosuchus spurensis* (MNA V9300, Parker, 2008a). Posterodorsally, the articular exhibits a small dorsally oriented triangular process (Fig. 3.10). The glenoid of the articular is mediolaterally broad for its articulation with the quadrate. The articulation surface for the lateral condyle of the quadrate is concave, mediolaterally compressed, and anteroposteriorly elongate, with a medial inclination in dorsal view. The medial articular surface of the glenoid is concave, circular in dorsal view, and is separated from the lateral articulation surface by a low ridge. Medially, the articular exhibits an anteroposteriorly oriented curved contact with the posterior process of the prearticular (Fig. 3.10). This contact terminates ventral to the glenoid, thus does not extend the entire length of the retroarticular process. Ventrally, the prearticular exhibits an elongate contact with the surangular and contacts the posteriorly tapering process of the angular medially, as observed in *Longosuchus meadei* (Parrish, 1994).

Dentition description

PEFO 49321 preserves several complete teeth, some of which are still in their respective alveoli within the maxillae (Fig. 3.1, 3.2). Because PEFO 49321 does not preserve the dentary, we interpret the isolated teeth as belonging to the preserved maxillae because they were found in proximity to each other. Additionally, if these teeth were derived from a dentary, they would likely be identical to those of the maxilla because most aetosaurs exhibit homodont dentition except *Typhothorax coccinarum* (Reyes et al., 2020). The isolated and in-situ teeth within the right maxilla are well preserved, being complete and relatively undistorted. The general anatomy of the dentition is best documented by an isolated left maxillary tooth (Fig. 3.11–3.14), which will serve as the main reference for the following description.

Maxillary teeth. The maxillary teeth of PEFO 49321 are bulbous, exhibit thecodont implantation (sensu Bertin et al., 2018), and are

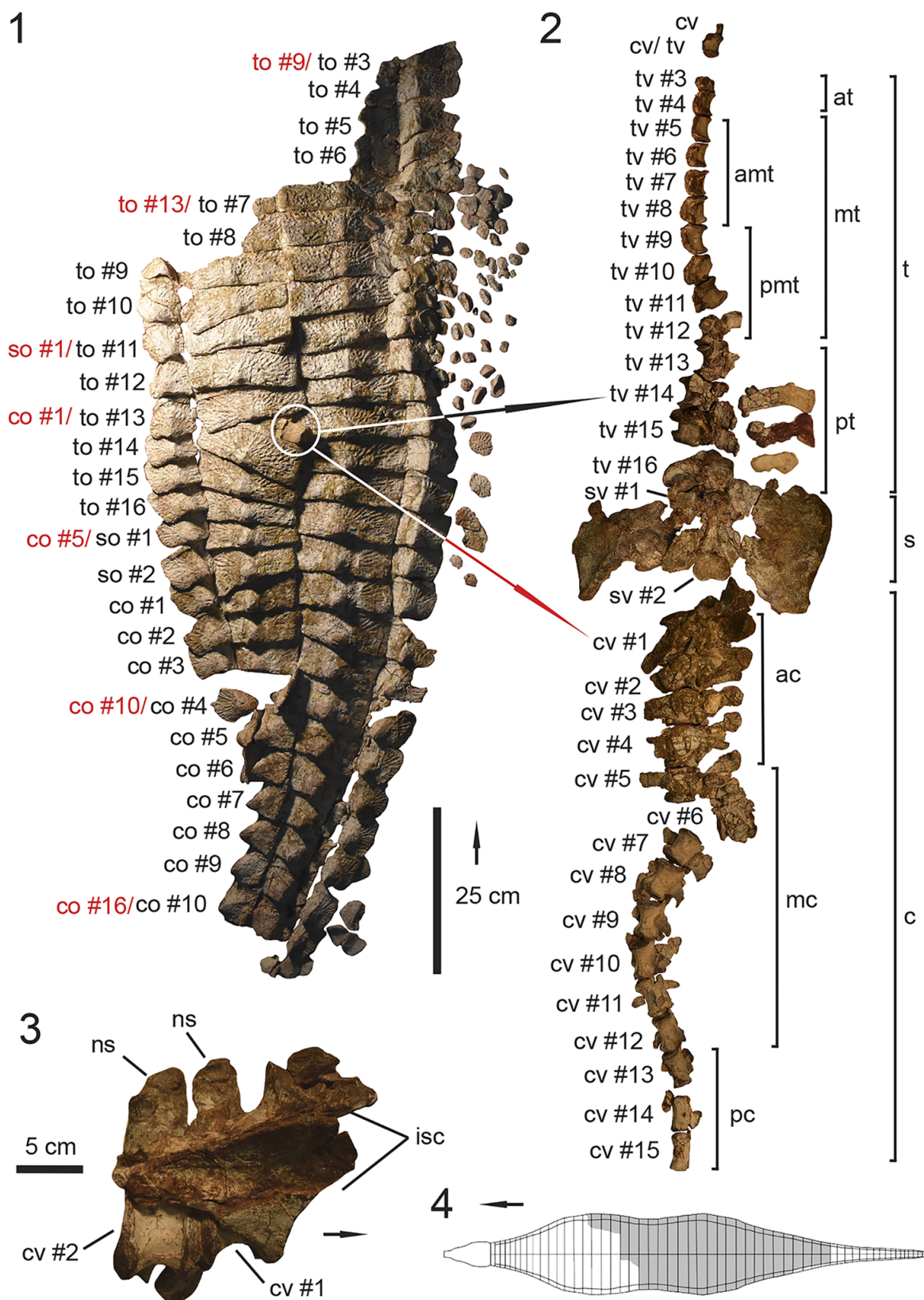


Figure 4. UMM 13950, holotype specimen of *Calyptosuchus welllesi*. (1) Articulated dorsal carapace in dorsal view; (2) associated vertebral column with pelvis in dorsal view in approximate anatomical position to the dorsal carapace in (1); (3) anteriormost caudal vertebrae with articulated ischia; (4) schematic of the aetosaurian dorsal carapace in dorsal view, where gray indicates regions preserved in UMM 13950. Anatomical interpretations based on this study are labeled in black and previous interpretations based on Parker (2018a), following those of Case (1932), are labeled in red, arrows also follow color labels, accordingly. ac = anterior caudal region; amt = anterior mid-trunk region; at = anterior trunk region; c = caudal region; co = caudal osteoderm; cv = caudal vertebra; isc = ischia; mc = mid-caudal region; mt = mid-trunk region; ns = neural spine; pc = posterior-caudal region; pmt = posterior mid-trunk region; pt = posterior-trunk region; s = sacral region; so = sacral osteoderm; sv = sacral vertebra; t = trunk region; to = trunk osteoderm; tv = trunk vertebra. Arrows indicate anterior direction.

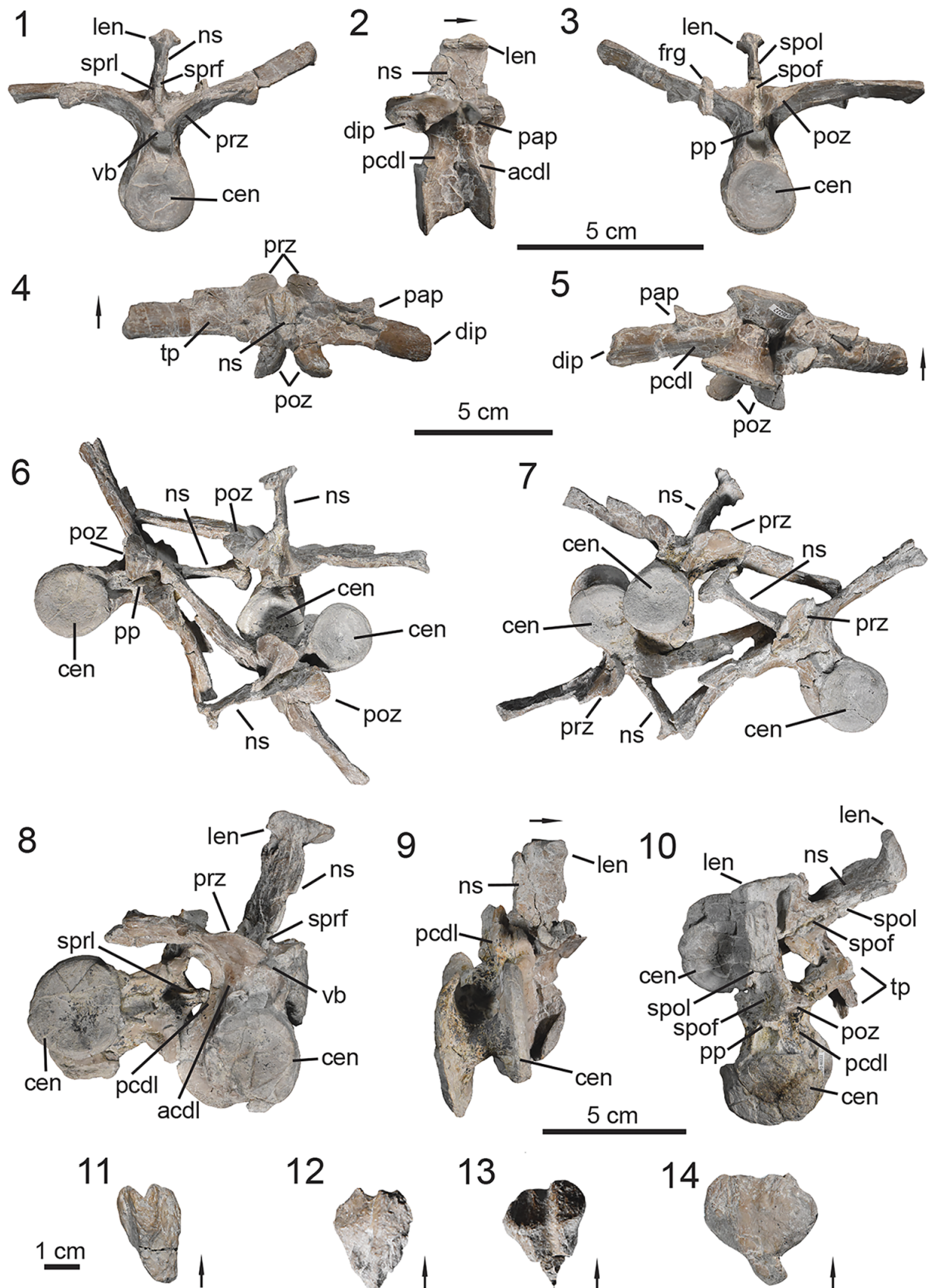


Figure 5. PEFO 46222, associated trunk vertebrae. (1–5, 11) Trunk vertebra #6; (6, 7, 12, 13) trunk vertebrae #10–12; (8–10, 14) trunk vertebrae #15–16; (11–14) lateral expansions of neural spines range. (1, 7, 8) Anterior views, (3, 6, 10) posterior views, (11–14) dorsal views, (5, 9) ventral views, (2, 9) lateral views. acdl = anterior centrodiapophyseal lamina; cen = centrum; dip = diapophysis; frg = bone fragment; len = lateral expansion of neural spine; ns = neural spine; pap = parapophysis; pcdl = posterior centrodiapophyseal lamina; pp = posteriorly projecting process; poz = postzygapophysis; prz = prezygapophysis; spol = spinopostzygapophyseal lamina; spof = spinopostzygapophyseal fossa; sprl = spinoprezygapophyseal lamina; tp = transverse process; vb = ventral bar. Arrows indicate anterior direction.

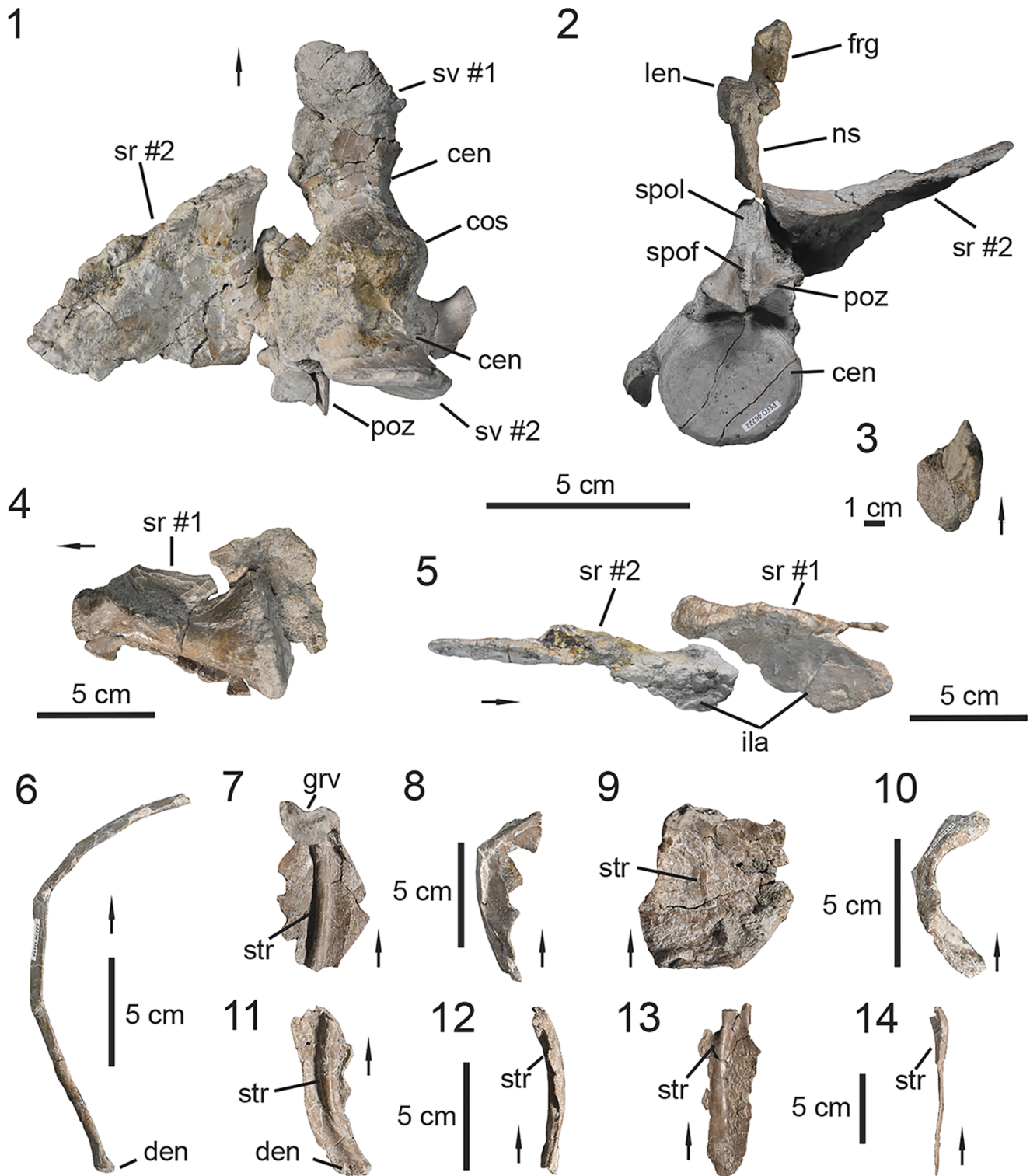


Figure 6. PEFO 46222, associated sacrum and ribs. (1, 2) Co-ossified sacral vertebrae; (3) lateral expansion of sacral vertebra #2 neural spine; (4, 5) sacral ribs; (6–14) trunk ribs. (1, 4) Ventral views, (2) posterior view, (3) dorsal view, (5) lateral/distal view, (7, 9, 11, 13) medial views, (6, 8, 10, 12, 14) anterior/posterior views. cen = centrum; cos = co-ossified sacral centra; den = distal end; frg = bone fragment; grv = groove; ila = ilium articulation; len = lateral expansion of neural spine; ns = neural spine; poz = postzygapophysis; spof = spinopostzygapophyseal fossa; spol = spinopostzygapophyseal lamina; sr = sacral rib; sv = sacral vertebra; str = strut. Arrows indicate anterior direction for vertebrae and proximal direction for ribs.

uniform in their anatomy, but become proportionately smaller distally in the tooth row. Unlike *Coahoamasuchus kahleorum* (TMM 31100-437, Parker, 2016a), the base of the teeth are slightly constricted (Fig. 3.13) but not to the extent observed in

Desmatosuchus smalli (TTU-P 9420, Small, 2002) or *Neoaetosaurus oides engaeus* (PULR 108, Desojo and Báez, 2007; Taborda et al., 2021). The mesiodistal width of the teeth is relatively unchanged until halfway between the base and apex. Apical to that point, the

distal margin remains straight with a slight mesial inclination until it reaches the apex, while the medial margin curves distally (Fig. 3.11). This results in the crown exhibiting a curved, distally oriented apex. However, the teeth are not truly recurved like those of *Aetosauroides scagliai* (UFSM 11505, Biacchi Brust et al., 2018; MCN-PV 2347, MCP-3450-PV, Paes Neto et al., 2021b) and *Coahomasuchus kahleorum* (TMM 31100-437, Parker, 2016a) because the apex is not positioned distal to the distal basal margin; instead, it is positioned just mesial to it (Fig. 3.11, 3.12). The curvature of the teeth in PEFO 49321 is most similar to the condition observed in *Aetosauros ferratus* (Schoch, 2007). There is no evidence of vertical fluting on the enamel surface of the teeth, which is observed in the dentition of *Stagonolepis olenkae* (ZPAL AbII/1995, Sulej, 2010) and *Stenomyti huangae* (DMNH V.60708, Small and Martz, 2013). At the point that the mesial and distal margins become confluent, the margins exhibit fine serrations (Fig. 3.14) composed of small triangular-shaped denticles similar to those of *Stagonolepis olenkae* (ZPAL AbII/1995, Sulej, 2010), but contrary to those observed in *Revueltosaurus callenderi* (PEFO 34561, Parker et al., 2021) and *Acaenasuchus geoffreyi* (PEFO 43699, Marsh et al., 2020) in which the denticles are large and round. The serrated edge forms the distal margin of the crown. However, on the mesial margin, the serrations originate on the lingual surface and curve onto the mesial margin of the crown. The crown exhibits a lingually oriented concave curvature near the apex similar to that of *Aetosauroides scagliai* (Paes Neto et al., 2021b). The labial surface of the crown apex is relatively more curved than the lingual surface (Fig. 3.13). In cross-section the teeth are mesiodistally ovate, but not to the extent observed in ziphodont teeth, which are labiolingually compressed. There is no evidence of tooth replacement in this specimen.

Vertebrae description

PEFO 46222 preserves a total of 13 vertebrae. Most of the vertebrae were collected semi-articulated within a 1-m² quadrant. The trunk vertebrae are poorly preserved in the holotype specimen UMMP 13950, thus the preserved vertebral column of PEFO 46222 provides new morphological understanding of the trunk series in *Calyptosuchus wellesi*.

Trunk vertebrae. PEFO 46222 preserves a total of 11 trunk vertebrae (= dorsal vertebrae; Parker, 2008a; Heckert et al., 2010; Desojo et al., 2012, 2013). The discovery of partial or relatively complete vertebral columns of various aetosaur taxa indicates that on average the trunk series in aetosaurs is composed of 16 vertebrae and exhibits a 1:1 ratio with the dorsal carapace osteoderms (Parker, 2008a). The holotype specimen (Fig. 4.2; UMMP 13950) preserves 14 trunk vertebrae (i.e., tv #3–16), but most of the vertebrae (i.e., tv #3–11) are poorly preserved and are only represented by their centra (Fig. 4.2). PEFO 46222 preserves most of the trunk vertebral series (Fig. 5); the most anterior vertebra represents tv #6 from the anterior middle trunk region (Fig. 5.1–5.5). The middle trunk vertebrae (i.e., tv #6–12) are well preserved with little taphonomic distortion, unlike those from the posterior trunk (i.e., tv #13–16), which are missing their respective transverse processes. Thus, PEFO 46222 allows us to assess the anatomy of trunk vertebrae that are missing or poorly preserved in UMMP 13950.

In general, the centra are amphicoelous with circular articular faces. The centra become proportionally larger towards the sacral region and exhibit a more ovate shape in the posteriormost trunk vertebrae (Fig. 5.8–5.10; tv #15–16). The faces of the centra exhibit well-developed rims and are positioned roughly in the same longitudinal plane (Fig. 5.2), unlike *Stagonolepis robertsoni* (Walker,

1961) and *Scutarx deltatylus* (Parker, 2016b) in which the posterior face is more dorsally offset than the anterior one in the more posterior vertebrae. As observed in UMMP 13950, the body of the centrum is transversely compressed and concave with a smooth surface lacking a ventral keel at the midline (Fig. 5.5, 5.9). These features give the centra a spool shape, which is characteristic among aetosaurs (Desojo et al., 2013). Laterally, the body of the centra are smooth, (Fig. 5.2), as observed in UMMP 13950, UMMP 7470, and several referred vertebrae from UCMP A269 (UCMP 139694, UCMP 139796, UCMP 139702; Parker, 2018a). There is no evidence of an ovate fossa on the lateral surface of the centrum in PEFO 46222, which is a feature that is subject to intraspecific variation and can become more developed through skeletal maturity, as observed in *Aetosauroides scagliai* (Paes Neto et al., 2021c). As observed in UMMP 13950, the trunk centra become more anteroposteriorly compressed in lateral view from the middle trunk to the posterior trunk in which the transverse width of the centrum becomes proportionately larger than the anteroposterior length of the body of the centrum (Fig. 5.2, 5.9). Anteriorly, the neural canal is transversely wider than it is dorsoventrally tall, giving the opening a quadrangular shape (Fig. 5.1). The inverse condition is exhibited by the posterior end of the neural canal in which the opening is dorsoventrally taller than it is transversely wide, giving it an ovate shape (Fig. 5.3).

The trunk vertebrae of PEFO 46222 exhibit both anterior and posterior centrodiaiphyseal lamina (sensu Wilson, 1999; = infra-diaiphyseal lamina, Desojo and Ezcurra, 2011), as observed in UMMP 7470 (Parker, 2018a), *Aetosauroides scagliai* (Desojo and Ezcurra, 2011; Paes-Neto et al., 2021a), *Scutarx deltatylus* (Parker, 2016b), and *Desmatosuchus spurensis* (Parker, 2008a). This condition is considered plesiomorphic within Archosauroomorpha (Ezcurra, 2016). In PEFO 46222 the posterior centrodiaiphyseal lamina is weakly developed in the middle trunk region (Fig. 5.2) and becomes more prominent in the posterior trunk vertebrae (Fig. 5.8), which also appears to be the case in UMMP 13950. The parapophyses are situated on the transverse process in all the known trunk vertebrae, indicating that no transitional cervical/trunk vertebrae are preserved in PEFO 46222 (Fig. 5.1–5.7). The positioning of the parapophyses on the transverse process is typical of aetosaurians (Desojo et al., 2013), a condition shared with the trunk vertebrae in extant crocodyliformes such as *Alligator mississippiensis* (Daudin, 1802) Frey, 1988, figs. 6, 7) and *Alligator sinensis* (Fauvel, 1879) (Cong et al., 1998, fig. 80). In general, the transverse processes project laterally, nearly perpendicular to the neural spine. They are anteroposteriorly broad with flat dorsal surfaces and transversely wide, around 2.0–2.5 times the transverse width of the centrum (Fig. 5.6, 5.7). The posterior trunk vertebrae #15–16 (Fig. 5.8–5.10) do not preserve enough of their transverse processes, so we are not able to confirm whether the ribs of PEFO 46222 are co-ossified to the transverse processes as described in *Scutarx deltatylus* (PEFO 34045, Parker, 2016b), *Desmatosuchus spurensis* (MNA V9300, Parker, 2008a), and the holotype of *Calyptosuchus wellesi* (UMMP 13950, Case, 1932; Long and Murry, 1995; Parker, 2018a). The postzygadiaiphyseal lamina has deep associated fossae on the dorsal and ventral surfaces of the transverse process in the middle trunk vertebrae of UMMP 7470 (Parker, 2018a, fig. 7). However, postzygadiaiphyseal lamina is absent in the trunk vertebrae of PEFO 46222 and there is no clear evidence of its presence in the holotype specimen (UMMP 13950) due to the poor preservation of the trunk vertebrae.

The vertebrae of PEFO 46222 lack hyposphene-hypantrum accessory articulations similar to other specimens of *Calyptosuchus wellesi* (Parker, 2018a). Hyposphene-hypantrum accessory

articulations are documented within *Desmotosuchus* (Parker, 2005, 2008a) and *Aetobarbakinoides brasiliensis* (Desojo et al., 2012). The prezygapophyses are inclined $\sim 40^\circ$ from horizontal and are connected at the midline by a small transversely flat shelf (= ventral bar, Parker, 2018a). This shelf marks the floor of the spinoprezygapophyseal fossa (sensu Wilson et al., 2011) at the base of the neural spine (Fig. 5.1). The postzygapophyses are also inclined $\sim 40^\circ$ from the horizontal and project slightly beyond the posterior face of the centrum. At the midline between the postzygapophyses there is a posteriorly oriented projection that rests on top of the ventral bar of the succeeding vertebra as in *Scutarx deltatylus* (Parker, 2016b). Additionally, there is a deep spinopostzygapophyseal fossa (sensu Wilson et al., 2011) between the postzygapophyses at the base of the neural spine, dorsal to the posteriorly oriented process.

The main body of the neural spine is transversely compressed and anteroposteriorly broad. It becomes proportionally broader sequentially in the vertebral column until it surpasses the anteroposterior length of the centra in trunk vertebrae #15–16 (Fig. 5.8–5.10). In the middle trunk region, the neural spines are 1.41–1.68 times taller dorsoventrally than the centrum (Fig. 5.1–5.7), while in the posterior trunk region they are 1.30–1.33 times taller. The neural spine exhibits both spinoprezygapophyseal (Fig. 5.1, 5.8) and spinopostzygapophyseal laminae (Fig. 5.3, 5.10), as observed in UMMP 7470 (Parker, 2018a) and UMMP 13950. Dorsally, the neural spine expands into a transversely broad and flat table-like structure. In dorsal view the ‘table’ exhibits a heart-shaped outline with the tapered end pointing posteriorly. The transverse width of the tops of the neural spines proportionately increase relative to the transverse width of the centrum down the vertebral column (Fig. 5.11–5.14). Overall, the trunk vertebrae become more robust towards the sacrum.

Sacral vertebrae. The previously known sacral anatomy of *Calyptosuchus wellsi* is based on UMMP 7470 and UMMP 13950, although the elements are distorted in the latter specimen (Case, 1922, 1929, 1932). The sacral vertebrae of PEFO 46222 are not well preserved (Fig. 6.1) and were recovered in series with the posterior trunk vertebrae (Figs. 5.8–5.10, S1). The body of the centrum is crushed and distorted anteriorly in sacral vertebra #1 (Fig. 6.1), but its anterior face is still mostly intact. The slightly ovate anterior face of sacral vertebra #1 is completely exposed and disarticulated from the posteriormost trunk vertebra (Fig. 5.8–5.10, S1). The neural arch of the anterior sacral vertebra is not preserved, and only a disarticulated sacral rib remains (Fig. 6.4, described below).

Sacral vertebra #2 of PEFO 46222 (Fig. 6.1, 6.2) is robust and well preserved, preserving the neural arch with an articulated sacral rib (described below) and a relatively uncrushed centrum with a slightly ovate articular face. Additionally, the centrum body is anteroposteriorly longer than the transverse width of the articular surface, unlike the more truncated posterior trunk vertebrae (Fig. 5.8, 5.9). The prezygapophyses are not preserved but the postzygapophyses are inclined approximately 30° from the horizontal and project slightly beyond the posterior face of the centrum (Fig. 6.1, 6.2). No posteriorly oriented ventral projection is discernable at the midline of the postzygapophyses. The neural spine is robust and exhibits a posterior spinopostzygapophyseal lamina and spinopostzygapophyseal fossa at its base (Fig. 6.2; sensu Wilson et al., 2011). Although the distal half of the neural spine is broken into a separate piece, when articulated the neural spine is 1.6 times taller than the centrum, a proportion similar to those of some middle trunk vertebrae. The dorsal transverse expansion of the neural spine (Fig. 6.3) is broad, robust, and more ovate than those in the trunk vertebrae, with a transverse width that is half that of the articular face of the centrum.

The centrum of sacral vertebra #1 (Fig. 6.1) is completely disarticulated from that of the posteriormost trunk vertebra (i.e., tv #16) (Fig. 5.8–5.10) in PEFO 46222, which is also observed in UMMP 13950 and UMMP 7470 (Case, 1932; Parker, 2018a). This indicates that these two vertebrae were not co-ossified to each other in PEFO 46222. Co-ossification of the posterior trunk vertebra with the first sacral vertebra (= dorsosacral, Griffin et al., 2017) has only been reported in taxa within the more inclusive clade Desmotosuchini (Long and Murry, 1995; Parker, 2008a, 2016a; Nesbitt, 2011; Griffin et al., 2017). Additionally, incorporation of the posteriormost trunk vertebra into the sacrum does not occur in the early-branching aetosaur *Aetosauroides scagliai* (Casamiquela, 1967; Heckert and Lucas, 2002a), which suggests that the incorporation of the dorsosacral in desmotosuchins is a derived state. In PEFO 46222 the two sacral vertebrae are ankylosed at the centra faces (Fig. 6.1). Among aetosaurs, co-ossification of the sacral vertebrae has only been documented in *Desmotosuchus smalli* (TTU-P 9419, Parker, 2005), *Desmotosuchus spurensis* (MNA V9300, TTU-P 10008, Long and Murry, 1995; Parker, 2008a), and *Longosuchus meadei* (TMM 31100-236).

Rib description

PEFO 46222 preserves several ribs from the same anatomical regions as the preserved vertebrae. Most of the ribs are disarticulated, however no trunk ribs are complete.

Trunk ribs. Several trunk ribs were intermixed with the semi-articulated trunk vertebrae recovered with PEFO 46222. The ribs are neither complete nor do they preserve the capitulum or tuberculum. We describe the general anatomy of the trunk ribs of *Calyptosuchus wellsi* based on PEFO 46222 and UMMP 13950. Proximally, the capitulum and tuberculum are differentiated by a transversely oriented shallow groove in dorsolateral view (Fig. 6.7). In proximal cross-section, the bone thickens dorsoventrally just anterior to the groove. Based on comparisons to *Scutarx deltatylus* (PEFO 34045, Parker, 2016b), this thickening is associated with the capitulum. The ribs flare out transversely from the transverse process, gradually descend ventrally, and arch more medially towards the distal end until they terminate at an ovate tip (Fig. 6.6). We note that there is one rib fragment with a strongly arched proximal end (Fig. 6.10). This suggests that the ribs may become strongly arched posteriorly in the trunk, as observed in *Typhothorax coccinarum* (PEFO 42506, Parker et al., 2023), however we cannot confirm this based on the preserved material of PEFO 46222.

The ribs are anteroposteriorly broad proximally with a compressed dorsolateral surface throughout the shaft. Ventromedially, there is variation between the preserved rib fragments near the proximal end. In the more complete fragment, the medial surface exhibits a well-developed strut near the proximal end with thin, gracile flanges extending towards the margins (Fig. 6.7). It is evident that the flanges and strut are confluent near the distal end of the rib, where the surface is flat, and the rib body becomes mediolaterally compressed (Fig. 6.11–6.14). This thin flaring of the bone near the proximal end of the rib is more pronounced in other fragments (Fig. 6.9, 6.10), suggesting that this happens sequentially towards the posterior region of the trunk. This condition is also observed in UMMP 13950 and is documented in *Desmotosuchus spurensis*, where the trunk (= dorsal) ribs become more expanded and thinner near the proximal end in the more posteriorly positioned trunk ribs (Parker, 2008a).

Sacral ribs. The anatomy of the sacral ribs in *Calyptosuchus wellsi* was briefly described by Case (1932) and Parker (2018a), however PEFO 46222 preserves both sacral ribs, allowing for a more

thorough description of their anatomy. The right sacral rib of sacral vertebra #1 (= anterior) is preserved but not attached to the centrum (Fig. 6.4, 6.5), but the left sacral rib of sacral vertebra #2 (= posterior) is still in articulation. Based on the articulated sacral rib, the sacral ribs are not shared between the two sacral vertebrae, but rather they are each restricted to a single vertebra (Nesbitt, 2011, character 208). Because of poor preservation, we cannot determine how the anterior sacral rib contacts the main body of an anterior sacral vertebra. However, based on the in-situ articulated sacral rib and UMMP 7470, the ribs were attached dorsolaterally on the centrum and partially on the ventral portion of the neural spine (Fig. 6.1). The anterior sacral rib was damaged during excavation, resulting in partial loss of the thin flange near the proximal end (Fig. 6.4; PEFO 46222). In dorsal view, the surface is flat and dorsoventrally broad. In ventral view, there is a well-developed and robust strut running the transverse width of the rib (Fig. 6.4). The strut is concave, giving the rib a strongly bowed appearance that opens ventrally in anterior/posterior view. In lateral view there is a deep groove that separates the ventral strut from the anteroposteriorly expanded dorsal sheet of bone (Fig. 6.5). Distally, the anterior sacral rib (for sacral #1) exhibits a transversely ovate articulation surface that is dorsoventrally thickened (Fig. 6.5). Thus, the anterior sacral rib has a large, robust contact with the medial surface of the ilium. This contact occurs just dorsal to the pubic peduncle, ventral to the preacetabular process, and is slightly shared with the posterior sacral rib. Additionally, there is a thin sheet of bone that dorsally overhangs the articulation surface and contacts the ilium (Fig. 6.4).

The left posterior sacral rib is complete and well preserved. The rib is anteroposteriorly expanded distally giving it a subtriangular shape in dorsal/ventral view (Fig. 6.1). Additionally, it is dorsoventrally thickest anteriorly and gradually thins posteriorly (Fig. 6.5), as seen in UMMP 7470 (Case, 1929). In the distal cross-section, the articulation surface is dorsoventrally thick anteriorly, where it partially shares the articulation surface of the anterior sacral rib (Fig. 6.5). This was described and well figured by Walker (1961, fig. 9) for *Stagonolepis robertsoni*. Because the posterior sacral rib becomes anteroposteriorly expanded distally, it exhibits a broad articulation with the ilium. This articulation extends posterodorsally on the medial surface of the ilium, terminating ventral to the postacetabular process. The posterior sacral rib is not bowed like the anterior sacral rib, nor does it exhibit a well-developed strut in ventral view. Overall, the anatomy of the sacral ribs and their contact with the ilium in *Calyptosuchus wellesi* resembles that of *Stagonolepis robertsoni* (Walker, 1961, fig. 9).

Pelvis description

PEFO 46222 preserves most of the pelvis, except the proximal portion of the left pubis. All the elements are disarticulated. Most of them were collected next to the associated sacral vertebrae.

Ilium. PEFO 46222 preserves both ilia. The right ilium is well preserved and serves as the main reference for the anatomical description of the element (Fig. 7). The left ilium is partly preserved and was accidentally damaged during excavation (i.e., found unexpectedly with a pickaxe while removing overburden). This resulted in the acetabular rim, ischiac peduncle, and part of the postacetabular process to be broken, and the breaks are delineated by fresh surfaces. The preacetabular process extends anteriorly but not beyond the anterior margin of the pubic peduncle, similar to the condition in *Scutarx deltatylus* (Parker, 2016b) and UMMP 7470 (Case, 1929). In the referred ilium UCMP 25941 from UCMP A269, the preacetabular process is positioned just dorsal to the pubic

peduncle (Long and Murry, 1995; Parker, 2018a), unlike the preacetabular process of *Neoaetosauroides engaeus*, which extends far anteriorly of the pubic peduncle (Desojo and Báez, 2005). The preacetabular process is a finger-like projection that hooks anteroventrally (Fig. 7.1). This resembles that of UMMP 7470 (Case, 1929) but is unlike that of UCMP 25941, the specimen from UCMP A269 (Long and Murry, 1995; Parker, 2018a), which is more triangular and robust in lateral view. The finger-like anatomy of PEFO 46222 is also shared with the early-branching *Aetosauroides scagliai* (PVL 2073, Casamiquela, 1967; Heckert and Lucas, 2002a), *Aetosaurus ferratus* (Schoch, 2007), and ?*Lucasuchus hunti* Long and Murry, 1995 (TMM 31100-1). In lateral view, the outline of the ilium between the preacetabular process and pubic peduncle is U-shaped (Fig. 7.1), as seen in UMMP 7470 (Case, 1929), but unlike that of UCMP 25941, which is more V-shaped. Although crushed, the ilium in the holotype specimen of *Calyptosuchus wellesi* (UMMP 13950, Case, 1932; Parker, 2018a) exhibits a reminiscent U-shape outline between the pubic peduncle and preacetabular process (Parker, 2018a, fig. 9).

Anteroposteriorly, the dorsal margin of the iliac blade ascends gradually from the preacetabular process to the postacetabular process and becomes slightly concave dorsal to the iliac body. The dorsal surface of the blade is rugose (Fig. 7.1, 7.2), presumably marking the attachment of the M. iliotibialis (Romer, 1956; Hutchinson, 2001; Schachner et al., 2011, 2019), although it is not as well defined as seen in UCMP 25941 (Long and Murry, 1995; Parker, 2018a). In dorsal view, the iliac blade is mediolaterally compressed and becomes expanded posteriorly (= squared off, Parker, 2016a, 2018a) at the postacetabular process (Fig. 7.2), as observed in UMMP 13950 and UMMP 7470. As typically seen in aetosaurs, the postacetabular process extends well beyond the posterior margin of the ischiac peduncle. In lateral view, the postacetabular process is knob-like with the 'neck' exhibiting a concave posterior margin between it and the acetabulum, a condition shared with UMMP 7470 (Case, 1929) and UCMP 25941 (Long and Murry, 1995; Parker, 2018a). The acetabulum is deeply concave and broad, being anteroposteriorly longer than it is dorsoventrally tall (Fig. 7.1), but not to the extent observed in UCMP 25941 (Parker, 2018a). As observed in UMMP 7470, the acetabulum of PEFO 46222 would have faced ventrolaterally due to the articulation between the ilium and sacral vertebrae (Parker, 2018a).

The ilium exhibits a well-developed supraacetabular crest, similar to that of *Scutarx deltatylus* (PEFO 31217, Parker, 2016b), *Stagonolepis* (NHMUK PV R4789, Walker, 1961; UOPB00150, Desmet et al., 2022), and *Aetosauroides scagliai* (PVL 2073, Casamiquela, 1967; Heckert and Lucas, 2002a). Just dorsal to the supraacetabular crest, the body of the ilium exhibits a shallow fossa (Fig. 7.1), as observed in UMMP 13950. However, it is not deep as described in *Scutarx deltatylus* (Parker, 2016b). This region is partially distorted in UMMP 7470. Ventrally, the margins of the ilium form a V-shaped ventrally projecting point at the midline of the acetabulum. The pubic peduncle is mediolaterally expanded with a flat surface in anterior view and exhibits a comma-shaped outline in ventral view. In contrast, the ischiac peduncle is also comma-shaped in ventral view but exhibits a sharp ridge in posterior view due to it being mediolaterally compressed. The medial surface exhibits prominent scars/attachment sites for the sacral ribs (Figs. 6.5, 7.3). There is a large ovate surface medial to the acetabulum, just dorsal to the pubic peduncle, which represents the attachment site of the anterior sacral rib. Posterodorsal to this ovate surface there is a crest that terminates at the postacetabular process. This serves as the main attachment site for the transversely expanded posterior sacral rib.

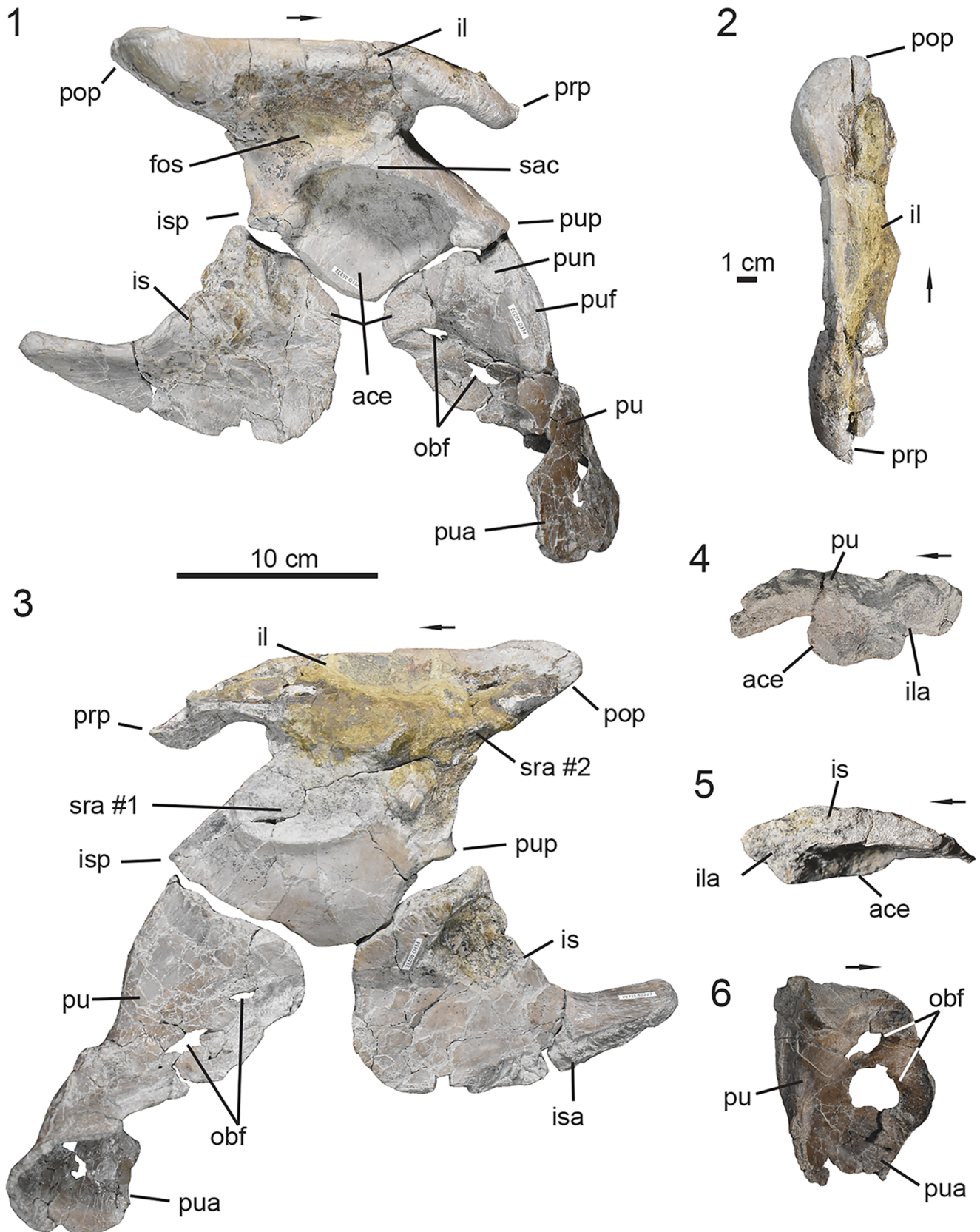


Figure 7. PEFO 46222, associated pelvic elements. (1–5) Right half of disarticulated pelvic girdle; (6) left pubis. (1, 6) Lateral views, (3) medial view, (2) dorsal view, (4, 5) proximal views. ace = acetabulum; fos = fossa; il = ilium; ila = ilium articulation; is = ischium; isa = ischium articulation; isp = ischiac peduncle; obf = obturator foramina; prp = preacetabular process; pop = postacetabular process; pu = pubis; pua = pubic apron; puf = pubic fossa; pun = pubic notch; pup = pubic peduncle; sac = supraacetabular crest; sra = sacral rib articulation. Arrows indicate anterior direction.

Pubis. The right pubis of PEFO 46222 is mostly complete although it is slightly crushed (Fig. 7.1). In contrast, the left pubis preserves the proximal two-thirds of the element (Fig. 7.6) but is not as crushed as the right pubis. Together, the preservation of the pubes allows for a description of the entire element, which is only proximally preserved in UMMP 7470 and partially obscured in UMMP 13950. The pubis of PEFO 46222 exhibits a dorsoventral height that is less than the anteroposterior length of the iliac blade as observed in UMMP 13950, but unlike the condition exhibited by *Desmatosuchus spurensis* (MNA V9300, Parker, 2008a) and *?Lucasuchus huntii* (TMM 31100-313, Long and Murry, 1995), in which the height of the pubis exceeds the length of the ilium. Proximally, the pubis exhibits a comma-shaped surface that matches the contact surface of the pubic peduncle on the ilium (Fig. 7.4). This is also the case in the referred pubis of *Calyptosuchus wellesi* (UCMP 23195, Parker, 2018a) from UCMP A269. More posteriorly, this surface expands ventrally for its contact with the anterior margin of the ischium. The acetabular portion of the pubis is strongly concave with a well-developed rim (Fig. 7.1), as seen in UCMP 23195 (Parker, 2018a) and UMMP 7470 (Case, 1929). Proximally, the shaft of the pubis is robust anteriorly and becomes more gracile posteriorly where it composes part of the pubic apron, as observed in UMMP 13950. On the lateral surface, the pubis exhibits a deep notch that originates just anterodorsal to the acetabular rim and runs anteroventrally on the anterior surface of the shaft as described in UMMP 7470 (Case, 1929; Parker, 2018a). There is a shallow fossa on the shaft posterior to that groove that extends parallel to the anterior margin.

The surface is smooth on the pubic apron portion of the element and exhibits faint rugosities near its medial margin (Fig. 7.3). This rugose surface presumably marks the attachment site of the M. puboischiofemoralis externus 1–3 (Hutchinson, 2001; Schachner et al., 2011). The perforate region of the pubic apron is often poorly preserved or obscured from view in taxa with a preserved pubis (i.e., *Aetosauroides scagliai*, Casamiquela, 1967; Heckert and Lucas, 2002a; *?Lucasuchus huntii* Long and Murry, 1995; *Aetosaurus ferratus*, Schoch, 2007; *Desmatosuchus spurensis*, Parker, 2008a; *Typothorax coccinarum*, Heckert et al., 2010; *Stenomyti huangae* Small and Martz, 2013), fortunately this region is well preserved in PEFO 46222. It is evident that the pubis in PEFO 46222 is perforated by two foramina (Fig. 7.1, 7.2, 7.6).

Currently, the presence of two foramina on the pubic apron in aetosaurs has only been unambiguously described in *Scutax deltatylus* (PEFO 31217, Parker, 2016b) and *Stagonolepis robertsoni* (NHMUK R4793, MCZD 4, Walker, 1961). This is unlike the condition observed in the aetosaurs *Neoaetosauroides engaeus* (PVL 3525, Desojo and Báez, 2005) and *Desmatosuchus smalli* (TTU-P 9419, Martz, 2008) where the pubis is perforated by only one foramen, the obturator foramen. In life, the single obturator foramen conveys the obturator nerve and associated blood vessels that partially innervate and vascularize the hindlimb (Romer, 1956; Hutchinson, 2001; Claessens and Vickaryous, 2012).

In PEFO 46222 the dorsally positioned foramen is ovate with a dorsomedial inclination, whereas the ventral foramen is significantly larger and semicircular (Fig. 7.6). The two foramina are separated by a thin plate of bone. Ventral to the foramina, the pubic shaft twists medially, and becomes broad and mediolaterally compressed with a similar thickness as the dorsal pubic apron portion (Fig. 7.1). Distally, the pubis exhibits a curved, mediolaterally compressed ventral margin. It lacks the distal expansion (= 'pubic boot', Gauthier, 1986; Nesbitt, 2011) present in *Desmatosuchus spurensis* (MNA V9300, Parker, 2008a), *Typothorax coccinarum* (TTU P-9214,

Martz, 2002), and *Aetosauroides scagliai* (PVL 2073, Casamiquela, 1967; Heckert and Lucas, 2002a).

Ischium. The left ischium of PEFO 46222 is well preserved with few signs of taphonomic distortion, unlike its right counterpart, which is slightly crushed with a distal process that is preserved as a separate piece. The element is anteroposteriorly longer than it is dorsoventrally tall. The main body of the ischium is broad and thickest mediolaterally near the acetabulum. Proximally, the ischium exhibits a comma-shaped cross-section (Fig. 7.5) matching that of the ischiac peduncle on the ilium. Unlike the pubis, the acetabulum is concave and shallow (Fig. 7.1). The acetabular rim is prominent near the proximal contact with the ilium (Fig. 7.5). Posteroventrally, the ischium tapers to a blunt, posteriorly oriented process unlike that of *Desmatosuchus spurensis* (Parker, 2008a) in which the posterior process hooks ventrally. In lateral view, it exhibits a concave posterior margin between its contact with the ilium and posterior process. The ischium exhibits a uniform mediolateral thickness posteroventral to the acetabulum. This is unlike the referred ischia of *Calyptosuchus wellesi* (UCMP 32148, UCMP 32148, Long and Murry, 1995; Parker, 2018a) from UCMP A269, which exhibit a 'rod-like' body posteriorly and fan out ventrally becoming more gracile.

Laterally, the expanded surface is generally flat and smooth but becomes more rugose near the anteroposteriorly straight ventral margin (Fig. 7.1). This rugose texture presumably marks the attachment site of M. puboischiofemoralis externus 3 (Hutchinson, 2001; Schachner et al., 2011). The medial contact between the ischia is well exposed; this contact runs the length of the ventral margin and is composed of a series of inclined ridges and grooves, indicating a strong interlocking contact between the ischia (Fig. 7.3). Previously, the presence of a notch was described on the anterior margin of the ischium in the referred specimens UCMP 32148 and UMMP 7470 (Parker, 2018a), however those notches are artifacts of preservation.

Carapace description

PEFO 46222 preserves approximately 30 osteoderms that are from various regions of the body. The majority of the osteoderms are well preserved, although some exhibit taphonomic distortion because of crushing or diagenetic cementation at PFV 456. The articulated carapace of the holotype specimen of *Calyptosuchus wellesi* (Fig. 4.1; UMMP 13950, Case, 1932) allows us to determine the relative anatomical position of the osteoderms recovered with PEFO 46222. Our recent examination of the carapace of UMMP 13950 indicates that previous interpretations by Parker (2018a), which followed those by Case (1932), are offset. Originally, Case (1932, p. 64) interpreted the neural spine protruding through the dorsal carapace as belonging to that of the first caudal vertebra (cv #1) and designated the carapacial row sequence based on that landmark (Fig. 4.1, 4.2). Our re-examination of the associated vertebral column indicates that this is not the case because the neural spines are complete and articulated from the 15th trunk vertebra through the mid-caudal region (Fig. 4.1–4.3). These observations, as well as the morphology and measurements (i.e., anteroposterior length, transverse width) of the lateral projections on the top of the neural spines, indicate that the neural spine protruding through the carapace belongs to the 14th trunk vertebra (Fig. 4.1–4.3). Thus, the carapace of UMMP 13950 preserves more of the anterior trunk region than previously recognized (Fig. 4.1, 4.4), which correlates with the associated vertebral column (Fig. 4.2).

Thanks to this new understanding we can compare PEFO 46222 to UMMP 13950 and assess the morphological variation of the osteoderms across the dorsal carapace with a higher fidelity. Previous studies (e.g., Case, 1932; Long and Ballew, 1985; Long and Murry, 1995; Parker, 2018a) were limited in their interpretations of the morphological variation of the dorsal carapace because of the articulated state of the holotype specimen, which obscures several anatomical features (i.e., anterior bar, ventral surface, lateral edge, flexure), or because of the ambiguity in determining which disarticulated elements were associated with specific individuals, which is the case for the referred elements from UCMP A269 (Parker, 2018a). The associated carapace of PEFO 46222 provides important insight into the positional morphological variation of the osteoderms within a single individual of *Calyptosuchus wellsi*.

Paramedian osteoderm description

PEFO 46222 preserves several complete paramedian osteoderms. This includes four individual right paramedian osteoderms that are imbricated and diagenetically cemented to each other in an articulated sequence. These imbricated osteoderms were collected adjacent to the posterior trunk vertebrae and partially diagenetically cemented to the medial surface of the right ilium. Counting from the 14th trunk osteoderm row, as indicated by the protruding 14th vertebra, it is evident that the articulated carapace of the holotype specimen UMMP 13950 (Fig. 4.1; Case, 1932) preserves osteoderms in anatomical sequence (Fig. 4.1) from the anterior trunk (to #3) through middle caudal (co #10) region. Case (1932, p. 61) noted that the transverse width of the paramedian osteoderms decreases posteriorly on the carapace of UMMP 13950, and we agree with that observation. As noted by Case (1932) and Parker (2018a), the dorsal eminence becomes more robust and well developed posteriorly along the dorsal carapace. We note that the anatomy of the lateral margin becomes less sigmoidal into the caudal region. Because PEFO 46222 preserves a similar region of the body as the holotype, we use these noted features of the carapace in UMMP 13950 as proxies to position the paramedian osteoderms of PEFO 46222 in a relative sequence. Additionally, several paramedian osteoderms articulate with some of the isolated lateral osteoderms. The holotype specimen of *Calyptosuchus wellsi* (UMMP 13950) indicates that the anatomy of the lateral osteoderms varies significantly between the regions of the dorsal carapace (Figs. 1, 4; Parker, 2018a). Thus, we used the anatomy of the lateral osteoderms as another proxy for determining the regional differentiation to which the isolated paramedian osteoderms are referable.

Middle trunk region. The middle trunk region encompasses trunk vertebrae and osteoderm rows numbering 5–12 (Figs. 1, 4). It is further subdivided into the anterior middle trunk region, encompassing rows 5–8 (Figs. 1, 4), and the posterior middle trunk region, which encompasses rows 9–12 (Figs. 1, 4). In PEFO 46222 the middle trunk region is composed of several complete paramedian osteoderms (Fig. 8) with three associated lateral osteoderms, which are characterized by a ‘wing’-like lateral flange. In dorsal view, the plates are rectangular with some exhibiting a slight anterolateral curvature. The paramedian osteoderms of this region exhibit the largest width-to-length ratios (W:L) and anteroposterior length of any of the preserved paramedian osteoderms, with an average W:L of 2.7 and anteroposterior length of 8.5 cm. In posterior view and lateral to the dorsal eminence, the paramedian osteoderms exhibit varying degrees of ventral arching at the center of ossification, causing the bone surface to be dorsally convex

(Fig. 8.3, 8.4). This is exemplified by a right paramedian osteoderm that is strongly arched (Fig. 8.4), similar to an isolated osteoderm of *Adamanasuchus eisenhardtiae* (PEFO 34638, Lucas et al., 2007a, fig. 3). This is likely associated with constriction of the trunk into a gracile ‘waist’ (Desojo et al., 2013), which occurs anterior to the sacral region in the middle to posterior trunk transition and has been documented in aetosaurs such as *Coahomasuchus kahleorum* (Heckert and Lucas, 1999).

The paramedian osteoderms of the middle trunk region exhibit a pronounced anterolateral triangular process of the anterior bar (Parker, 2018a), however this process varies in its inclination in dorsal view throughout this region. In the anterior middle trunk region, the process projects parallel to the horizontal plane in dorsal view (Fig. 8.1) and becomes anterolaterally inclined in the posterior middle trunk region (Fig. 8.2). The sigmoidal nature of the lateral margin of the paramedian osteoderms vary in the middle trunk region; it ranges from being weakly to moderately sigmoidal (Fig. 8.1, 8.2, 8.7, 8.8). Additionally, the lateral margin exhibits an embayed surface positioned just posterior to the anterolateral process for overlap of the adjacent lateral osteoderm. The anterior bar also exhibits an anteromedial process that projects anteriorly. It has been noted that the anterior margin of the anterior bar is ‘scalloped’ in the paramedian osteoderms of *Calyptosuchus wellsi* (UMMP 7470, Parker, 2018a). PEFO 46222 indicates that this scalloped margin is not consistent across all the paramedian osteoderms of this region; it is weak in the anterior trunk region (Fig. 8.1), whereas in the more posteriorly positioned osteoderms it is moderately to well incised (Fig. 8.2, 8.8). The medial edge is roughly anteroposteriorly straight, although on some of the osteoderms the edge curves slightly medially, just posterior to the anterior bar. The medial edge lacks the interlocking tongue-and-groove articulation surface that is seen in *Desmatosuchus* (Long and Ballew, 1985; MNA V9300, Parker, 2008a). In the middle trunk region, the dorsal eminence is positioned more medially on the posterior border of the plate. It is weakly developed, being a relatively low boss with a slight keel that originates from the posterior margin of the anterior bar (Fig. 8.1, 8.2). In posterior view, the eminence exhibits a mound-like curved outline (Fig. 8.4, 8.10).

The dorsal ornamentation is composed of well-incised pits and grooves radiating from the eminence (Fig. 8.1). However, in several of the preserved paramedian osteoderms, the dorsal ornamentation is broken by large, deep, anteroposteriorly oriented grooves with straight margins (Fig. 8.2, 8.8). Ventrally, there is a ridge and rounded swelling of the bone associated with the groove on the dorsal surface (Fig. 8.10, 8.11). It is possible that this is associated with predation or scavenging (i.e., bite traces), which has also been documented in the osteoderms of *Typothorax coccinarum* (PEFO 34869, Drymala et al., 2021). Alternatively, this damage may be pathological in origin, although testing that hypothesis requires further analysis outside the scope of the present study. In the absence of this abnormal swelling and damage of the bone, the ventral surface is smooth with a weak, transversely oriented ventral strut (sensu Long and Ballew, 1985; Fig. 6.5) and an embayed posterior margin (Fig. 8.5, 8.6), which overlaps the anterior bar of the succeeding paramedian osteoderm, as described by Parker (2018a).

Posterior trunk and sacral region. The posterior trunk region encompasses trunk osteoderm rows #13–16 and the succeeding sacral region is composed of two sacral osteoderm rows (Figs. 1, 4). UMMP 13950 indicates that the paramedian osteoderms in the posterior trunk and sacral regions are similar in anatomy to those of the mid trunk region. These regions can be differentiated from each

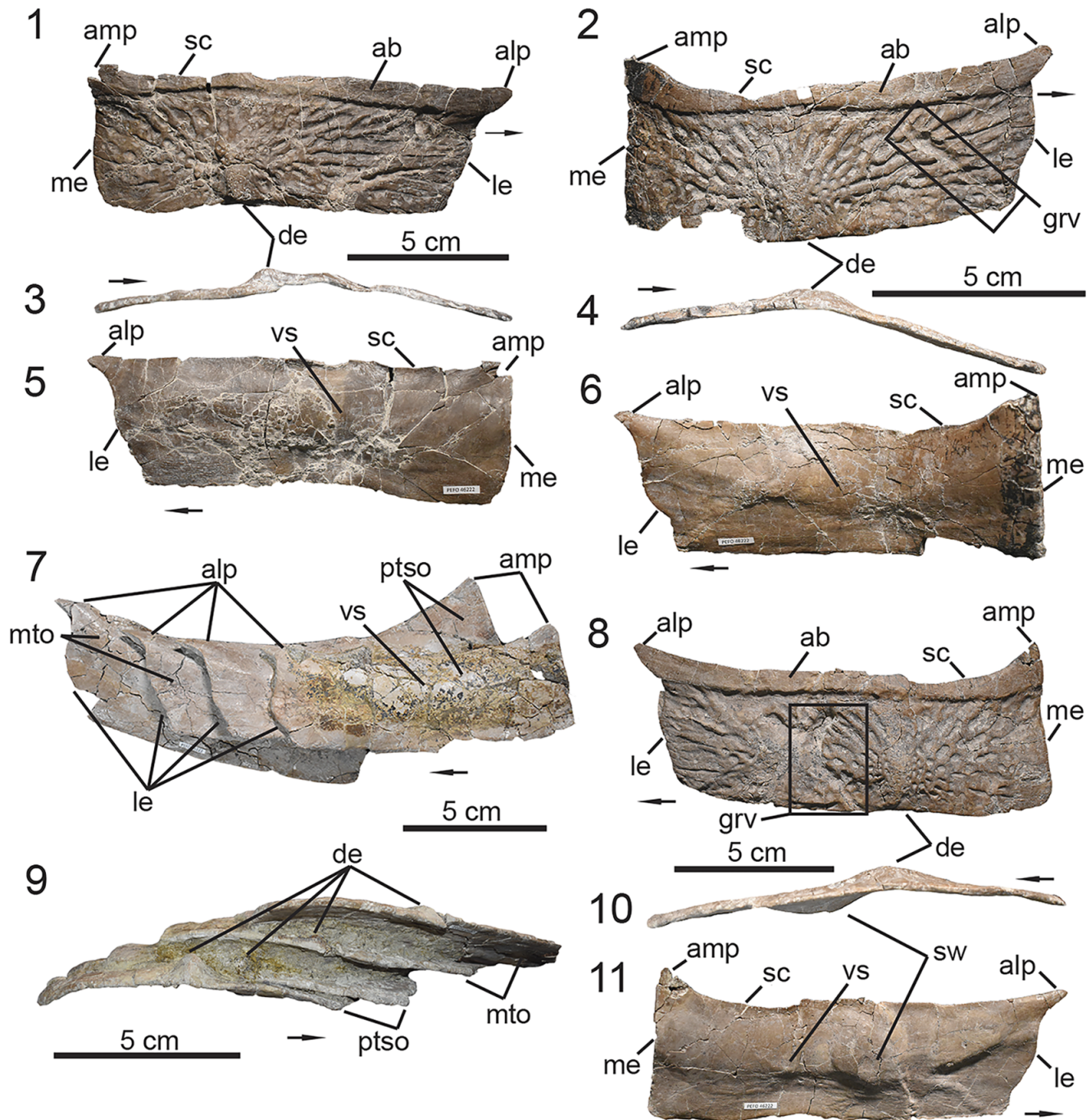


Figure 8. PEFO 46222, associated mid-trunk paramedian osteoderms. (1–6) Isolated osteoderms showing the variation in anatomy within the mid-trunk region; (7, 9) four imbricated paramedian osteoderms that include osteoderms derived from the posterior trunk and/or sacral regions; (8, 10, 11) isolated paramedian osteoderm with possible pathology that is observed across the carapace of PEFO 46222. (1, 2, 8) Dorsal views, (5–7, 11) ventral views, (3, 4, 9, 10) posterior views. ab = anterior bar; alp = anterolateral process; amp = anteromedial process; de = dorsal eminence; grv = groove; le = lateral edge; me = medial edge; mto = mid-trunk osteoderm; ptso = posterior-trunk / sacral osteoderm; sc = scalloped; sw = swelling; vs = ventral strut. Arrows indicate lateral direction.

other based on the anatomy of the respective lateral osteoderms. The articulated carapace of UMMP 13950 indicates that the lateral osteoderms in the posterior trunk and sacral regions lack the 'wing'-like lateral flange that is characteristic of the middle trunk region (Fig. 4.1), instead they exhibit a square-like outline in dorsal view with a quadrangular lateral flange.

Two paramedian osteoderms referable to the posterior trunk region are imbricated and diagenetically cemented to two other

osteoderms from the middle trunk region (Fig. 8.7, 8.9). Linear measurements of these imbricated osteoderms indicate that they exhibit an average W:L of 2.5 and an anteroposterior length of 7.9 cm. These osteoderms are slightly arched from the medial edge to the dorsal eminence and transversely flat lateral to the eminence in posterior view (Fig. 9.3). Additionally, they exhibit a slight anterolateral curvature in dorsal view (Fig. 9.1), as observed in the posterior middle trunk region (Fig. 8.8). The preserved elements

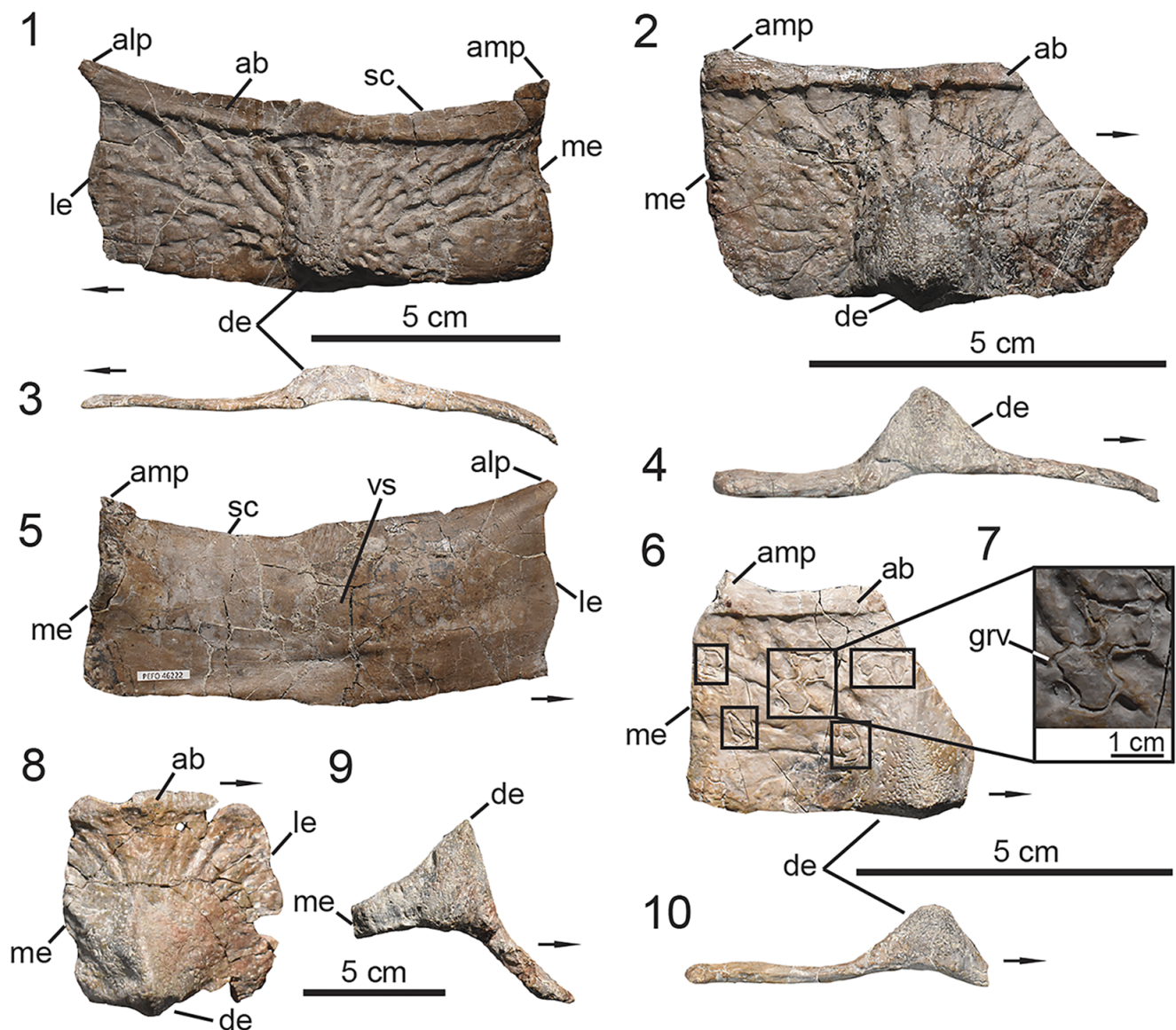


Figure 9. PEFO 46222, associated posterior trunk/sacral and caudal paramedian osteoderms. (1, 3, 5) Isolated paramedian osteoderm derived from the posterior trunk or sacral region; (2, 4, 6–10) caudal paramedian osteoderms; (6, 7, 10) caudal osteoderm showing possible invertebrate traces on the dorsal surface. (1, 2, 6–8) Dorsal views, (5) ventral view, (3, 4, 9, 10) posterior views. ab = anterior bar; alp = anterolateral process; amp = anteromedial process; de = dorsal eminence; grv = groove; le = lateral edge; me = medial edge; sc = scalloped; vs = ventral strut. Arrows indicate lateral direction.

indicate that the triangular anterolateral process of the anterior bar gradually becomes less pronounced moving posterior in the trunk series (Fig. 8.7). The orientation of this process is predominantly inclined anterolaterally. The anterior margin of the anterior bar is moderately 'scalloped', unlike those of the posterior middle trunk region where the scalloping of the anterior bar is well developed. A complete left paramedian osteoderm articulates with an associated square-like lateral osteoderm, indicating that the lateral margin is moderately sigmoidal in the posterior trunk and sacral regions (Fig. 9.1), a condition also observed in those osteoderms that are imbricated and diagenetically cemented (8.7). This particular osteoderm exhibits a slightly lower W:L of 2.3 and an anteroposterior length of 7.5 cm, indicating that it succeeds the imbricated osteoderms described above. The medial margins of the paramedian osteoderms are as described for those of the middle trunk region (Fig. 8). The dorsal eminence in the posterior trunk and sacral region is taller and more transversely expanded than those of

the middle trunk region. The eminence is a more prominent boss that has a weak keel anteriorly and is rounded or 'mound-shaped' in posterior view (Fig. 9.3). The eminence itself is not medially situated; instead, it is positioned at the midline of the posterior border (Fig. 9.1). This aligns with the sequential transverse shortening of the paramedian osteoderms in the carapace (Case, 1932), which gradually positions the dorsal eminence closer to the medial edge of the osteoderm. The gradual change of the dorsal eminence from the mid trunk to sacral region in PEFO 46222 is best observed in the imbricated osteoderms (Fig. 8.9). The dorsal ornamentation is characterized by well-incised grooves and ridges radiating from the eminence. The ventral surface is smooth and exhibits a weak, transversely oriented ventral strut.

Caudal region. PEFO 46222 preserves three caudal paramedian osteoderms from the right side (Fig. 9.2, 9.6, 9.8). Two of these elements are not fully preserved, missing the lateral extent of the element, which prohibits calculation of their respective width-to-

length ratios. However, it is evident that caudal osteoderms are transversely shorter than the paramedian osteoderms of the trunk and sacral regions. The key feature that supports their referral to the caudal region is the presence of a tall, robust, blunt pyramidal dorsal eminence with an anterior keel (Fig. 9.4, 9.9, 9.10). The holotype specimen of *Calyptosuchus wellsi* (UMMP 13950, Case, 1932) preserves most of the caudal carapace, and it is evident that only in this region do the dorsal eminences become this prominent (Fig. 4.1; Parker, 2018a). Additionally, the caudal paramedian osteoderms become more flexed distally on the tail. Thus, the anatomy of the eminence along with the flexure of the osteoderm provide the best proxy in determining the anatomical position of these caudal elements. The paramedian caudal osteoderms are referable to middle caudal rows #5–10 (Figs. 1, 4). Two of these elements are rectangular in dorsal view (Fig. 9.2, 9.6), whereas the other exhibits a more square-like outline (Fig. 9.8). Comparison with UMMP 13950 indicates that the square-like osteoderm is positioned more posteriorly in the caudal region near caudal row #10 (Figs. 1, 4).

The preserved osteoderms are anteroposteriorly shorter than those from the trunk and sacral region with an average anteroposterior length of 7.15 cm. This shortening occurs gradually from the mid trunk to mid caudal region, as observed in UMMP 13950. The general anatomy of the dorsal eminence is the same in the preserved elements, only varying in their respective heights. The height of the eminence is directly correlative to the transverse shortening of the paramedian osteoderm in the caudal region, thus the eminence becomes taller and more robust in the more caudally positioned elements within the middle caudal region of *Calyptosuchus wellsi* (Figs. 4.1, 6.4, 9.9, 9.10). In the posteriormost caudal paramedian osteoderms, the eminence exhibits a height that is equivalent to the anteroposterior length of the osteoderm (Fig. 9.8, 9.9). Additionally, the dorsal eminence is positioned closer to the medial edge than those in the trunk and sacral regions. The dorsal ornamentation is composed of grooves and ridges radiating from the eminence. However, in the more posteriorly positioned osteoderm the dorsal surface is dominated by the eminence rather than the ornamentation (Fig. 9.8). Thus, the ornamentation is not as well incised as those from the trunk and sacral regions. One of the caudal paramedian osteoderms exhibits several shallow channels incised faintly onto the bone surface forming irregular loops that are inconsistent with the ornamentation on the dorsal surface (Fig. 9.6, 9.7). We hypothesize that these looped channels may represent osteophagous invertebrate traces similar to those described from other Triassic assemblages (Paes Neto et al., 2016). Alternatively, they may represent evidence of root etching on the bone surface. However, those patterns tend to exhibit a randomized and/or irregular pattern with channels that are interconnected on the bone surface (Francischini et al., 2020). Ventrally, the preserved elements lack a ventral strut and exhibit a smooth surface with a more deeply embayed posterior margin for the overlap of the succeeding osteoderm.

Lateral osteoderm description

PEFO 46222 preserves several lateral osteoderms that act as the main anatomical landmarks for our divisions of the preserved carapace. Aetosaur lateral osteoderms are composed of dorsal and lateral flanges divided by a pronounced flexure (Parker, 2007; Desojo et al., 2013). At the point of this flexure, the dorsal surface exhibits an eminence, usually in the form of a keel or spine (Desojo et al., 2013). The lateral osteoderms of PEFO 46222 exhibit a predominantly obtuse flexure between the dorsal and lateral

flanges that is laterally convex in posterior view (Fig. 10.4–10.6, 10.8), similar to other taxa within the Stagonolepidoidea (Parker, 2016a, 2018a; Reyes et al., 2020). The lateral osteoderms are overlapped anteriorly by the anterolateral projection of the adjacent paramedian osteoderm, unlike the condition exhibited by desmatosuchin taxa where the overlapping projection is on the lateral osteoderm (Parker, 2007, 2016a). They exhibit a well-developed anterior bar, pyramidal-shaped dorsal eminences that contact the posterior margin, and a surface ornamentation consisting of grooves and ridges radiating from the eminence (Fig. 10.1–10.3). Together the anatomy of the lateral and paramedian osteoderms of PEFO 46222 support its referral to *Calyptosuchus wellsi* (Long and Ballew, 1985).

Middle trunk region. PEFO 46222 preserves several lateral osteoderms that are associated with paramedian osteoderms of the mid trunk region. These osteoderms exhibit a significantly larger lateral flange compared to the dorsal flange (Fig. 10.1, 10.2). The outline of the dorsal flange is triangular in dorsal view. The medial edge of the dorsal flange is sigmoidal along its contact with the lateral margin of the adjacent paramedian osteoderm. The anteromedial edge of the anterior bar is incised for reception of the anterolateral process of the anterior bar in the adjacent paramedian osteoderm. The angle of incision varies between the lateral osteoderms (Fig. 10.1, 10.2), which matches the variation observed in the projection of the anterolateral process of the paramedian osteoderms throughout the dorsal carapace. The lateral flange of these lateral osteoderms is triangular in dorsal view and exhibits an anterolateral ‘wing-like’ appearance (sensu Parker, 2018a), in which the posterior margin curves anteriorly until it meets the anterior margin at a rounded tip (Fig. 10.2; Parker, 2018a). This anatomy is associated with lateral osteoderms positioned in the middle trunk region of UMMP 13950 (Figs. 1, 4). When measuring from the dorsal eminence, the transverse width of the lateral wing varies between these lateral osteoderms. The lateral flange exhibits a larger width the more anteriorly located it is in the middle trunk region and becomes gradually reduced posteriorly in the sequence.

There is also variation in the dorsal eminence on the middle trunk lateral osteoderms. The more anteriorly located elements exhibit a low pyramidal eminence with an anteroposteriorly elongate keel at the midline (Fig. 10.4, 10.5; Parker, 2018a). However, unlike the condition observed in an isolated lateral osteoderm (UCMP 136744) referred to *Calyptosuchus wellsi* from UCMP A269, the dorsal eminence does not project beyond the posterior margin (Parker, 2018a). The flexure between the dorsal and lateral flange varies between these lateral osteoderms. The more anteriorly positioned lateral osteoderms exhibit a flexure of nearly 90° between the dorsal and lateral flanges in posterior view (Fig. 10.4), whereas the succeeding lateral osteoderms exhibit a more obtuse flexure in comparison (Fig. 10.5). This variation in the flexure of the lateral osteoderm is also well documented in *Desmatosuchus spurensis* (MNA V9300, Parker, 2008a, fig. 27), in which the osteoderms become more acutely flexed in the middle trunk region.

Posterior trunk and sacral regions. PEFO 46222 preserves a left lateral osteoderm (Fig. 10.3, 10.6) that articulates with a paramedian osteoderm referable to the posterior trunk or sacral region of the dorsal carapace. The element exhibits a sigmoidal medial edge similar to the middle trunk lateral osteoderms, although the anterior bar is not well incised due to the decreased prominence of the anterolateral process of the adjacent paramedian osteoderm (Fig. 10.3). The dorsal flange no longer exhibits a triangular outline

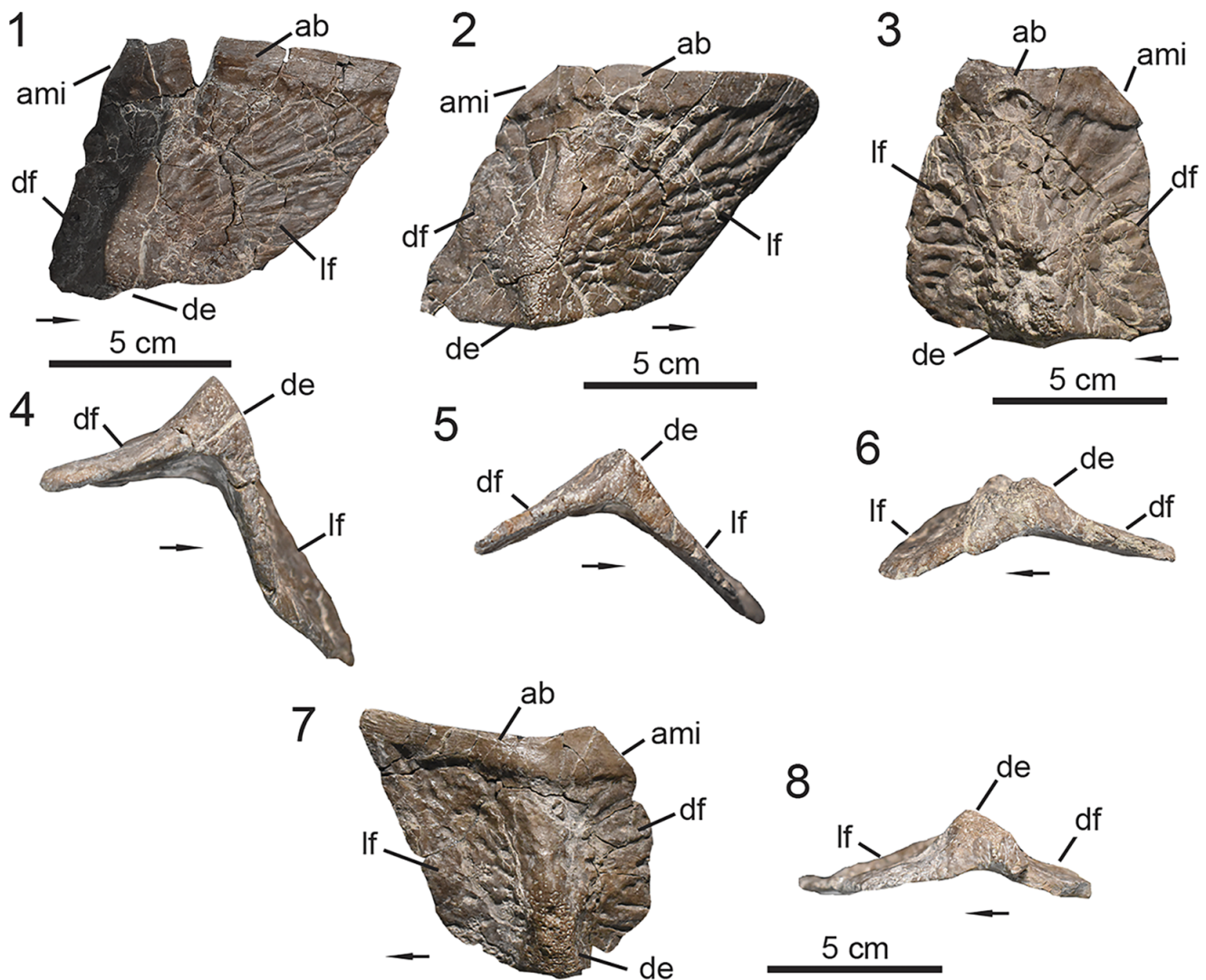


Figure 10. PEFO 46222, associated lateral osteoderms. (1, 2, 4, 5) Mid-trunk lateral osteoderms; (3, 6) posterior trunk/sacral lateral osteoderms; (7, 8) caudal lateral osteoderms. (1–3, 7) Dorsal views, (4–6, 8) posterior views. ami = anteromedial incision; ab = anterior bar; de = dorsal eminence; df = dorsal flange; lf = lateral flange. Arrows indicate lateral direction.

in dorsal view, instead it is more rectangular. The lateral flange lacks the triangular-shaped ‘wing’ (sensu Parker, 2018a) that is characteristic of the middle trunk laterals. Instead, it exhibits a transverse width similar to the dorsal flange, giving the element a squared outline in dorsal view with a wide obtuse flexure in posterior view (Fig. 10.3, 10.6). The dorsal eminence is partially eroded near the apex, but it is evident that it was moderately developed and exhibited an anteroposteriorly oriented keel on the dorsal surface similar to those from the trunk.

Caudal region. PEFO 46222 preserves a left lateral caudal osteoderm (Fig. 10.7, 10.8) that is referable to the anterior caudal region based on comparisons to UMMP 13950 (Fig. 4.1). It exhibits well-incised radial ornamentation, a low pyramidal eminence that is anteriorly keeled, and a transversely short triangular lateral flange that is slightly wider than the dorsal flange with an anterolateral inclination (Fig. 10.7). Although the lateral flange is similar to those from the middle trunk region, the osteoderm exhibits a wide, obtuse flexure of nearly 180° (Fig. 10.8). The dorsal flange exhibits a rectangular outline in dorsal view similar to those in the posterior trunk and sacral regions. However, the medial edge is weakly sigmoidal in comparison to the more anteriorly positioned lateral osteoderms.

Referred specimens

UMMP 7470, trunk and sacral vertebrae, paramedian osteoderms, and a relatively complete pelvic girdle preserving the right ilium, right pubis, and co-ossified ischia (Case, 1922, 1929); UCMP 27225, dentary fragment, cervical centra, paramedian, lateral, and ventral osteoderms (Parker, 2018a); UCMP 25941 and UCMP 32148, associated left ilium and ischium, respectively (Long and Murry, 1995); and approximately 400 catalogued elements from UCMP A269 (the *Placerias* Quarry, Parker, 2018a, supplemental material).

New referred PEFO specimens. PEFO 46222, an associated skeleton preserving elements from the trunk through caudal region including paramedian and lateral osteoderms, vertebrae, ribs, and a disarticulated pelvic girdle; PEFO 49321, an associated skeleton preserving paramedian and lateral osteoderms as well as skull elements including the left and right maxillae with teeth, the right jugal, the left quadratojugal, the left quadrate, the left laterosphenoid, the right surangular, the right prearticular, and the right articular.

Rationale for referral of PEFO specimens. PEFO 46222 and PEFO 49321 preserve osteoderms that are rectangular in dorsal view, indicating they are paramedian osteoderms derived from two

medial anteroposterior columns of the dorsal carapace (Parker and Martz, 2010). The paramedian osteoderms lack a beveled edge on the posterodorsal margin, unlike *Tecovasuchus chatterjeei* Martz and Small, 2006 (TTU-P 545), *Paratypothorax* sp. (TTU-P 09169, Martz et al., 2013; PEFO 3004, Lucas et al., 2006), *Kocurypelta silvestris* (ZPAL V.66/1, Czepiński et al., 2021), and *Venkatasuchus armatum* Haldar, Ray, and Bandyopadhyay, 2023 (ISIR267/1-7), which exhibit this anatomy in the trunk and caudal regions. The dorsal ornamentation of the paramedian osteoderms in PEFO 46222 and PEFO 49321 is composed of a strong radial pattern of ridges and grooves radiating from the eminence, unlike *Typothorax coccinarum* (TTU-P 9214, Martz, 2002; NMMNH P-12964, Heckert et al., 2010), *Redondasuchus rineharti* Spielmann et al., 2006 (NMMNH P-43311), *Kryphioparma caerula* (UCMP 165173, Reyes et al., 2023), and *Sierittasuchus macalpini* Parker, Stocker, and Irmis, 2008 (UMMP 60817), which exhibit well-incised oblong to circular pits across the dorsal surface, or *Apachesuchus heckerti* Spielman and Lucas, 2012, which is primarily devoid of ornamentation. Anteriorly, the trunk paramedian osteoderms exhibit a thickened well-developed anterior bar unlike paratypothoracins (e.g., *Rioarribasuchus chamaensis* Zeigler, Heckert, and Lucas, 2003), which exhibit a weakly developed anterior bar (Parker, 2007; Martz et al., 2013; Czepiński et al., 2021; Haldar et al., 2023; Reyes et al., 2024), *Desmatosuchus spurensis* (UMMP 7476, Case, 1922; MNA V9300, Parker, 2007, 2008a), which exhibits a depressed surface (= anterior lamina, sensu Long and Ballew, 1985; Parker, 2005, 2008a), or *Garzapelta muelleri* (Reyes et al., 2024), which exhibits presacral osteoderms with a flat and smooth anterior margin. The anterior bar exhibits both strongly projecting anterolateral and anteromedial projections, similar to *Scutarx deltatylus* (Parker, 2016b). The anterolateral process on the paramedian osteoderm overlaps the anterior surface of the adjacent lateral osteoderm, unlike desmatosuchins (Parker, 2007). More specifically, the trunk paramedian osteoderms of PEFO 46222 and PEFO 49321 exhibit a 'scalloped' anterior margin of the anterior bar, a weakly developed ventral strut, and a low, rounded, anteriorly keeled eminence in the trunk series that becomes more pronounced, tall, robust, and pyramidal caudally; a condition shared with *Scutarx deltatylus* (Parker, 2016b) and *Adamanasuchus eisenhardtae* (Lucas et al., 2007a). The dorsal eminence contacts the posterior margin, a condition shared with most taxa except *Desmatosuchus* (Parker, 2005, 2008a), *Lucasuchus huntii* (Long and Murry, 1995), *Neoaetosauroides engaeus* (Desojo and Báez, 2005), and paratypothoracins (Parker, 2007). Additionally, PEFO 46222 and PEFO 49321 preserve asymmetrical osteoderms with dorsal and lateral flanges, flexed at the center of ossification, and articulate with paramedian osteoderms, indicating they are lateral osteoderms from the two outer columns of the dorsal carapace (Parker and Martz, 2010). The lateral osteoderms are broadly flexed, similar to those of non-desmatosuchin and non-typothoracine taxa (Parker, 2007). The dorsal eminence is a low keeled triangular boss, unlike desmatosuchins, which exhibit a conical spike (Parker and Martz, 2010), or paratypothoracins, which exhibit a dorsoventrally flattened horn (Parker, 2007).

The suite of characters described above supports the referral of PEFO 46222 and PEFO 49321 to the more inclusive clade Calyp-tosuchini n. clade, which includes *Calyptosuchus wellesi*, *Scutarx deltatylus*, and *Adamanasuchus eisenhardtae* (Parker, 2016a). Those three taxa are further differentiated from each other based on a combination of characters and autapomorphies of the trunk paramedian osteoderms. *Scutarx deltatylus* exhibits a strong dorsal protuberance on the posteromedial dorsal surface, which is an autapomorphic condition of the taxon (Parker, 2016b). In

Adamanasuchus eisenhardtae (Lucas et al., 2007a) the dorsal surface exhibits an unornamented triangular area on the dorsal surface of the posteromedial corner, which is an autapomorphy of the taxon (Parker, 2016a, b), as well as a strongly incised 'cut-off' posterolateral corner for its contact with the adjacent lateral osteoderm shared with paratypothoracins (e.g., PEFO 3004). In *Calyptosuchus wellesi* (Parker, 2018a) the posteromedial corner is flat and exhibits radial ornamentation instead of a protuberance or unornamented area and lacks a strongly incised ('cut-off' corner) posterolateral margin. Thus, the osteoderm anatomy of PEFO 46222 and PEFO 49321 aligns with that of *Calyptosuchus wellesi* (Long and Ballew, 1985) following the revision by Parker (2018a).

Ontogenetic assessment

PEFO 46222, UCMP 27225, UMMP 7470, and UMMP 13950 are considered skeletally mature, based on the complete co-ossification of the neurocentral sutures of the preserved cervical and trunk vertebrae and the fusion of the sacral centra (see Griffin et al., 2021). PEFO 49321 does not preserve any vertebrae, however the proportional size of its paramedian osteoderms (Fig. S2) suggests that it was of similar size to PEFO 46222, and possibly skeletal maturity.

Remarks

The diagnosis for *Calyptosuchus wellesi* (Long and Ballew, 1985) by Parker (2018a) is mostly retained. We modified it based on our reassessment of the holotype specimen UMMP 13950 and referred pelvis UMMP 7470, which corrects some of the original interpretations by Case (1932), and the new morphological understanding provided by PEFO 49321 and PEFO 46222 (this study). *Calyptosuchus wellesi* remains a biostratigraphically informative taxon because it is currently restricted to the Adamanian Late Triassic Land Vertebrate Estimated Holochronozone (Martz and Parker, 2017).

Results

Phylogenetic analyses

Maximum parsimony. The strict consensus of Run 1 (Fig. 14.1) recovered UCMP 27225, PEFO 49321, PEFO 46222, UMMP 7470, and UMMP 13950 in a polytomy at the base of the Stagonolepididae. Because of the inconclusive nature of this quantitative analysis, we incorporated these specimens into a composite OTU of *Calyptosuchus wellesi*, assuming that they are indeed referable to the taxon, in order to explore the influence these specimens would have on the topological position of *C. wellesi* and the topology of the Aetosauria. Run 2 (Fig. 14.2) resulted in a strict consensus tree that recovers *Aetosauroides scagliai* as the earliest branching aetosaur, as seen in the strict consensus trees presented by Parker (2016a) and Reyes et al. (2020, 2024). The Stagonolepidoidea (Parker, 2016a) is apparent (Fig. 14.2) but is missing *Calyptosuchus wellesi* (composite OTU) and *Neoaetosauroides engaeus*, which are taxa traditionally recovered within this clade (Parker, 2016a; Reyes et al., 2020, 2024; Paes Neto et al., 2021c). In our analysis (Fig. 14.2) they are recovered in a large polytomy at the base of the Stagonolepididae, which is predominantly composed of taxa from the Aetosaurinae. The Desmatosuchini remains stable and composed of *Gorgetosuchus pekinensis* Heckert et al., 2015, *Sierittasuchus macalpini*, *Longosuchus meadei*, *Lucasuchus huntii*, *Desmatosuchus smalli*, and *Desmatosuchus spurensis*, as observed

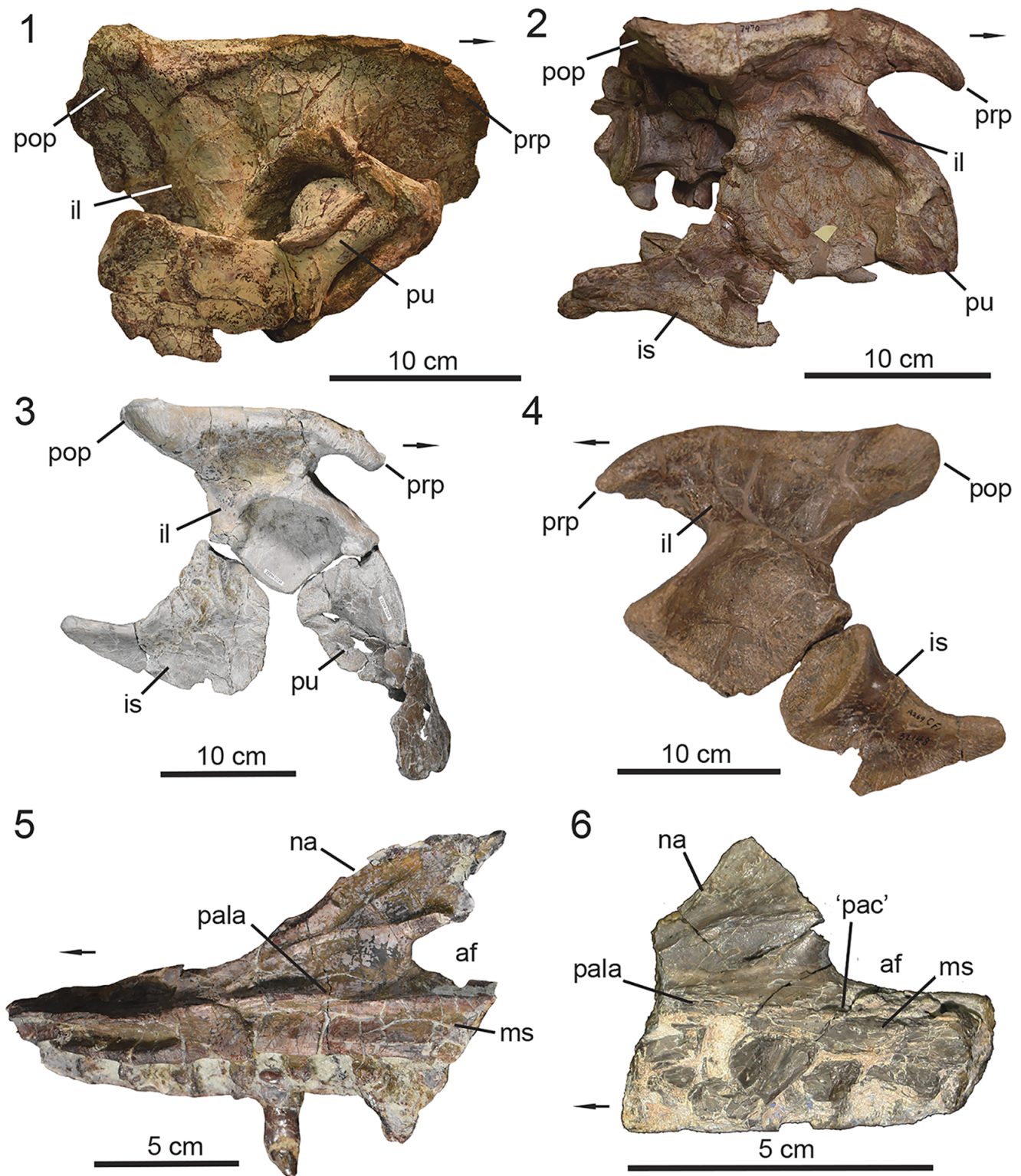


Figure 11. Taxonomic assessment of elements referred to *Calyptosuchus wellsi* from A269. (1) UMMP 13950, partial right portion of pelvis; (2) UMMP 7470, right aspect of partial pelvic girdle; (3) PEFO 46222, right half of disarticulated pelvis; (4) UCMP 25941 and UCMP 32148, associated pelvis from UCMP A269; (5) PEFO 49321, fragment of right maxilla; (6) UCMP 195193, fragmentary right maxilla. (1–4) Lateral views, (5, 6) medial views. af = antorbital fenestra; il = ilium; is = ischium; ms = medial shelf; na = nasal articulation; 'pac' = misidentified 'pneumatic accessory cavity'; pala = palate articulation; pu = pubis; prp = preacetabular process; pop = postacetabular process. Arrows indicate anterior direction.

in previous studies (Parker, 2016a; Reyes et al., 2020, 2024; Paes Neto et al., 2021c; Halder et al., 2023).

Bayesian inference. The Bayesian consensus of Run 1 (Fig. 15.1) recovered UCMP 27225, PEFO 49321, PEFO 46222, UMMP 7470, and UMMP 13950 within an inclusive clade that includes *Scutarx*

deltatylus, *Adamanasuchus eisenhardtae*, *Neoetosauroides engaeus*, and *Stenomylus huangae*. In this clade PEFO 46222 and PEFO 49321 are sister taxa. These specimens are recovered basal to UMMP 7470 and UCMP 27225, where the latter is directly basal to *Scutarx deltatylus* and *Adamanasuchus eisenhardtae*, two taxa that exhibit

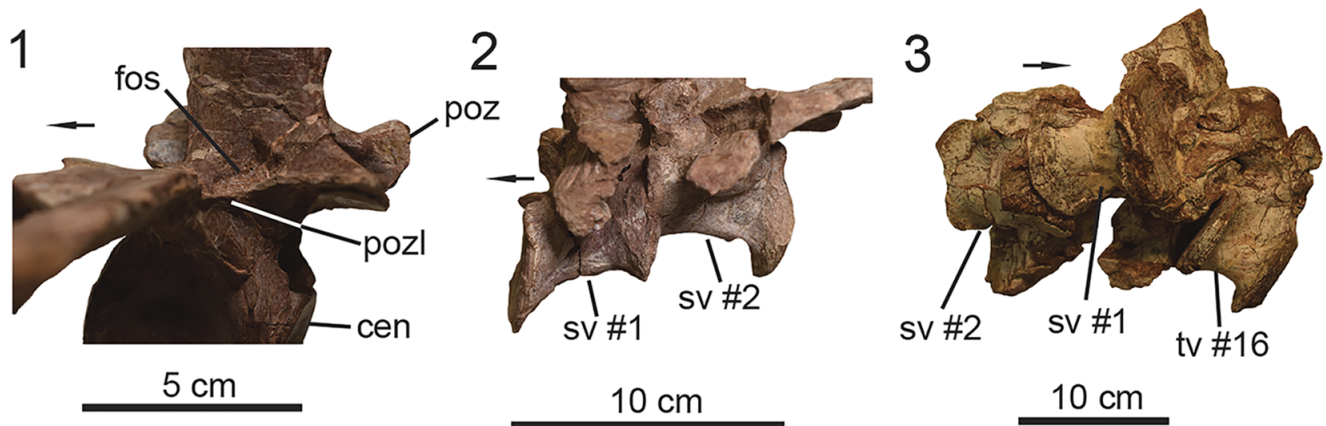


Figure 12. Noted areas of intraspecific variation within *Calyptosuchus wellesi*. (1) Postzygapophyseal lamina present in the middle trunk vertebra of UMMP 7470; un-co-ossified sacral vertebrae in (2) UMMP 7470 and (3) UMMP 13950. (1, 2) Lateral views, (3) ventral view. cen = centrum; fos = fossa; poz = postzygapophysis; pozl = postzygapophyseal lamina; sv = sacral vertebra; tv = trunk vertebra. Arrows indicate anterior direction.

a similar osteoderm anatomy to *Calyptosuchus wellesi* and often are recovered in an inclusive clade (= Calyptosuchini n. clade; Parker, 2016a, b; Reyes et al., 2020; Paes Neto et al., 2021c). UMMP 13950 is positioned basally within the clade and separated from the PEFO 46222, PEFO 49321, UMMP 7470, and UCMP 27225 by *Neoaetosauroides engaeus* and *Stenomyti huangae*, which are recovered as sister taxa. The recovery of these two taxa within this clade does make sense qualitatively because they exhibit a very similar dorsal osteoderm anatomy to *Calyptosuchus wellesi* (UMMP 13950). UCMP 27225 preserves a dentary, cervical vertebrae, and cervical osteoderms, which are elements that are absent in UMMP 7470, PEFO 46222, and PEFO 49321. UMMP 13950 preserves fragmentary cervical vertebrae, however these elements are represented by partial centra. The topological position of UCMP 27225 is due to this specimen preserving anatomy of the cervical region, which cannot be compared quantitatively to the UMMP or PEFO specimens because they do not preserve that anatomy, but they are comparable with those of *Scutarx deltatylus* (Parker, 2016b). UMMP 7470 preserves a limited number of paramedian osteoderms and trunk vertebrae along with an articulated pelvic girdle—elements that are preserved in UMMP 13950, PEFO 46222, and PEFO 4932. However, the topological position of UMMP 7470 is influenced by the lack of data of its lateral osteoderms and the presence of zygapophyseal laminae on the trunk vertebrae, a condition shared with *Scutarx deltatylus* (Parker, 2016b).

We reject the referral of UCMP 27225, PEFO 46222, PEFO 49321, and UMMP 7470 to *Scutarx deltatylus* and *Adamanasuchus eisenhardtae* because the paramedian osteoderms of these specimens lack the unornamented triangular protuberance on the posteromedial corner that is autapomorphic to *S. deltatylus* or the ‘cut-off’ corner observed in *A. eisenhardtae* (Lucas et al., 2007a, Parker, 2016a, b). Although they exhibit similarities to the dorsal osteoderms of *Neoaetosauroides engaeus* and *Stenomyti huangae*, the stratigraphic and geographical occurrences of the specimens in question do not support their referral to either of these taxa. *Neoaetosauroides engaeus* is known exclusively from the Los Colorados Formation of Argentina (Desojo and Báez, 2007), while *S. huangae* is only documented from outcrops of the Chinle Formation (or its equivalent) in northwestern Colorado (Small and Martz, 2013). Additionally, *Neoaetosauroides engaeus* and *Stenomyti huangae* are both restricted to the Revueltoian estimated holochron (215–207 Ma, sensu Martz and Parker, 2017) (Small and Martz, 2013; Kent et al., 2014; Parker, 2016a), unlike the UCMP, PEFO, and UMMP specimens in question, which are restricted to the

Adamanian estimated holochron (224–215 Ma, sensu Martz and Parker, 2017). Based on the topological position of UCMP 27225, PEFO 46222, PEFO 49321, and UMMP 7470, their anatomical similarities to UMMP 13950, the stratigraphic relationship between UCMP 27225 and the PEFO specimens within the Chinle Formation as well as that of the UMMP specimens within the Dockum Group, and our rationale for rejecting their referral to *Neoaetosauroides engaeus*, *Stenomyti huangae*, *Scutarx deltatylus*, and *Adamanasuchus eisenhardtae*, we support the referral of UCMP 27225 and UMMP 7470 to *Calyptosuchus wellesi*, as originally proposed by Parker (2018a), and refer the new PEFO specimens to this taxon.

The Bayesian consensus of Run 2 (Fig. 15.2) resulted in a fully resolved tree with a topology that is similar to the strict consensus trees presented by Parker (2016a, fig. 7), Reyes et al. (2020, fig. 8), Paes Neto et al. (2021c, fig. 8), and the Bayesian consensus tree presented by Reyes et al. (2024, fig. 11d). The Aetosauria is composed of two major clades, Aetosaurinae and Stagonolepidoidea (Parker, 2016a), however several taxa shifted in their topological position. *Aetosauroides scagliai* is no longer recovered as a non-stagonolepidid aetosaur; instead, it is recovered as a sister taxon of the Stagonolepidoidea (Fig. 15.2). The topological position of *Stenomyti huangae* remains unstable as it is recovered within the Stagonolepidoidea in our analysis but has also been recovered at the base of the Aetosaurinae (Parker, 2016a; Reyes et al., 2020, 2024) or in a polytomy at the base of the Aetosauria (Paes Neto et al., 2021c; Haldar et al., 2023). Although the anatomy of *Stagonolepis robertsoni* is most similar to that of *Calyptosuchus wellesi*, our Bayesian analysis recovers it basal to the Desmatosuchini alongside *Stagonolepis olenkae* as observed in Reyes et al. (2024). The inclusive clades Desmatosuchini, Typothoracinae, and Paratypothoracini are recovered as seen in previous studies (Parker, 2016a; Reyes et al., 2020, 2024; Paes Neto et al., 2021c; Haldar et al., 2023). It is evident that the addition of four new characters and rescored did not influence the topological position of *Calyptosuchus wellesi* because it still forms an inclusive clade (= Calyptosuchini n. clade) with *Scutarx deltatylus* and *Adamanasuchus eisenhardtae*.

Discussion

Obturator foramina within the Aetosauria

Prior to the discovery of PEFO 46222, the presence of two foramina had only been documented on the pubic apron within the pubis of *Scutarx deltatylus* (PEFO 31217, Parker, 2016b) and *Stagonolepis*

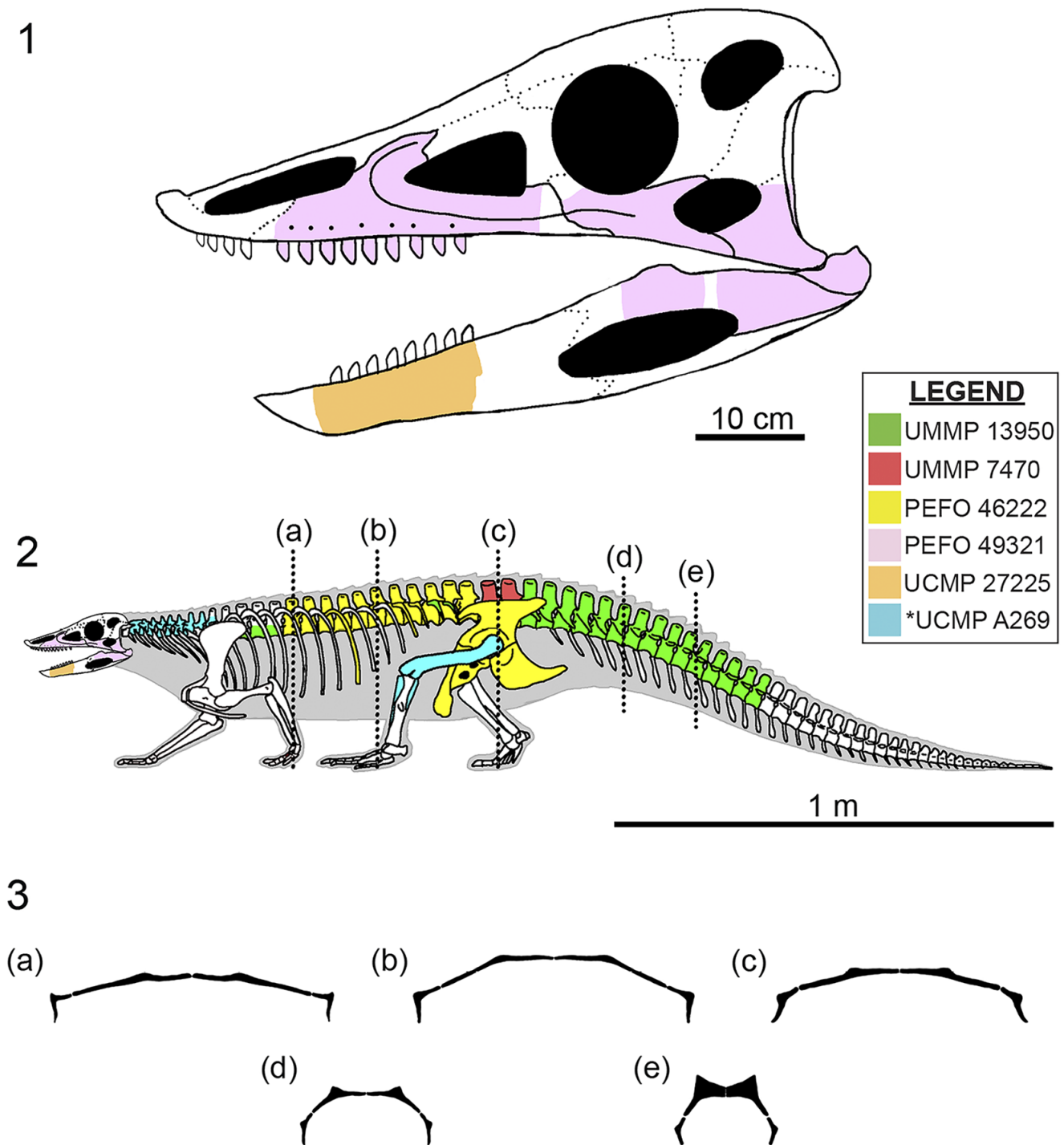


Figure 13. Hypothetical reconstructive illustrations of *Calyptosuchus welllesi*. (1) Skull reconstruction in left lateral view based on PEFO 49321 and UCMP 27225, and the closely related taxa *Neoaetosauroides engaeus* (Desojo and Báez, 2007) and *Scutarx deltatylus* (Parker, 2016b). Dotted lines indicate hypothetical contacts. Colored regions indicate anatomy preserved. (2) Skeletal reconstruction in left lateral view. The osteoderms are excluded, but the carapace is incorporated into the silhouette of the body. The reconstruction of *Stagonolepis robertsoni* (Walker, 1961) served as the template, but was modified accordingly based on the anatomy of UCMP 27225, PEFO 46222, PEFO 49321, UMMP 7470, UMMP 13950, and specimens referred to *C. welllesi* from UCMP A269 (the Placerias Quarry) by Parker (2018a). Colored regions based on specimen(s) that best exemplify the anatomy. The specimens from UCMP A269 are incorporated into a single label (* = fossil locality). (3) Transverse cross-sections of the dorsal carapace through (a) anterior middle trunk, (b) posterior middle trunk, (c) sacral, and (d) anterior portion and (e) middle portion of the middle caudal regions. Cross-sections (not to scale) of the dorsal carapace are based on PEFO 46222; sectioned regions are represented by vertical dashes in (2).

robertsoni (NHMUK R4793, MCZD 4, Walker, 1961). Small and Martz (2013, p. 407) described “two shallow notches” in the broken pubic apron of a pubis (DMNH V.34565) referred to *Stenomyti huangae*, suggesting that the pubic apron of this taxon may have also been perforated by two foramina as observed in *Scutarx deltatylus* (Parker, 2016b), *Stagonolepis robertsoni* (Walker, 1961),

and *Calyptosuchus welllesi* (PEFO 46222, Fig. 7). Recently, Desmet et al. (2022) suggested that the pubis of *Stagonolepis olenkae* also exhibits two ‘obturator foramina’ based on a right pubis (UOPB01143) that is part of an associated pelvis collected from the Upper Triassic strata in Krasiejów, Poland (Desmet et al., 2022). This is a region where *S. olenkae* is the only documented

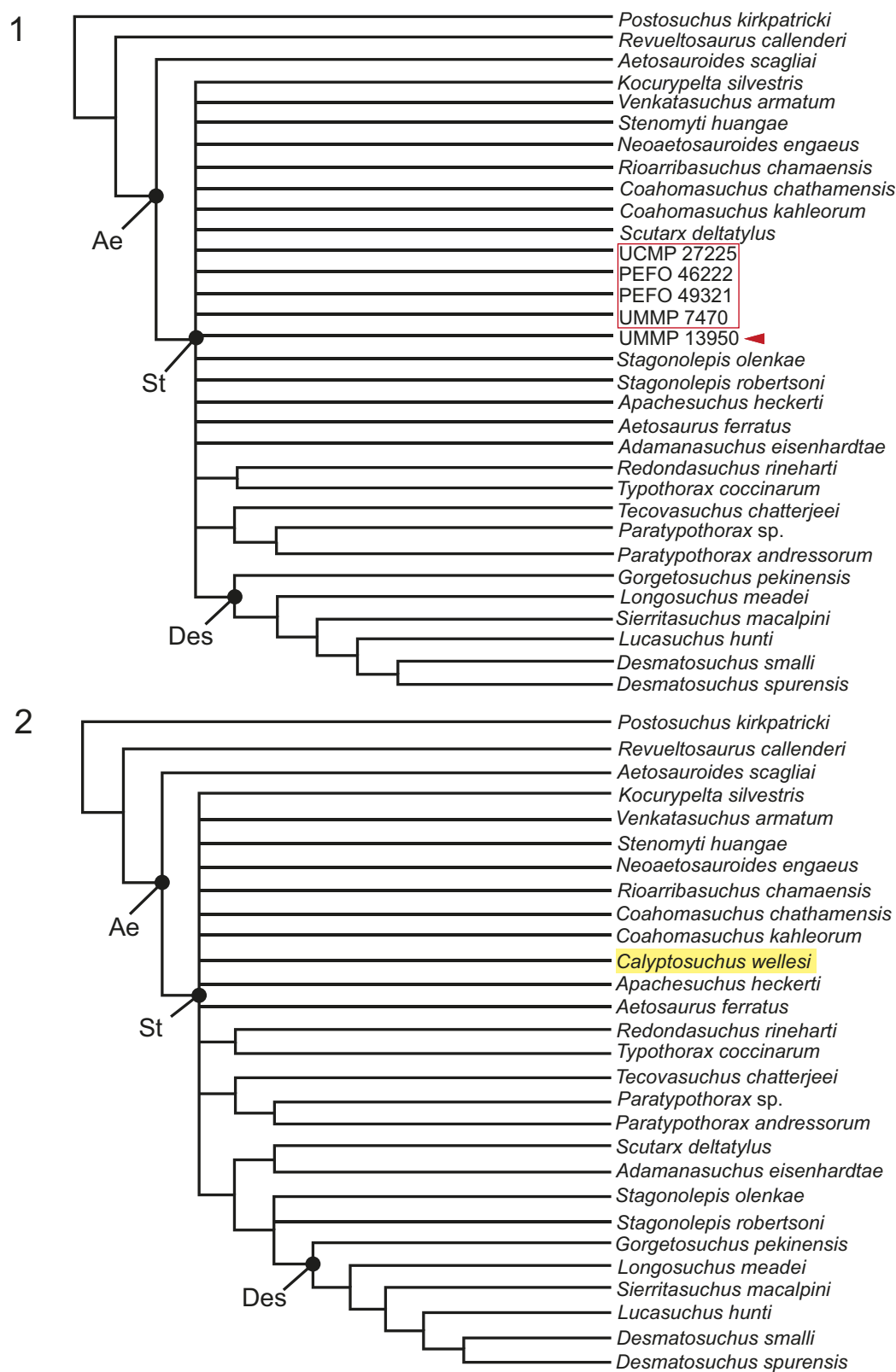


Figure 14. Maximum parsimony phylogenetic analyses. (1) Run 1: Strict consensus of the holotype specimen of *Calyptosuchus wellsi*, UMMP 13950 (indicated by red arrow), with other referred individuals (indicated by red-bounded box). (2) Run 2: Strict consensus of composite OTU *Calyptosuchus wellsi* (indicated by yellow highlight). Ae = Aetosauria; Des = Desmatosuchini; St = Stagonolepididae.

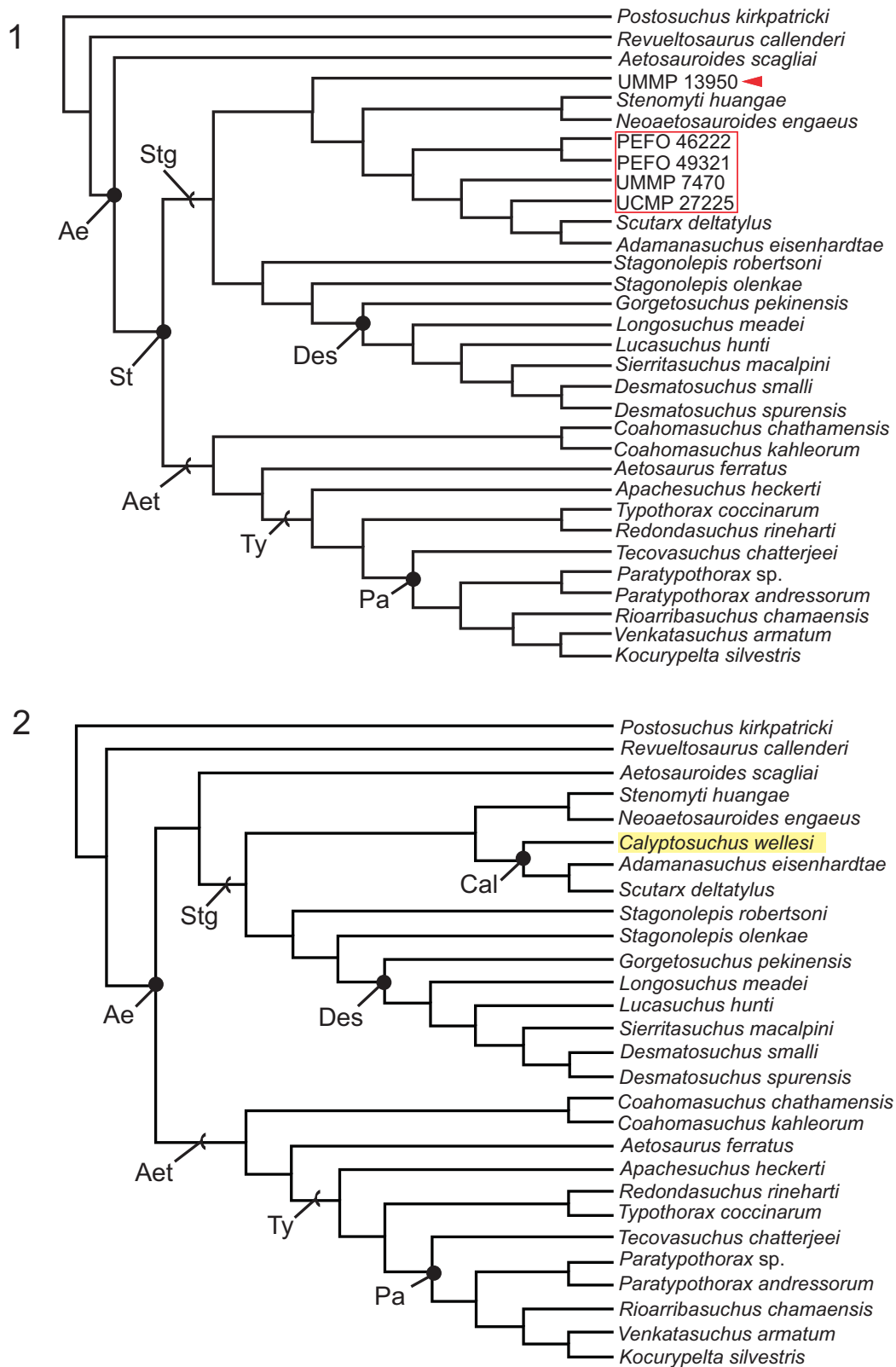


Figure 15. Bayesian inference phylogenetic analyses. (1) Run 1: Bayesian consensus cladogram of the holotype specimen of *Calyptosuchus welllesi*, UMMP 13950 (indicated by red arrow), with other referred individuals (indicated by red-bounded box). (2) Run 2: Bayesian consensus cladogram of composite OTU *Calyptosuchus welllesi* (indicated by yellow highlight). Ae = Aetosauria; Aet = Aetosaurinae; Cal = Calyptosuchini n. clade; Des = Desmatosuchini; Pa = Paratypothoracini; St = Stagonolepididae; Stg = Stagonolepidoidea; Ty = Typothoracinae.

aetosaurian within the Upper Triassic (Keuper) strata (Dzik and Sulej, 2007; Sulej, 2010; Antczak, 2015; Parker, 2016a; Teschner et al., 2022). However, pelvic material described from the same region by Drożdż (2022) suggests otherwise. Drożdż (2022) described several pelvic elements, including several pubes, that were recovered in association with dorsal paramedian osteoderms, which support their referral to *Stagonolepis olenkae*. This new material indicates the presence of only one obturator foramen within a well-preserved right pubis (ZPAL AbIII/3266) of *Stagonolepis olenkae*.

Desmet et al. (2022, fig. 11) described the presence of two 'obturator foramina' in UOPB01143, however the associated figures of this element do not support their interpretation; the 'obturator foramina' are labeled in lateral view, however in medial view there is no evidence of perforation on the bone surface. Instead, the bone surface is smooth and well preserved. Based on this, we interpret the two 'obturator foramina' described in UOPB01143 by Desmet et al. (2022) as taphonomic indentations of the bone surface, and the actual obturator foramen, or foramina, are not preserved. Thus, we follow the description of Drożdż (2022) and interpret *Stagonolepis olenkae* as exhibiting one obturator foramen similar to *Neoaetosauroides engaeus* (PVL 3525, Desojo and Báez, 2005) and *Desmatosuchus smalli* (TTU-P 9419, Martz, 2008; Martz et al., 2013). However, in recent years, several researchers (e.g., Lucas et al., 2007b; Antczak, 2015; Górnicki et al., 2021; Desmet et al., 2022) have suggested that *Stagonolepis olenkae* (Sulej, 2010) may be a junior synonym of *Stagonolepis robertsoni* (Walker, 1961) and attributed the few morphological differences of the skull and postcrania to intraspecific variation (i.e., sexual dimorphism, ontogenetic variation). Under this interpretation, the number of foramina within the pubis of *Stagonolepis robertsoni* would be considered variable. Further study is required to assess the taxonomic status of *Stagonolepis olenkae* (Sulej, 2010) and its relationship to *Stagonolepis robertsoni* (Walker, 1961).

It is evident that the number of foramina that perforate the pubic apron is variable within the Aetosauria (Parker, 2016b). The perforated region of the pubis is not preserved within the early-branching aetosauroid *Aetosauroides scagliai* (PFV 2073, Casamiquela, 1967; Heckert and Lucas, 2002a), thus inhibiting our ability to determine the plesiomorphic state of this condition within the clade. However, the presence of one obturator foramen within the non-aetosaur aetosauriformes *Acaenasuchus geoffreyi* (UCMP 285841, Marsh et al., 2020) and *Revueltosaurus callenderi* (PEFO 36875, Parker et al., 2021) suggests that this is the plesiomorphic condition within the Aetosauria and the presence of two foramina in *Scutarx deltatylus* (Parker, 2016b), *Stagonolepis robertsoni* (Walker, 1961), and *Calyptosuchus wellsi* (Fig. 7; PEFO 46222) is a derived condition. Outside of the Aetosauria, the presence of two foramina is also documented within the non-archosaur archosauriform *Euparkeria capensis* Broom, 1913, and the sauropodomorph *Sarhsaurus aurifontanalis* Rowe, Sues, and Reisz, 2011 (Marsh and Rowe, 2018), indicating that this condition convergently evolved within aetosaurs.

Among taxa that exhibit two foramina within the pubis, the dorsal foramen is considered homologous with the single obturator foramen observed in the pubis of most archosauromorphs (Ezcurra, 2016; Parker, 2016a). However, the obturator foramen is lost within crocodyliforms (Claessens and Vickaryous, 2012), turtles, and some dinosaurs (Hutchinson, 2001). In the literature, the ventral foramen has been referred to as a 'pubic foramen' (Rowe et al., 2011), 'secondary pubic foramen' (Hutchinson, 2001), or 'thyroid fenestra' (Walker, 1961). However, a thyroid fenestra is actually an opening that develops within the puboischadic plate

and is completely or partially enclosed by the pubis and ischium (Romer, 1956; Ezcurra, 2016); among saurian reptiles this condition is observed in lepidosauromorphs, tanystropheids, and trilophosaurids (Ezcurra, 2016; Pritchard and Sues, 2019). It is possible that this ventral foramen is homologous with the thyroid fenestra, however this requires further study. The function of the ventral foramen is presently not understood but it likely served a similar function as the single obturator foramen. It is possible that the obturator nerve and associated vessels split into two separate branches before exiting through the pubic apron, a feature that typically happens external to the pubis (Romer, 1956; Hutchinson, 2001; Claessens and Vickaryous, 2012).

Intraspecific variation within the Aetosauria

The influence of ontogeny is poorly understood among extinct archosaurs, particularly within the Aetosauria (Nesbitt et al., 2017; Griffin et al., 2021; Paes-Neto et al., 2021a). In recent years, histological analyses have provided insight into the intraspecific variation within the clade. Authors who studied skeletal growth documented a shift from highly vascularized, woven-fibered tissue to less-vascularized, lamellar tissue in the cortex of several taxa, indicating a shift in the rate of skeletal growth early in ontogeny (e.g., de Ricqlès et al., 2003; Werning, 2013; Scheyer et al., 2014; Taborda et al., 2015; Cerda et al., 2018; Hoffman et al., 2019; Ponce et al., 2023; Teschner et al., 2023). This new understanding has led to a new hypothesis in which the complexity in the dorsal ornamentation of paramedian osteoderms correlates with the transition in tissue vascularization (Hoffman et al., 2019).

Aetosauroides scagliai has been used as a sample taxon to explore the relationship between body size and growth rate within the Aetosauria because the taxon is known from several specimens that cover an array of body sizes (Taborda et al., 2013, 2015; Cerda et al., 2018). These authors determined that the lines of arrested growth (LAG) count varied significantly between similar-sized individuals and hypothesized that this disparity could be attributed to sexual dimorphism. Additionally, histological studies on *Typothorax coccinarum* indicate a discordance between skeletal maturity and body size, which is related to the variation in the timing of the co-ossification of the neural arch and centrum across the vertebral column (Parker et al., 2023).

Although aetosauroid elements, particularly their osteoderms, are commonly reported from Late Triassic strata (Desojo et al., 2013), most taxa are not represented by a large enough sample size that includes individuals at various ontogenetic stages and/or share homologous skeletal elements; the exception being the early-diverging aetosauroid *Aetosauroides scagliai* (Desojo and Ezcurra, 2011). The ontogenetic series of *Aetosauroides scagliai* indicates that phylogenetically informative characters such as the lateral fossae on the vertebral centra and centrodiapophyseal laminae are ontogenetically variable within the trunk vertebrae of *A. scagliai* (Paes-Neto et al., 2021a). This understanding resulted in a new hypothesis in which *Polesinesuchus aurelioi* Roberto-Da-Silva et al., 2014, a taxon documented exclusively through a skeletally immature specimen (ULBRA PVT003), represents a skeletally immature individual of *Aetosauroides scagliai* (Paes-Neto et al., 2021a). Thus, this brings to question the taxonomic status of small-bodied 'dwarf' aetosauroid taxa that are based on skeletally immature specimens (e.g., *Coahomasuchus chathamensis*, Heckert et al., 2017; Hoffman et al., 2019; *Aetosaurus ferratus*, Schoch, 2007; Schoch and Desojo, 2016; Scheyer et al., 2014; *Polesinesuchus aurelioi*, Roberto-Da-Silva et al., 2014; Paes-Neto et al., 2021a). Small-bodied taxa are present within

the Aetosauria (Desojo et al., 2013), as exemplified by *Sierritasuchus macalpini* (Parker et al., 2008). Historically, this taxon was hypothesized to either represent a juvenile of *Desmatosuchus* (Long and Murry, 1995) or *Longosuchus meadei* (Parker, 2002) due to the small body size of the type specimen UMMP V6081. However, histological analysis of UMMP V60817 indicated that the individual was not skeletally immature (Parker et al., 2008; Parker, 2016a). Similarly, Heckert and Lucas (2002b) hypothesized that small (< 25 mm) dorsal osteoderms collected from UCMP V7308 (Blue Hills locality) represented juvenile individuals of *Calyptosuchus* (= '*Stagonolepis*') *wellesi*, which is also documented from this locality based on UCMP 27225 (Long and Murry, 1995; Parker, 2018a), because of their size. However, revision of these osteoderms indicated these elements are referable to the aetosauriform *Revueltosaurus callenderi* (Parker et al., 2021).

Our new understanding of the anatomy of *Calyptosuchus wellesi* provides new insight into the intraspecific variation of the postcranial skeleton within the Aetosauria. Based on skeletal proxies including the proportional size of the ilia and complete co-ossification of the centra with their respective neural arches (Brochu, 1996), we hypothesize that PEFO 46222, UMMP 7470, and UMMP 13950 are of similar skeletal maturity. However, to independently assess that hypothesis, further histological sampling is needed because recent studies indicate that there is a disparity in the timing of the co-ossification of the neurocentral suture across archosaurs (Irmis, 2007; Griffin et al., 2021; Parker et al., 2023). PEFO 46222 records the only occurrence of co-ossification of the centra in the sacral vertebrae of *Calyptosuchus wellesi* (Fig. 6.1), a condition that was previously only documented in the desmatosuchins *Desmatosuchus* (Parker, 2005, 2007, 2008a) and *Longosuchus meadei* (TMM 31100-236). However, co-ossification of the sacral vertebrae is absent in UMMP 13950 (Fig. 12.3) and UMMP 7470 (Fig. 12.2) indicating that this is an area of intraspecific variation that may be attributed to ontogeny or sexual dimorphism. Although the sacral vertebrae in PEFO 46222 are co-ossified to each other, the posteriormost trunk vertebra is not co-ossified with the first sacral vertebra (Figs. 5, 6; = dorsosacral, Griffin et al., 2017). Among aetosaurs, incorporation of the dorsosacral into the sacrum is documented within *Desmatosuchus* (MNA V9300, Parker, 2008a), *Longosuchus meadei* (TMM 31100-236, Griffin et al., 2017), and ?*Lucasuchus huntii* (TMM 31100-313, Long and Murry, 1995). Thus, the absence of a dorsosacral in PEFO 46222 suggests that its incorporation is a derived condition of desmatosuchins.

PEFO 46222 preserves relatively complete vertebrae for most of the trunk series, a region that is poorly preserved in the holotype specimen UMMP 13950 (Fig. 4.2). Similar to *Aetosauroides scagliai* (Paes-Neto et al., 2021a), we document variation of the laminae within the trunk vertebrae of a single specimen of *Calyptosuchus wellesi*. In PEFO 46222, the posterior centrodiapophyseal lamina is weakly developed in the middle trunk region (Fig. 5.2) and becomes more prominent in the posterior trunk region (Fig. 5.8). Based on this observation, we hypothesize that the posterior centrodiapophyseal lamina may be more incipient in the anterior trunk region, but we cannot confirm this due to limited specimens and preservation. A well-defined postzygadiapophyseal lamina has been described in the middle trunk vertebrae of *Calyptosuchus wellesi* based on UMMP 7470 (Fig. 12.1; Parker, 2018a). However, that morphological feature is absent in PEFO 46222 (Fig. 5.3, 5.7), indicating that this state is variable in the taxon. Due to the poor preservation of the middle trunk vertebrae in UMMP 13950, we are unable to assess the presence of postzygadiapophyseal laminae in that specimen.

In addition to the noted variation in the vertebral column of *Calyptosuchus wellesi*, PEFO 46222 also provides more clarity on the

variation of the osteoderms across the dorsal carapace of the taxon (Figs. 8, 9, 15). We document variation associated with morphological characters of the anterior bar in paramedian osteoderms including the presence of a scalloped edge, anterior triangular projection, and the anterolateral process in the trunk region (Parker, 2016a). The scalloped edge and anterior triangular projection vary in how prominent or well incised they are across the same region of the carapace. Additionally, the anterolateral process varies in its lateral inclination with no real consistent pattern, however, as noted by Parker (2018a), it does reduce in its prominence/size caudally in the carapace. Our re-examination of the articulated carapace in UMMP 13950 indicates that the lateral edge of the paramedian osteoderms is weakly sigmoidal in the mid- through posterior-trunk region and is more straight in the caudal region, a feature that is also reflected in the adjacent lateral osteoderms.

Status of elements referred to *Calyptosuchus wellesi* from the Placerias Quarry

The new specimens from PEFO bring to question the taxonomic affinities of elements from the Placerias Quarry (UCMP A269) referred by previous authors to *Calyptosuchus wellesi* (e.g., Long and Murry, 1995; Parker, 2018a). UCMP 195193 is a partial right maxilla referred to *Calyptosuchus wellesi* by Parker (2018a) and is characterized by the presence of a 'pneumatic accessory cavity' (Fig. 11.6). However, when comparing this anatomical feature to that of *Stenomys huangae* (Small and Martz, 2013), *Desmatosuchus smalli* (Small, 2002), and *Stagonolepis* (Walker, 1961; Sulej, 2010; Parker, 2018b), it is evident that the 'pneumatic accessory cavity' described within UCMP 195193 is not homologous to those observed within the mentioned taxa because it is not characterized as an anteroposteriorly oriented pit positioned anteroventral to the junction of the anterior and ventral margins of the antorbital fenestra. Thus, the 'pneumatic accessory cavity' within UCMP 195193 is likely a taphonomic feature and is absent in this specimen as observed in PEFO 46222. However, this reinterpretation and the presence of a deep antorbital fossa that is delineated ventrally by a ridge on the lateral surface do support the referral of UCMP 195193 to *Calyptosuchus wellesi*, as originally proposed by Parker (2018a).

An isolated sacral vertebra (UCMP 139785) was originally referred to *Calyptosuchus wellesi* because it was not co-ossified to another trunk or sacral vertebra (Parker, 2018a), a condition characteristic of *Desmatosuchus* (Parker, 2005, 2008a), which is also present at UCMP A269 (Parker, 2018a; von Baczko et al., 2021). However, PEFO 46222 indicates that co-ossification of the sacral vertebrae, albeit variable, is a condition also exhibited by *Calyptosuchus wellesi* (Fig. 9.1). Thus, referral of the isolated sacral vertebra UCMP 139785 remains tentative.

Historically, the pelvic anatomy of *Calyptosuchus wellesi* was based on an associated left ilium and ischium (UCMP 25941 and UCMP 32148, respectively) from UCMP A269 (Fig. 11.4; Long and Murry, 1995; Parker, 2018a) due to the poor preservation of UMMP 13950 (Fig. 11.1) and distortion of UMMP 7470 (Fig. 11.2). Together, UMMP 13950, UMMP 7470, and PEFO 46222 (Fig. 12.1–12.3) provide a composite picture of the pelvic anatomy in *Calyptosuchus wellesi*, thus allowing us to assess the referral of UCMP 25941 and UCMP 32148 to *C. wellesi*. The ilia are similar in size across these individuals, yet they vary in the shape of the preacetabular process, inclination of the iliac blade, roundness of the postacetabular process, the outline of the ilium between the preacetabular process and pubic peduncle in lateral view, and the width of the acetabulum (Fig. 11.1–11.4). Additionally, the ischia do not share a rod-like body that becomes ventrally gracile near the ischiadic symphysis.

It is unlikely that UCMP 25941 and UCMP 32148 are referable to *Desmatosuchus*. The pelvic anatomy of *Desmatosuchus* is currently exemplified by that of MNA V9300, a specimen of *D. spurensis* that preserves a complete pelvic girdle that is heavily distorted and exhibits crushed preacetabular processes of the ilia (Parker, 2008a), thus, limiting the utility of MNA V9300 in our comparison. However, the acetabular region of UCMP 25941 does bear a resemblance to that of a partial ilium preserved within the holotype of *Desmatosuchus spurensis* (UMMP 7476, Parker, 2008a), which exhibits a poorly preserved preacetabular process and body, and is missing the postacetabular process. A recently prepared pelvic girdle (TTU-P 9419) from MOTT 3624 (the Post Quarry) that is referable to *Desmatosuchus smalli*, which is also reported from UCMP A269 (von Baczko et al., 2021), preserves nearly complete ilia that are undistorted, only missing their preacetabular processes. Based on TTU-P 9419, the postacetabular process of *Desmatosuchus* is not expanded and exhibits a posterodorsally inclined iliac blade in lateral view, which are conditions unlike that of UCMP 25941.

Although the anatomy of UCMP 25941 and UCMP 32148 from UCMP A269 show variation from the pelvic girdles of UMMP 13950, UMMP 7470, and PEFO 46222 (Fig. 11), their referral to *Calyptosuchus wellsi* remains contentious because they were collected in a quadrant dominated by osteoderms and vertebrae of that taxon (see Parker, 2018a). It is possible that the morphological variation observed in the pelvic girdles of these specimens is attributable to intraspecific variation, similar to the observed variation in the co-ossification of their sacral vertebrae (Fig. 12). Alternatively, although UCMP 25941 and UCMP 32148 are unlikely to be referable to *Desmatosuchus* (see above), they could be referable to either the typothoracine *Kryphioparma caerulea* (Reyes et al., 2023) or ambiguous paratypothoracin (Parker, 2005, 2007) that are also documented within UCMP A269 (Parker, 2007; Reyes et al., 2023; Parker and Haldar, 2024). Unfortunately, those taxa are known solely from their osteoderms and the loss of original association within UCMP A269 (Parker, 2018a) inhibits our ability to refer the pelvis in question to either taxon. Thus, the referrals of UCMP 25941 and UCMP 32148 to *Calyptosuchus wellsi* remain tentative. A better understanding of the intraspecific variation of the pelvic girdle in aetosaurians is needed to unambiguously reject their referral to *Calyptosuchus wellsi*.

Aetosaur ecology

Since the beginning of the twenty-first century, the ecology of aetosaurs has been a topic of high interest among aetosaur researchers (e.g., Small, 2002; Desojo and Báez, 2007; Desojo and Vizcaíno, 2009; Heckert et al., 2010; Sulej, 2010; Desojo and Ezcurra, 2011; Desojo et al., 2013; Biacchi Brust et al., 2018; von Baczko et al., 2018, 2021; Reyes et al., 2020; Paes Neto et al., 2021b; Taborda et al., 2021). This is due to the discoveries and/or reports of new specimens preserving dentigerous material for a variety of aetosaur taxa (e.g., *Aetosauroides scagliai*, *Calyptosuchus wellsi*, *Coahomasuchus kahleorum*, *C. chathamensis*, *Paratypothorax andressorum*, *Stenomylus huangae*, *Stagonolepis olenkae*, *Typothorax coccinarum*), which have brought to light the extent of the anatomical disparity in their dentition across the clade (Reyes et al., 2020; Paes Neto et al., 2021b). Based on this new understanding, their dentition can be generalized into three morphotypes: (1) a basally constricted, peg-like tooth with a bulbous, spade-like crown with fine serrations, as exemplified by *Desmatosuchus* (Small, 2002), *Stagonolepis* (Walker, 1961; Sulej, 2010; Antzack, 2015), and

Neoaetosauroides engaeus (Desojo and Báez, 2007); (2) a slightly basally constricted tooth with an apicobasally straight distal margin and curved mesial margin that meet at an apex that does not project distally beyond the basal margin, as exemplified by *Aetosaurus ferratus* (Schoch, 2007), *Stenomylus huangae* (Small and Martz, 2013), *Paratypothorax andressorum* (Schoch and Desojo, 2016), and *Calyptosuchus wellsi* (Fig. 3.11–3.14); and (3) a non-basally constricted tooth with a serrated and recurved crown with an apex that projects distally beyond the basal margin, as exemplified by *Aetosauroides scagliai* (Biacchi Brust et al., 2018; Paes Neto et al., 2021b) and *Coahomasuchus* (Parker, 2016a; Heckert et al., 2017). Currently, only *Typothorax coccinarum* exhibits a heterodont dentition that is composed of two of the mentioned morphotypes (Reyes et al., 2020).

Historically, it was hypothesized that aetosaurs represented an herbivorous group of archosaurs (Walker, 1961). However, because of the recognized disparity in their dentition, it is now hypothesized that aetosaurs were likely an omnivorous/faunivorous group (Small, 2002; Desojo and Báez, 2007; Desojo et al., 2013; von Baczko et al., 2018; Reyes et al., 2020; Paes Neto et al., 2021b). This hypothesis is further supported by the presence of recurved, serrated teeth in the clade (e.g., *Aetosauroides scagliai*, Biacchi Brust et al., 2018; Paes Neto et al., 2021b; *Coahomasuchus*, Parker, 2016a; Heckert et al., 2017; Parker et al., 2025), which is suggestive of a faunivorous ecology and rejects the previous hypothesis that they were strictly herbivorous animals (e.g., Walker, 1961). Additionally, the absence of taxa with ‘herbivorous-like’ teeth that are basally constricted and exhibit large denticles further weakens the hypothesis that aetosaurs were a herbivorous clade because this morphotype is typically associated with a herbivorous ecology (Parker et al., 2005) and is observed in other Late Triassic archosaurs such as the aetosauriforms *Revueltosaurus callenderi* (Parker et al., 2021) and *Acaenasuchus geoffreyi* (Marsh et al., 2020), as well as silesaurid dinosauriforms (e.g., Martz and Small, 2019). Thus, the dental morphology of *Calyptosuchus wellsi* (Fig. 3.11–3.14) does not align with that associated with a strictly herbivorous ecology, further bolstering the hypothesis that aetosaurs were likely an omnivorous/faunivorous group.

Calyptosuchus wellsi is recovered as a relative of *Neoaetosauroides engaeus*, *Stagonolepis*, and desmatosuchins within the Stagonolepidoidea (Fig. 15). However, its dentition is unlike that of those taxa, suggesting that the dentition among calyptosuchins may have diverged from the peg-like tooth exhibited by other stagonolepidoids. By proxy, this would suggest that calyptosuchins may have exhibited a different ecology from those taxa. If so, the variation in dentition among stagonolepidoids may correlate with why calyptosuchins and *Desmatosuchus* are often recovered together within fossiliferous localities (e.g., PFV 456, Reyes et al., 2023; UCMP A269, Parker, 2018a; MOTT 3624, Martz et al., 2013) in Norian-age strata of the southwestern United States (Parker and Martz, 2011). Their coexistence may indicate niche partitioning because these taxa likely would not have been in direct competition for resources (i.e., food), as suggested by the dental variation between *Calyptosuchus wellsi* (Fig. 3.11–3.14) and *Desmatosuchus smalli* (Small, 2002).

Conclusions

The discovery of two new specimens referable to *Calyptosuchus wellsi* from Petrified Forest National Park prompted re-interpretation of the holotype specimen (UMMP 13950) and provided new data on the cranial anatomy, ecology, positional variation, and intraspecific variation of the taxon (Fig. 13). The

first unambiguous cranial material of *Calyptosuchus wellsi* (PEFO 49321) indicates that its skull anatomy (Fig. 13.1) is similar to that of *Stagonolepis olenkae* and *Neoetosauroides engaeus*. Additionally, it highlights the disparate anatomy of the dentition within the Aetosauria, providing more support for the hypothesis that some members of the clade were more omnivorous/faunivorous than previously recognized (Desojo and Ezcurra, 2011; von Baczko et al., 2018, 2021; Reyes et al., 2020; Paes Neto et al., 2021b).

Aetosaurs, particularly their osteoderms, are considered biostratigraphically informative across the southwestern USA because they provide a means of temporally constraining Upper Triassic strata in the region (Long and Murry, 1995; Heckert and Lucas, 2000; Parker and Martz, 2011; Parker, 2016a; Martz and Parker, 2017), and their dorsal and lateral osteoderms play a key role in our ability to assess taxonomic affinities (Parker and Martz, 2010, 2011; Parker, 2016a). Thus, it is important that we understand the degree of variation within the dorsal carapace to improve phylogenetic and biostratigraphic hypotheses (Reyes et al., 2024). The associated skeleton of PEFO 46222 adds new understanding of the osteoderm anatomy and positional variation within the dorsal carapace of *Calyptosuchus wellsi* (Fig. 13.2, 13.3), thus refining our ability to document isolated osteoderms of *Calyptosuchus wellsi* and utilize them as a biostratigraphic marker to correlate Late Triassic strata across the southwestern USA (Parker and Martz, 2011).

PEFO 46222 also adds new insight into both the positional and intraspecific variation within the vertebral column of *Calyptosuchus wellsi*, particularly the documentation of co-ossified sacral vertebrae. This indicates that the co-ossification of the sacral vertebrae is more widely shared across the Aetosauria than previously recognized and suggests that it is likely associated with ontogeny or sexual dimorphism. This new anatomical understanding of *Calyptosuchus wellsi* expands our understanding of the inter- and intraspecific variation within the postcranial skeleton of aetosaurs.

The coding of polymorphic characters for *Calyptosuchus wellsi* did not influence its hypothesized topological position within the Aetosauria. The documentation of two foramina within the pubic apron of *Calyptosuchus wellsi* indicates that this state is more widely distributed across the Aetosauria than previously recognized and is a synapomorphy of the new clade Calyptosuchini. The recovery of *Stagonolepis robertsoni* as a non-calyptosuchin stagonolepidoid suggests that our current matrix needs to be further expanded to account for more morphological patterns within the clade because *S. robertsoni* exhibits a strong resemblance to *Calyptosuchus wellsi* as opposed to desmatosuchins. Our taxonomic reassessment of specimens previously referred to *Calyptosuchus wellsi* highlights the issue surrounding our ability to identify isolated elements from UCMP A269. The loss of original association inhibits our ability to refer many specimens, most of which remain taxonomically ambiguous, to known taxa or determine if they represent new, previously unrecognized species with a high degree of confidence (Parker, 2018a; Reyes et al., 2023).

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Competing interests. The authors declare none.

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