5-22-2018

Morphological and histological description of small metoposaurids from Petrified Forest National Park, AZ, USA and the taxonomy of Apachesaurus

Bryan M. Gee
University of Toronto Mississauga & Petrified Forest National Park, bryan.gee@mail.utoronto.ca

William G. Parker
Petrified Forest National Park

Taylor & Francis
Taylor & Francis Group

ARTICLE

Check for updates

Morphological and histological description of small metoposaurids from Petrified Forest National Park, AZ, USA and the taxonomy of *Apachesaurus*

Bryan M. Gee [a,b] and William G. Parker [b]

aDepartment of Biology, University of Toronto Mississauga, Mississauga, Ontario, Canada; bDivision of Science and Resource Management, Petrified Forest National Park, Petrified Forest, Arizona, USA

ABSTRACT

Metoposaurids are Late Triassic temnospondyls that are abundant components of freshwater depositional settings. Although metoposaurids are represented by hundreds of specimens in collections around the world, the vast majority pertain to large-bodied, relatively mature individuals, and as a result, the early stages of ontogeny are still poorly characterised. Small-bodied metoposaurids from North America have traditionally been assigned to *Apachesaurus gregorii*, interpreted as a diminutive taxon, but this interpretation has not been rigorously tested. Here we provide a morphological description of two new small-bodied metoposaurid specimens from Petrified Forest National Park, AZ, USA. Both provide various anatomical details that improve our understanding of small-bodied metoposaurids and their taxonomic placement within Metoposauridae. Furthermore, we perform a histological analysis on associated intercentra of these specimens, which indicates that these are relatively immature individuals. These findings support the growing consensus that *Apachesaurus* is a juvenile metoposaurid, thereby providing additional data regarding the early stages of metoposaurid ontogeny and evidence of the persistence of large-bodied forms into the late Norian. Accordingly, these findings merit a reevaluation of the taxonomic validity and diagnosis of the taxon and of the previous interpretations of its paleobiology.

Introduction

Metoposaurids are Late Triassic temnospondyls identified by the anterior placement of their orbits in contrast to other Mesozoic stereospondyls (e.g. Hunt (1993); Schoch (2008)). Although numerous taxa have been named from North America (e.g. Branson and Mehl 1929), only three are presently recognised as valid: *Koskinonodon perfectus* Case (1922), '*Metoposaurus*' *bakeri* Case (1931), and *Apachesaurus gregorii* Hunt (1993). Metoposaurids typically reach an adult size in excess of two meters with the exception of *A. gregorii*. Although metoposaurids are common constituents of Upper Triassic deposits, the vast majority of specimens belong to large-bodied, presumably mature, individuals with skull lengths in excess of 30 cm and occasionally exceeding 60 cm. Relatively complete skulls of these large-bodied metoposaurids number in the hundreds from mass death assemblages alone (e.g. Colbert and Imbrie 1956; Dutuit 1976; Sulej 2007; Lucas et al. 2016). Conversely, only a few dozen skulls that belong to small-bodied metoposaurids are known (Table 1), and the vast majority of these are extremely fragmentary. Descriptions of small-bodied metoposaurids are even rarer. Most of those specimens, which were assigned to *Apachesaurus*, are figured or described in a relatively generic sense (e.g. Hunt 1993; Long and Murry 1995; Spielmann and Lucas 2012). The handful of more thorough descriptions are limited to material that is more fragmentary or poorly-preserved than that used to diagnose large-bodied taxa (e.g. TMM 31099-12B, TTUP 9216 [Davidow-Henry 1987, 1989]; MNA V8415 [Zanno et al. 2002]; PEFO 35292 [Gee

and Parker 2017]). As a result, even the general ontogeny of metoposaurids (let alone that of specific taxa) is poorly constrained. Various studies have explored metoposaurid ontogeny using quantitative (e.g. Colbert and Imbrie 1956; Sulej 2007; Rinehart et al. 2009; Lucas et al. 2016) and histological (e.g. Steyer et al. 2004; Konietzko-Meier and Sander 2012; Konietzko-Meier et al. 2013; Konietzko-Meier and Klein 2013; Gee et al. 2017; Teschner et al. 2018) methods. However, those studies have either characterised a limited portion of the ontogenetic trajectory due to incomplete sample ranges or focused on postcranial material when current metoposaurid taxonomy rests almost entirely on cranial features (e.g. Hunt 1993).

The poor understanding of metoposaurid ontogeny in turn complicates metoposaurid taxonomy. This is particularly salient with regard to *Apachesaurus gregorii*, which is interpreted as a terrestrially inclined, diminutive metoposaurid with a much smaller adult body size than all other taxa (e.g. Hunt 1993; Spielmann and Lucas 2012). *Apachesaurus* is known primarily from isolated intercentra and fragmentary skull materials that were first collected from Arizona, New Mexico, and Texas in the early to mid-20th century (Gregory 1980). The first taxonomic assignment of this material was to *Anaschisma*, a large-bodied genus known from the Popo Agie Formation (late Carnian) of Wyoming, on the perceived basis of shared shallow otic notches in the holotypes of *An. browni* (UC 447) and *An. brachygnatha* (UC 448) (Gregory 1980). The shallow otic notches of these specimens are, in fact, an artefact that is exaggerated by plaster reconstruction in this region

---

Table 1. Listing of previously described or figured specimens of small metoposaurids. Specimens that were listed in the text without clear description of their material are not included. As there is no established quantitative metric for determining if a metoposaurid is 'small,' we rely primarily on the descriptions of these specimens by past authors. Because the elongate intercentra are a not a reliable feature for taxonomic differentiation of North American taxa (see Gee et al. 2017), and material should not be ascribed solely based on size, this list reflects only cranial material even though a much large number of specimens comprising various postcranial elements exists in collections. In general, a size threshold of a total skull length less than 30 cm characterizes the listed specimens. Page and figure numbers are provided for publications that describe a large number of specimens and/or taxa except when a specimen is only listed as a referred specimen with no further description or figuring. Taxonomic assignments reflect those provided by the listed references, although taxa have been updated to account for taxonomic acts such as synonymy. Specimens that cannot be referred to a particular taxon under an apomorphy-based identification system are marked by an asterisk (*). Although the holotype of *Dictyocephalus elegans* (AMNH 5661) is considered too fragmentary to be identified beyond Temnospondyli indet., it is included here as it has often been referenced in the literature as a small metoposaurid. This list should not be considered exhaustive, particularly because older works are less likely to have included scale bars or another appropriate reference measurements. Undoubtedly, material of small metoposaurids remains unprepared and undescribed in many collections. Institutional abbreviations: AMNH, American Museum of Natural History; MNA, Museum of Northern Arizona; MNHN, Museum National d'Histoire Naturelle; NM, New Mexico; NMMNH, New Mexico Museum of Natural History & Science; PEFO, Petrified Forest National Park; PPHM, Panhandle-Plains Historical Museum; SMNS, Staatliches Museum fur Naturkunde Stuttgart; TMM, Texas Memorial Musuem; TTU/TTUP, Texas Tech University Paleontology (abbreviation listed as in original reference); UCMP, University of California Museum of Paleontology; UM, University of Missouri; YPM, Yale Peabody Museum.

Taxon	Specimen	Locality	Reference
Apachesaurus gregorii	PEFO 16759	Chinle Fm, Arizona	this study
Apachesaurus gregorii	*NMMNH P-37069	Redonda Fm, New Mexico	Spielmann and Lucas (2012, figure 16A-D)
Apachesaurus gregorii	*NMMNH P-16948	Redonda Fm, New Mexico	Spielmann and Lucas (2012, figure 16E)
	*NMMNH 16948	Redonda Fm, New Mexico	Hunt (1993, figure 13C)
Apachesaurus gregorii	*TTUP 9126	Dockum Group, Texas	Hunt (1993, figure 13F)
			Spielmann and Lucas (2012, figure 17B)
	*TTU-P09126	Dockum Group, Texas	Martz et al. (2013, p. 6, figure 4)
Apachesaurus gregorii	*TTUP 9237	Dockum Group, Texas	Davidow-Henry (1987, p. 24–27)
			Hunt (1993, figure 13D)
			Davidow-Henry (1989, p. 280–285)
Apachesaurus gregorii	*UCMP 82/39/37	Chinle Fm, Arizona	Davidow-Henry (1987, p. 27–30)
			Hunt (1993, figure 13H)
	*UCMP V82250/171591		Spielmann and Lucas (2012, figure 18)
Apachesaurus gregorii	UCMP 63845	Redonda Fm, New Mexico	Hunt (1993, p. 84, figure 12–13)
			Spielmann and Lucas (2012, p. 15–25, figures 9–12)
Apachesaurus gregorii	*UCMP V6148/63852	Redonda Fm, New Mexico	Spielmann and Lucas (2012, figures 15A-B)
Apachesaurus gregorii	*UCMP V6148/63846	Redonda Fm, New Mexico	Spielmann and Lucas (2012, figures 15C,17A)
Apachesaurus gregorii	*UCMP V7308/175145	Chinle Fm, Arizona	Zanno et al. (2002)
Apachesaurus gregorii	*YPM 4201	Redonda Fm, New Mexico	Gregory (1980, p. 130, figure 7.2)
			Hunt (1993, figure 13E)
			Spielmann and Lucas (2012, figure 14A-B)
Apachesaurus gregorii	*YPM 4202	Redonda Fm, New Mexico	Spielmann and Lucas (2012, figure 14C-D)
'Dictyocephalus elegans'	*AMNH 5661	Cumnock Fm, North Carolina	Leidy (1856)
			Colbert and Imbrie (1956, figure 2)
Dutuitosaurus ouazzoui	MNHN XIII/12/65	Timezgadouine Fm, Morocco	Dutuit (1976, plate 32)
Dutuitosaurus ouazzoui	MNHN XIII/38/65	Timezgadouine Fm, Morocco	Dutuit (1976, plate 34)
Koskinonodon perfectus	UM 517	Popo Agie Fm, Wyoming	Branson and Mehl (1929, p. 65–73)
Koskinonodon perfectus	*MNA V8415	Chinle Fm, Arizona	Zanno et al. (2002)
Koskinonodon perfectus	*PEFO 35392	Chinle Fm, Arizona	Gee and Parker (2017)
Koskinonodon perfectus	PPHM WT 3011	Dockum Group, Texas	Lucas et al. (2016, figure 30C-D)
Koskinonodon perfectus	TMM 31099-12B	Dockum Group, Texas	Hunt (1993, figure 8A-B)
			Sawin (1945, p. 393, Table 1)
Metoposauridae indet.	PEFO 40023	Chinle Fm, Arizona	this study
Metoposaurus diagnosticus	SMNS 56633	Weser Fm, Germany	Sulej (2002, p. 538)
			Milner and Schoch (2004, p. 239–240, figure 2)
'Metoposaurus' bakeri	YPM PU 21742	Wolfville Fm, Nova Scotia	Baird (1986, p. 128)
			Hunt (1993, p. 77, figure 6)

(e.g. Branson and Mehl 1929; BMG pers. obs.), a point overlooked by Gregory. A succession of other workers in the 1980's discussed the possibly for *Apachesaurus* to be a novel species of various existing genera (summarized by Hunt 1989, p. 296) but did not formalize it through a taxonomic act. The taxon was finally formalized by Hunt (1993); since then, it has been revised only by Spielmann and Lucas (2012). The elongate intercentra considered diagnostic for the taxon (Hunt 1993; Milner 1994; Spielmann and Lucas 2012) are the most commonly recovered and referred material of *Apachesaurus*. In general, material of small-bodied metoposaurids has traditionally been referred to this taxon. However, this is often in spite of the absence of any preserved apomorphies that would differentiate it from juveniles of a large-bodied taxon under the interpretation of *Apachesaurus* as a diminutive metoposaurid (e.g. Long and Murry 1995).

Various features of *Apachesaurus* have been cited as evidence of its identification as a mature yet diminutive taxon (e.g. posterior position of the pineal foramen, dissimilarity to juveniles of some other taxa) and as a terrestrial form (e.g. poorly developed lateral line system) (Hunt 1993, p. 85). However, many of these interpretations relied on a small sample size of juveniles of large-bodied taxa, ontogenetic features of phylogenetically distant temnospondyls, and highly fragmentary material of *Apachesaurus* itself. The diagnosis of *Apachesaurus* comprises 13 characters, but most specimens preserve a minority of the 12 cranial characters (sensu Spielmann and Lucas 2012), and only the holotype (UCMP 63845) preserves the entire set. Furthermore, although *Apachesaurus* is considered to be an abundant late Norian taxon, the vast majority of the material that supports

that claim consists of isolated, elongate intercentra. However, it has long been recognized that the large-bodied taxon *Dutuitosaurus* from Morocco also possesses elongate intercentra (Dutuit 1976; Hunt 1993). Additionally, that feature was demonstrated to be unreliable for species discrimination by Gee et al. (2017) who found that elongation is a feature seen in juvenile individuals of North American metoposaurid taxa. Material that is referable to *Apachesaurus* based on the cranial characters and not on the basis of size is thus rare. The absence of coeval large-bodied forms, cited by past authors as evidence for the taxon's relative maturity (e.g. Hunt 1993), may reflect ecological partitioning between juveniles and adults. The latter idea was first proposed by recent workers (e.g. Rinehart et al. 2009; Lucas et al. 2016) as an explanation for the paucity of small-bodied, immature metoposaurids in older horizons. More recently, that hypothesis has also been explored in support of the alternative interpretation of *Apachesaurus* as a juvenile of a typically large-bodied taxon (e.g. Gee and Parker 2017; Gee et al. 2017). If adults and juveniles were geographically separated, settings inhabited by small-bodied metoposaurids could plausibly be preserved in a biased sample in the same way that mass death assemblages typically preserve only mature forms.

Here we present a description of partial skulls and associated postcrania of two small-bodied metoposaurids (PEFO 16759, PEFO 40023) from the late Norian of Petrified Forest National Park (PEFO), Arizona. The primary objective of this study is to further assess the morphology and systematics of small-bodied metoposaurids and the hypothesized diminutive adult size of *Apachesaurus* based on previous findings that contradict this interpretation. Both new specimens share a number of morphological features with the holotype of *Apachesaurus*. More importantly, histological sampling of associated intercentra of each specimen indicates that each individual was relatively immature at the time of death. Both specimens conform well in this regard to the general ontogenetic trajectory of intercentra of North American taxa that was described by Gee et al. (2017). These findings thus corroborate previous studies (e.g. Gee et al. 2017) in providing support for interpretations of *Apachesaurus* as a juvenile stage of a large-bodied metoposaurid. Given the absence of conclusive evidence that supports the original interpretation of the taxon as a diminutive metoposaurid, we are confident in designating *Apachesaurus* as a juvenile life stage of a taxon for which material of adults are presently unknown. Based on this interpretation, we maintain the taxonomic validity of *Apachesaurus* but provide a detailed revision of the diagnosis.

Materials and methods

Specimens

PEFO 16759 – partial skull with partial, articulated left mandible, nearly complete interclavicle and clavicles, and nineteen associated intercentra from RAP (*Revueltosaurus, Apachesaurus, Pseudopalatus*) Hill (PFV 216).

PEFO 40023 – nearly complete skull with semi-complete, articulated mandibles, a partial interclavicle and partial clavicles, ten associated to articulated intercentra, and miscellaneous postcrania (e.g. ribs, partial ilium) from Dinosaur Hill (PFV 040). Note that this locality is also referred to in the published literature as the Inadvertent Hills or Lacey Point Quarry, UCMP V82250 (Parker 2002).

We compared these specimens to published figures and descriptions of metoposaurids, particularly those of small-bodied specimens (e.g. Zanno et al. 2002; Spielmann and Lucas 2012). The holotype of *Apachesaurus* (UCMP 63845) has also been examined first-hand.

Geological provenance and age

PEFO 40023 was collected from Dinosaur Hill (PFV 040; Parker 2002), stratigraphically positioned in the Petrified Forest Member (Norian) of the Chinle Formation, by Adam Marsh (PEFO) and WGP in 2015. PEFO 16759 was collected from RAP Hill (PFV 216), also from the Petrified Forest Member, by Adrian Hunt (then of the Mesalands Dinosaur Museum) in the late 1990s. Both localities are blue paleosol horizons interpreted as low-energy abandoned channels and floodplain ponds by Loughney et al. (2011). Dinosaur Hill is slightly higher in the Chinle Formation than RAP Hill and is stratigraphically equivalent to Zuni Well Mound (PFV 215; Parker and Martz 2011), from which another small metoposaurid with associated intercentra (PEFO 35392) was described and histologically analysed (Gee and Parker 2017) (Figure 1). Material of *Apachesaurus* has previously been reported but never described from RAP Hill (e.g. Hunt and Wright 1999). Detailed descriptions of the fauna and depositional settings of these localities can be found in Therrien and Fastovsky (2000) and Loughney et al. (2011).

Preparation of specimens

Both specimens were prepared by BMG and WGP using a HW-70 microscribe and pin vises. Acryloid B-72 was used as an adhesive for reassembling PEFO 16759, and Butvar B-76 was used as a consolidant for both specimens. Specimens were photographed with a Panasonic Lumix DMC-LX100 digital camera; figures were compiled with Adobe Photoshop and Illustrator CS6. Comparative specimen measurements of the skulls were made using digital photographs and are presented in Table 2.

Intercentra measurements

Intercentra were measured using digital calipers (Table 3). Measurement parameters for the three axes follow those used by Konietzko-Meier et al. (2013) and Gee et al. (2017). Width was measured across the anterior articular surface between the parapophyses for all elements, including the atlas and axis. Height was measured across the same surface. Length was measured along the ventral surface between the articular surfaces. Determination of axial position was based primarily on the work of Sulej (2007) on
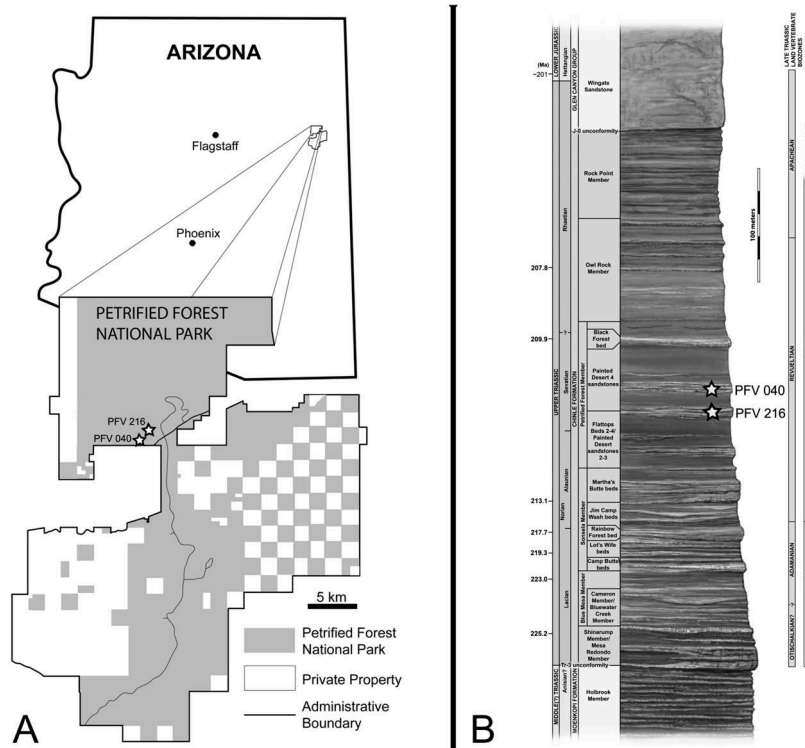
Figure 1. Geographic and stratigraphic provenance of PEFO 16759 and PEFO 40023. (A) Map of Petrified Forest National Park, modified from Parker and Irmis (2005); (B) stratigraphic column of Petrified Forest National Park modified from Martz et al. (2012). Stratigraphy follows Martz and Parker (2010) and Martz et al. (2012). Radioisotopic dates are from Ramezani et al. (2011).

Table 2. Comparative measurements of the holotype of *Apachesaurus gregorii* (UCMP 63845) and described skulls of small-bodied metoposaurids from Gee and Parker (2017) and this study. A 'greater than' value is provided for UCMP 63845 because the skull is nearly complete anteroposteriorly, lacking only the premaxillae, so the total preserved length is a reasonable estimate of its full length.

Measurement	UCMP 63845	PEFO 35292	PEFO 16759	PEFO 40023
Total skull length	> 18.2 cm	-	-	21.5 cm
Posterior postparietal – posterior orbit	10.3 cm	15.4 cm	8.4 cm	12.5 cm
Posterior postparietal – posterior pineal	3.9 cm	5.6 cm	-	-
Greatest width	13.7 cm	25.3 cm	13.4 cm	18.3 cm
Anterior orbit – anterior premaxilla	> 4.6 cm	-	-	5.9 cm

Metoposaurus krasiejowensis, which in turn derived from that of Dutuit (1976) on *Dutuitosaurus ouazzoui*.

Histological analysis

Because of the general uniformity in size, consistency in general axial position (e.g. presacral), and lack of precise axial position (e.g. sixth presacral), intercentra were evaluated for their overall completeness and condition in selection of elements for histological sectioning. Two trunk intercentra of each specimen were sampled (Figures 8(e,f), 9(a-d)). We interpret those of PEFO 16759 to pertain to the mid-trunk region. Those of PEFO 40023 are interpreted to pertain to the anterior trunk region. Following previous studies (e.g. Konietzko-Meier et al. 2013; Gee et al. 2017), intercentra were sectioned in both sagittal and transverse profiles. Histological preparation methods followed those of Gee et al. (2017, p. 8–9), with preparation of sections conducted at the Royal Ontario Museum (ROM), Toronto, Canada. Thin sections were imaged using a Nikon Instruments AZ100 Multizoom microscope fitted with AZ-Plan Apo 0.5 and

AZ-Fluor 5 objective lenses, an AZ-RP rotatable polariser plate, and a DS-Fi2 digital camera mount and with NIS-Elements imaging software.

Systematic palaeontology

Temnospondyli Zittel (1888) sensu Schoch (2013)
Stereospondyli Zittel (1888) sensu Yates and Warren (2000)
Metoposauridae Watson (1919)
Apachesaurus Hunt (1993) sensu Spielmann and Lucas (2012)
Apachesaurus gregorii Hunt (1993) sensu Spielmann and Lucas (2012)

Holotype

UCMP 63845, nearly complete skull from the Redonda Formation, Dockum Group, NM

Referred specimens

PEFO 16759, partial skull with pectoral girdle, mandible, intercentra; see Appendix 2 of Spielmann and Lucas

Table 3. Measurement data for intercentra associated with PEFO 16759 and PEFO 40023. Letter subdesignations are created solely for the purpose of this study. Positions are determined based on Sulej (2007). For PEFO 16759, all sub-letter designations correspond to those in Figure 8 except for specimens J-K; these are the two intercentra on the interclavicle (see Figure 6). For PEFO 40023, specimens A-H correspond to those in Figure 9; specimens I-K are the three articulated intercentra seen in Figures 3 and 7.

Specimen	Sub-letter	Width (mm)	Length (mm)	Height (mm)	W:L	Position
PEFO 16759	A	22.93	8.28	11.52	2.77	Atlas
	B	20.42	12.67	14.76	1.38	Mid-trunk
	C	15.02	11.75	12.88	1.28	Mid-trunk
	D	16.64	10.96	12.97	1.51	Mid-trunk
	E	16.40	11.03	13.24	1.24	Mid-trunk
	F	16.59	12.12	13.38	1.37	Mid-trunk
	G	15.28	12.30	12.67	1.24	Presacral
	H	15.36	-	11.95	-	Presacral
	I	-	10.33	12.66	-	Presacral
	J	-	12.80	-	-	Presacral
	K	-	14.18	-	-	Presacral
	L	17.39	13.06	-	1.33	Presacral
	M	-	11.93	14.52	-	Presacral
	N	13.35	12.97	-	1.03	Presacral
	O	-	11.60	-	-	?
	P	13.68	-	12.25	-	?
	Q	12.70	12.45	-	1.06	Presacral
	R	10.81	-	-	-	Presacral
	S	16.49	-	15.14	-	?
	T	14.39	13.71	-	1.05	Presacral
	U	-	14.3	-	-	Presacral
PEFO 40023	A	22.33	15.43	20.16	1.45	Anterior trunk
	B	21.93	14.22	19.36	1.54	Anterior trunk
	C	22.48	15.03	21.10	1.50	Anterior trunk
	D	22.19	14.55	20.35	1.52	Anterior trunk
	E	-	13.93	20.39	-	Anterior trunk
	F	19.87	12.72	18.91	1.56	Anterior trunk
	G	-	14.61	20.49	-	Perisacral
	H	19.61	15.10	18.46	1.30	Caudal
	I	23.39	-	-	-	Atlas
	J	22.15	9.84	-	2.25	Axis
	K	19.56	9.70	-	2.01	3rd

(2012, p. 116) for previously referred specimens not personally examined here.

Revised diagnosis

Metoposaurid characterised by the following autapomorphies: an occiput that does not project posteriorly; narrow cultriform process that tapers at the mid-length; reduced lacrimal excluded from the orbital margin; symmetrical, pentagonal squamosal with an anterior process that is not greatly transversely deflected; rounded, trapezoidal foramen magnum; dorsoventrally shorter oblique crest of the pterygoid; minimal expression of accessory paraquadrate foramen.

Remarks

Because *Apachesaurus gregorii* cannot be supported as being synonymous with another described taxon, nor can all 13 of the autapomorphies of Spielmann and Lucas (2012) be confidently determined to be being ontogenetically influenced, the taxon is maintained here. However, the revised diagnosis presented here (seven characters) removes features included by Spielmann and Lucas (2012) that are shared with other taxa or that can be reasonably questioned because of confounding influences by ontogeny, taphonomy, or intraspecific variation. Detailed explanations of the rationale for the validity of each character are provided in Appendix 1. Although taxonomic diagnoses are typically based on skeletally mature material in order for phylogenetic analyses to properly compare morphologies across taxa, such material that could be referred to *Apachesaurus* remains unknown.

Institutional abbreviations

MNHN, Muséum National d'Historie Naturelle, Paris, France; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; PEFO, Petrified Forest National Park, Petrified Forest, Arizona, USA; PPHM and WT, Panhandle-Plains Historical Museum, Canyon, Texas, USA; TMM, Texas Vertebrate Paleontology Collections, The University of Texas at Austin, Austin, Texas, USA; TTUP, Museum of Texas Tech, Lubbock, Texas, USA; UC, Field Museum, Chicago, Illinois; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA; YPM VPPU, Yale Peabody Museum, Princeton Collection, New Haven, Connecticut, USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Description

PEFO 16759 consists of a partial skull articulated with a partial left mandible, the interclavicle, and both clavicles. The skull is also associated with 19 isolated intercentra, mandible fragments, and various isolated postcrania (e.g. partial ribs); non-metoposaurid

material (e.g. *Revueltosaurus* teeth) is also catalogued under the same number. Most of the intercentra associated with the specimen are disarticulated and spread between four small blocks; none of the blocks articulate with each other. An additional seven intercentra were found isolated, including an atlas. Based on their conserved size relative to two intercentra that lie ventral to the interclavicle in a more confident association with the cranial material, we consider it reasonable to associate them with the skull. Even if they belong to another individual, it would be of a comparable size and presumed ontogenetic maturity, which is the primary consideration for the histological analysis.

PEFO 40023 consists of a nearly complete skull articulated with both mandibles, the atlas-axis complex and the third vertebral position, the interclavicle, and both clavicles. The axis and the third intercentra are articulated with elongate elements that we interpret as partial ribs. Seven intercentra were found posterior to the third vertebral position and are assigned to the specimen on the basis of a comparable size, the relative association, and their designation as anterior trunk intercentra. The skull has been variably fractured, often along sutural contacts, in a fashion such that different regions of the skull are broken off and angled, often ventromedially. The left side of the skull is more heavily fragmented, and the characterization of the cranial elements is derived primarily from the right side. Only the skull roof is present, exposed in both dorsal and ventral profiles with the loss of the palate. The right mandible is nearly complete, although it is broken posteriorly around the end of the tooth row. The left mandible lacks a large portion of the ventral surface. The three pectoral elements overlie each other, with the right clavicle being positioned ventral to the interclavicle, which in turn overlies the left clavicle. All three elements are only partially complete posteriorly, which is in part due to damage sustained during collection. Comparative measurements of these specimens were made with the holotype of *Apachesaurus* (Spielmann and Lucas 2012, figure 9) and with another small-bodied metoposaurid from PEFO that was described by Gee and Parker (2017) (PEFO 35392). These are presented in Table 3.

Skull roof

The metoposaurid skull roof is highly conserved relative to other temnospondyl clades. The description of the cranial elements presented here is considered representative of both specimens (Figure 2–3), with deviations noted where applicable; these specimens are also compared to other metoposaurid taxa where possible.

The premaxilla is a small element that forms the tip of the snout. It contacts the maxilla posterolaterally and the nasal posteromedially to frame the narial opening, which is visible on the right side of PEFO 40023 (Figure 3). At least four vacant tooth sockets are exposed ventrally. The left premaxilla is identified on the basis of the continuous rostral margin when viewed anteriorly. The premaxilla is a conserved element aside from minor variation in the relative contribution to the narial margins. The contribution to the lateral medial margin and the development of the lateral line on the premaxilla, two features that differ between *Apachesaurus* and large-bodied metoposaurids, cannot be characterised in PEFO 40023.

Neither specimen preserves the maxillae or the lacrimals. Fragments of either may be present in PEFO 40023 but cannot be confidently identified as such.

The prefrontal is a polygonal bone with significant variation intraspecifically and interspecifically, ranging from crescentic to pentagonal; this is best illustrated in descriptions of mass death assemblages (e.g. Sulej 2007; Lucas et al. 2016). Its sutural contacts remain consistent insofar as it sutures to the lacrimal laterally, to the maxilla anterolaterally, to the nasal anteromedially, to the frontal medially, and to the postfrontal posteriorly, forming the medial and anterior margin of the orbit, but the precise nature of these contacts (e.g. straight versus oblique versus curved sutures) is variable. In PEFO 40023, both prefrontals are defined by their contributions to the medial orbital margin (Figure 3). They are nearly complete, although the posterior end of the left prefrontal may be broken near to or at the suture with the postfrontal. In the case of the latter, the prefrontal's contribution to the medial margin would be approximately equal to that of the postfrontal. The anterolateral margins are poorly defined or obscured.

The nasal is a rectangular element that sutures to the premaxilla anteriorly, to the maxilla laterally, to the prefrontal posterolaterally, and to the frontal posteriorly. The nasals are lost in PEFO 16759. In PEFO 40023, the right nasal is complete, but it has been dislodged such that it overrides the anterior portion of the frontals and a portion of the prefrontal, resulting in the shape of the naris being slightly altered (Figure 3). The left nasal is more dislodged, is incomplete posteriorly, and is obscured anteriorly by various other elements. Contact of the nasal with the lacrimal is a variable feature of metoposaurids but cannot be characterised here.

The frontal is an elongate, rectangular element that is expanded anterolaterally before tapering slightly posteriorly. It is sutured to the nasal anteriorly, to the prefrontal anterolaterally, to the postfrontal posterolaterally, and to the postparietal posteriorly. The frontals are complete in PEFO 40023. The left frontal is fractured at about the mid-length, with the posterior fragment slightly uplifted; both frontals are overlapped anteriorly by the displaced right nasal (Figure 3). The posteromedial tapering of the frontals is variable among metoposaurids. Typically, the element gradually expands posterolaterally to the sutural junction with the pre- and postfrontal and then tapers. The posterior tapering is most pronounced in *Dutuitosaurus* (e.g. MNHN XIII/36/66 [Dutuit 1976, figure 2, plate 6]) and '*Metoposaurus*' *bakeri* (e.g. UMMP 13005 [Case 1931, figure 1]). Spielmann and Lucas (2012, p. 15) state that the tapering is less pronounced in *Apachesaurus* compared to most other metoposaurids save for *Arganasaurus*, but their comparative figure (Spielmann and Lucas 2012, figure 13) does not indicate appreciable differences between *Apachesaurus, Koskinonodon perfectus*, and *M. diagnosticus*. The posterior tapering of the element is generally more abrupt in *Apachesaurus* and '*M.*' *bakeri* (e.g. UMMP 13005 [Case 1932]; UCMP 63845 [Spielmann and Lucas 2012]), a condition seen in PEFO 40023. However the degree and nature of tapering also appear to vary intraspecifically in *K. perfectus* based on the figures of Lucas et al. (2016, figures 27–34 [compare, for example, WT 3116–1 with PPHM 9). This variation is reduced in *M. krasiejowensis*, but
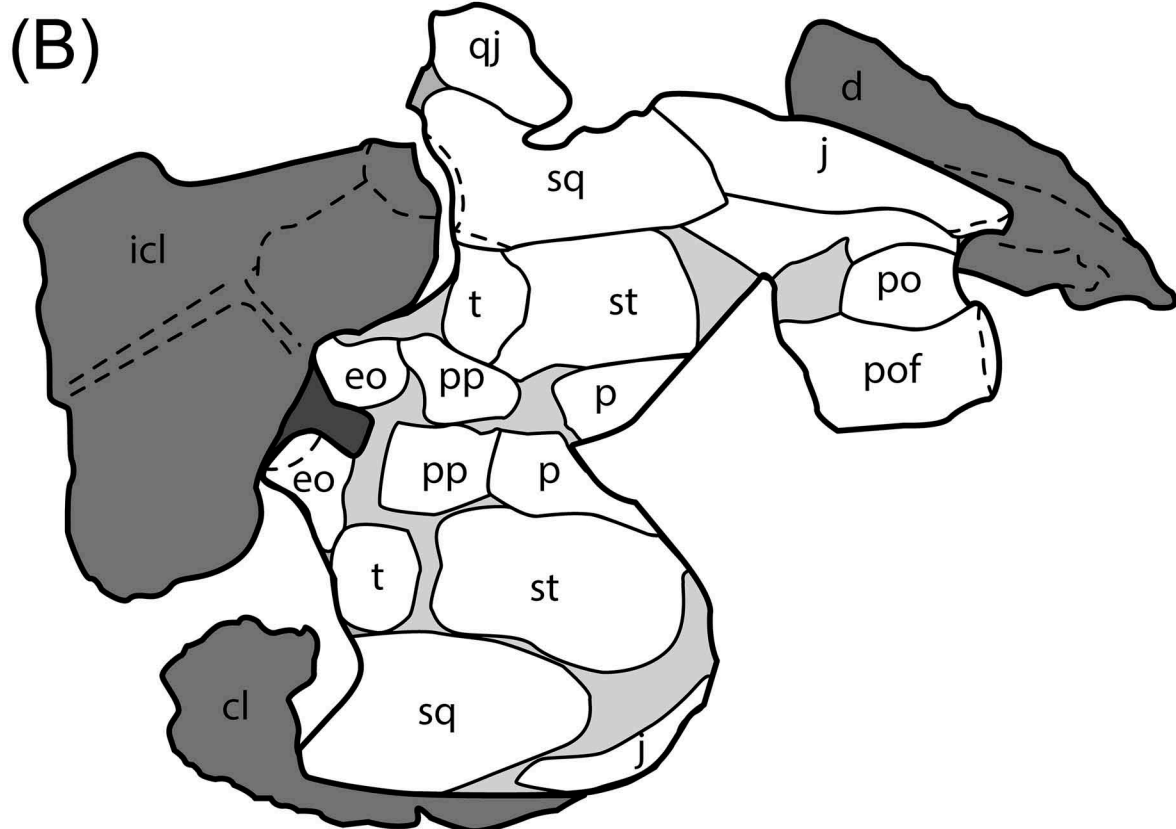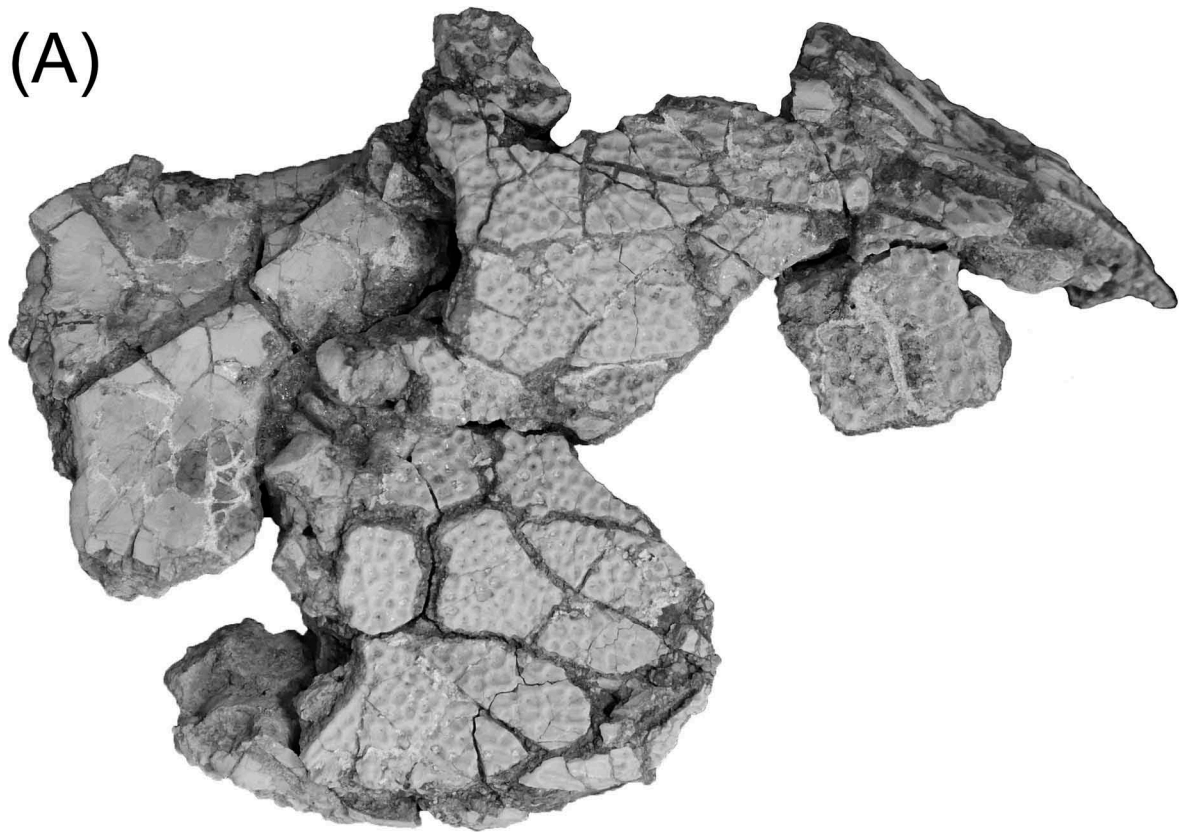
Figure 2. Dorsal profile of PEFO 16759. (A) photograph; (B) outline drawing. Darkest grey represents sediment-infilled areas. Abbreviations: cl, clavicle; d, dentary; eo, exoccipital; icl, interclavicle; j, jugal; p, parietal; po; postorbital; pof; postfrontal; pp, postparietal; qj, quadratojugal; sq, squamosal; st, supratemporal; t, tabular. Scale bar equals 5 cm.

Figure 3. Dorsal profile of PEFO 40023. (A) photograph; (B) outline drawing. Darkest grey represents sediment-infilled areas; black represents holes. Abbreviations: cl, clavicle; d, dentary; f, frontal; ic, intercentrum; icl, interclavicle; j, jugal; n, nasal; p, parietal; pf, prefrontal; pmx, premaxilla; po, postorbital; pof, postfrontal; pp, postparietal; qj, quadratojugal; r, rib; sq, squamosal; st, supratemporal; t, tabular. Scale bar equals 5 cm.

significant asymmetry between the frontals within an individual is also noted (e.g. ZPAL ABIII/358, Sulej 2007, figure 13).

The postfrontal is an elongate, polygonal element that is sutured to the frontal medially, to the prefrontal anterolaterally, to the postorbital laterally, to the supratemporal posterolaterally, and to the parietal postermedially. The postfrontals are present in both specimens, but those of PEFO 16759 are represented only a minute sliver sutured posteriorly to the supratemporal on the right, and by the anteriormost region at the posterior orbital margin on the left. In PEFO 40023, the right postfrontal is broken anteriorly, with a small portion, containing the orbital margin, being slightly dislodged; the remainder of the element is articulated with the right frontal. The left postfrontal can only be tentatively identified by the position of elements relative to the fragmentary orbit and by comparison with the right side. It is fragmented in several locations and as with the other left lateral elements, slopes ventromedially.

The postorbital is an elongate, polygonal element that is sutured to the jugal laterally, to the squamosal posterolaterally, to the supratemporal posteromedially, and to the postfrontal medially. It gradually expands transversely toward the posterior region and contributes to the posterior orbital margin. The postorbitals are present in both specimens but are represented in PEFO 16759 only by the anterior portion of the left postorbital at the orbital margin (Figure 2). In PEFO 40023, the right postorbital appears complete, although the posteriormost region is difficult to characterise because of dislodging of the elements on this side. The left postorbital is present but is fractured in several places and identified on the basis of its relative position and by comparison with the right side (Figure 3).

The parietal is an elongate, rectangular element that is sutured to the frontal anteriorly, to the postfrontal anterolaterally, to the supratemporal laterally, and to the postparietal posteriorly. The parietals normally frame the pineal foramen medially in the posterior third of the anteroposterior length, but this opening is not demarcated in either specimen. In PEFO 16759, the right parietal is broken at the anteromedial region, forming a trapezoidal shape with an anterior edge sloping anterolaterally. The left parietal is similarly preserved only posteriorly and is almost entirely overlain by the left supratemporal. In PEFO 40023, the right parietal is mostly intact, although it is broken at the mid-length with minor dislodging and rotated away from the posterior margin of the frontal. The left parietal is angled steeply anteroventromedially and is incomplete anteriorly. The element is conserved in shape and sutural contacts among metoposaurids. Illustrations of *Arganasaurus* (e.g. Spielmann and Lucas 2012, figure 13) indicate that *Arganasaurus* has a broader parietal with a more pentagonal profile compared to the rectangular profile of other taxa. However, photographs of specimens (e.g. MNHN XIX/3/66 [Dutuit 1976, plates 49–50]) indicate a far less disparate morphology.

The postparietal is a rectangular element, longer anteroposteriorly than mediolaterally, which contributes to the posteromedial margin of the skull table. It sutures to the tabular laterally, to the supratemporal anterolaterally, and to the

parietal anteriorly. The postparietals are present in both specimens, but they are either damaged or partially obscured. The right postparietal of PEFO 16759 is partially overlain medially by its counterpart, which in turn is overlain by the left tabular (Figure 2). The right postparietal of PEFO 40023 is similarly overlain by its counterpart; the left postparietal is missing an anteromedial region (Figure 3). The morphology and sutural contacts of the postparietal are conserved among metoposaurid taxa.

The supratemporal is an elongate, pentagonal element similar to the squamosal and of a comparable length and width to the parietal. It is sutured to the postorbital anteriorly, to the squamosal laterally, to the tabular, posteriorly, to the postparietal posteromedially, and to the parietal medially. In PEFO 16759, both supratemporals are nearly complete, although each is fractured in several places anteriorly. The lateral and medial margins are anteroposteriorly oriented. They taper anteriorly to a point that is medially positioned and directed (Figure 2). In PEFO 40023, the supratemporals are identified by their relative position and are more fragmentary (Figure 3).

The jugal is an elongate element that is typically sutured to the maxilla anteriorly and ventrolaterally, to the lacrimal anteromedially, to the postorbital medially, to the squamosal posteriorly, and to the quadratojugal posterolaterally; it also contacts the prefrontal in taxa with a lacrimal excluded from the orbit, which is unclear in these specimens. In PEFO 16759, the left jugal is partially complete, lacking the posterolateral region that would suture to the quadratojugal and the anteriormost region that forms the anterolateral orbital margin (Figure 2). In PEFO 40023, the left jugal appears to have been mostly lost, save for a few isolated fragments along the lateral margin (Figure 3). The right jugal is fully exposed, but broken at about the mid-length, with the posterior portion significantly shifted upward. The anterior portion that comprises the lateral orbital margin has been slightly medially shifted into the orbit and lies at the same level of the tooth row on the dentary (Figure 3).

The tabular is a small rectangular element, longer mediolaterally than anteroposteriorly, and contributes to the posteromedial margin of the skull table. It sutures to the squamosal laterally, to the supratemporal anteriorly, and to the postparietal medially. It also forms the medial margin of the otic notch. The tabulars are present in both specimens, although the left tabular of PEFO 16759 is partially obscured by the overlying squamosal, and the left tabular of PEFO 40023 is mostly absent. A particularly important feature for metoposaurid taxonomy is the tabular horn, found in all large taxa, but not in *Apachesaurus*. There is no tabular horn in PEFO 16759, nor is there any evidence of one having been broken off; however, the more complete right tabular has also been weathered at the corners. Conversely, a partial tabular horn lacking the distal-most portion is present in the larger PEFO 40023 (Figure 3). Both the horn and the otic notch of this specimen are not as developed as in larger metoposaurids, but they are more pronounced than in *Apachesaurus* (e.g. UCMP 63845 [Spielmann and Lucas 2012, figures 9–10]) and in PEFO 16759. The depth of the otic notch is comparable to a previously described juvenile metoposaurid (PEFO 35392)

(Gee and Parker 2017). The tabular horn appears relatively susceptible to taphonomic damage in all large metoposaurid taxa for which a reasonably large sample size is known and either sufficiently well-described or figured (e.g. *Dutuitosaurus, Metoposaurus krasiejowensis; Koskinonodon perfectus*) (Dutuit 1976; Sulej 2007; Lucas et al. 2016), so its absence in any given specimen must be carefully examined for taphonomic influence.

The squamosal is a large, pentagonal element characterised by lateral and medial margins that are nearly straight antero-posteriorly and that taper to an anterior point. It is sutured to the quadratojugal laterally, to the jugal anterolaterally, to the post-orbital anteromedially, to the supratemporal laterally, and to the tabular posteromedially, where it forms the majority of the otic notch dorsally and laterally. The squamosal is also readily iden-tifiable by its differential ornamentation, which consists primar-ily of a pattern of elongate grooves that radiate anteriorly and laterally from a posteromedial center of smaller pits near the tabular. In PEFO 16759, the right squamosal is nearly complete, although the anteriormost region is fragmented; the lateral margin appears essentially intact and may be broken along the suture with the absent quadratojugal (Figure 2). The sensory groove is well-defined along this margin. The left squamosal is more fragmentary, preserving the posterior region that contri-butes to the otic notch, some of the medial portions, and the anterior portion that sutures to the postorbital and the jugal (Figure 2). In PEFO 40023, the right squamosal is broken into several pieces but is essentially complete (Figure 3). A ventro-lateral portion of the element that would have framed the para-quadrate foramen is also present in occipital view, though the foramen itself is not preserved. The left squamosal is fractured into too many pieces to provide any additional information. The morphology of the squamosal varies among metoposaurids with regard to a lateral expansion; this can be seen, for example, in

Koskinonodon perfectus (e.g. WT 3114, WT 3011–3 [Lucas et al. 2016, figures 34A, 34E]) in which it is often proportionately wider, resulting in an expanded temporal lobe. Otherwise, its sutural contacts are consistent across taxa. Illustrations of *Arganasaurus* (e.g. Spielmann and Lucas 2012, figure 13) indi-cate that *Arganasaurus* has a more triangular squamosal. However, specimen photographs (e.g. MNHN XIX/3/66 [Dutuit 1976, plate 49A]) do not support this and instead indicate a comparable morphology to other taxa. The lack of a medial deflection of the anterior process is considered diagnos-tic for *Apachesaurus* (Spielmann and Lucas 2012). The anterior tip of the squamosals of PEFO 16759 are not significantly deflected in either direction. Conversely, the right squamosal of PEFO 40023 appears more medially deflected in a comparable fashion to large metoposaurids (Figures 2 and 3). We note however that the anterolateral margin in PEFO 40023 is not well-defined because of the displacement of the posterior por-tion of the postorbital.

The quadratojugal is a small, elongate element that forms the posterolateral corner of the skull with both a dorsal and a lateral exposure and that sutures to the maxilla anterolaterally, to the jugal anteriorly, and to the squamosal medially. Neither quadra-tojugal is well-preserved in PEFO 16759. The element appears to have been sheared off along the suture with the squamosal on the right side (Figure 2). There is only a small posterolateral portion of the left quadratojugal that is identifiable in occipital profile. In PEFO 40023, only the right quadratojugal is confidently identifi-able. It is slightly dislodged from the skull and rotated into a more vertical orientation, rendering it difficult to identify the precise contours (especially because of the displaced squamosal and jugal). It is readily identifiable in ventral profile (Figure 7) where the smooth ventral margin is positioned lateral to the mandible.

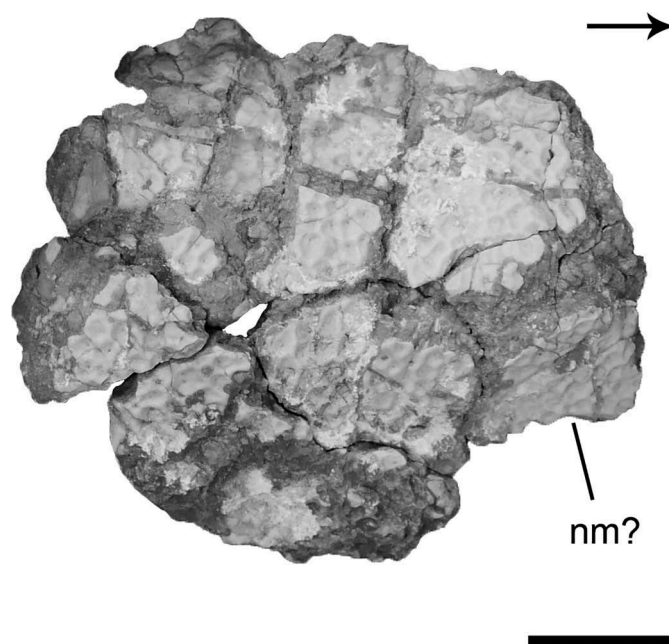An additional ornamented cranial fragment is catalogued under PEFO 16759 (Figure 4). A small portion of a smooth,

Figure 4. Skull fragment of PEFO 16759. (A) photograph in dorsal profile; (B) photograph in ventral profile. Arrow points anteriorly. Abbreviation: nm, narial margin. Scale bar equals 2 cm.

curved surface at the margin is likely to be the right narial opening, with most of the fragment pertaining to the ante-romedial region of the skull. If this identification is correct, the elements that are present would include a large portion of the nasals and possibly portions of the anteromedial lacrimal, the anterior prefrontal, and the anterior frontal. However, the element is heavily fractured, with no clear sutures or other landmark features (e.g. lateral line groove) visible, and a fit between this fragment and the larger skull roof was not found. It cannot be excluded that it could pertain to a second individual.

In neither specimen does the basicranial region appear to be preserved; that of PEFO 16759 is represented only by the displaced occipital condyles, which project extremely far posteriorly and were probably pushed out during dorsoventral compression of the skull. In occipital view, a portion of the falciform crest and the pars supraquadrata are visible on the left side ventral to the quadratojugal and the squamosal; other aspects are obscured. No basicranial elements can be confidently identified in PEFO 40023.

The palatal region of PEFO 16759 cannot be exposed, either due to overlying postcranial elements or because of the fragility of the specimen in relation to the encrusting matrix. The pectoral elements are closely adhered to the ventral surface of the skull roof, suggesting that the palatal elements may not be preserved. All of the elements exposed ventrally in PEFO 40023 pertain to the skull roof or to the mandible.

The ornamentation of the skull roof is obscured in some regions of both skulls but is typical for that of metoposaurids. The vast majority of the skull roof is characterised by small, circular pits with foramina, although most of these are partially infilled with encrusting matrix. The squamosal, jugal, and quadratojugal also feature elongate, radiating grooves, which facilitated the identification of some more fragmentary or dislodged elements. Lateral line grooves are mostly unidentifiable and may not have been fully developed (as in the holotype of *Apachesaurus*).

Mandible

A large fragment of the left mandible has been pressed against the side of the skull of PEFO 16759, overlapping the jugal and possibly the other elements of the lateral skull margin (Figure 5(a)). The jaw is bent medially and features a prominent dorsoventral kink. The ventral and lateral elements (e.g. splenial, postsplenial, angular) are markedly ornamented. The mandibular ornamentation is conserved among metoposaurids and consists of a small centre of circular pitting toward the posteroventral margin of the angular. From this centre, elongate grooves radiate outward in all directions, being most elongate at the anterior regions of the jaw. Because of the deformation of the jaw and the absence of identifiable sutures, we cannot confidently identify the position of this fragment. Based on the absence of circular pitting save for a few isolated pits, it appears that the fragment pertains to the mid-length of the jaw. It would thus preserve portions of the dentary, the angular, the postsplenial, and possibly the splenial in lateral profile and the dentary, the postsplenial, and possibly the splenial in ventral profile. The absence of landmarks, such as the Meckelian foramen, complicates identification. Fragments of bone that lie medial to the mandible in ventral profile may pertain to the medial wall of the adductor chamber (Figure 6), but it is impossible to confidently determine. This is in agreement with the predicted position for a mandible articulated with the skull roof. Tooth positions are mostly obscured or weathered such that a tooth count estimate is not feasible. Other tooth-bearing fragments of a temnospondyl mandible are catalogued under PEFO 16759 (Figure 5(b–c)), but they cannot be confidently associated with the mandible or the skull.

Both mandibles of PEFO 40023 are articulated with the skull (Figures 3 and 7). The left mandible is missing a large ventral portion, but both mandibles are essentially complete along their length. They are fractured in a similar fashion toward the posterior end such that the two portions form a
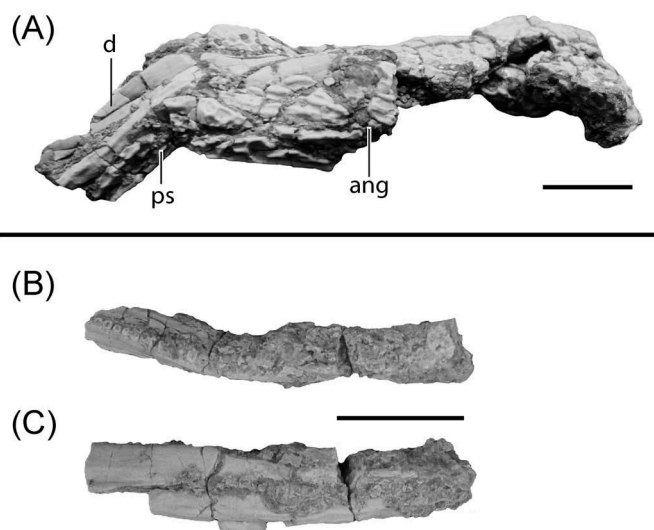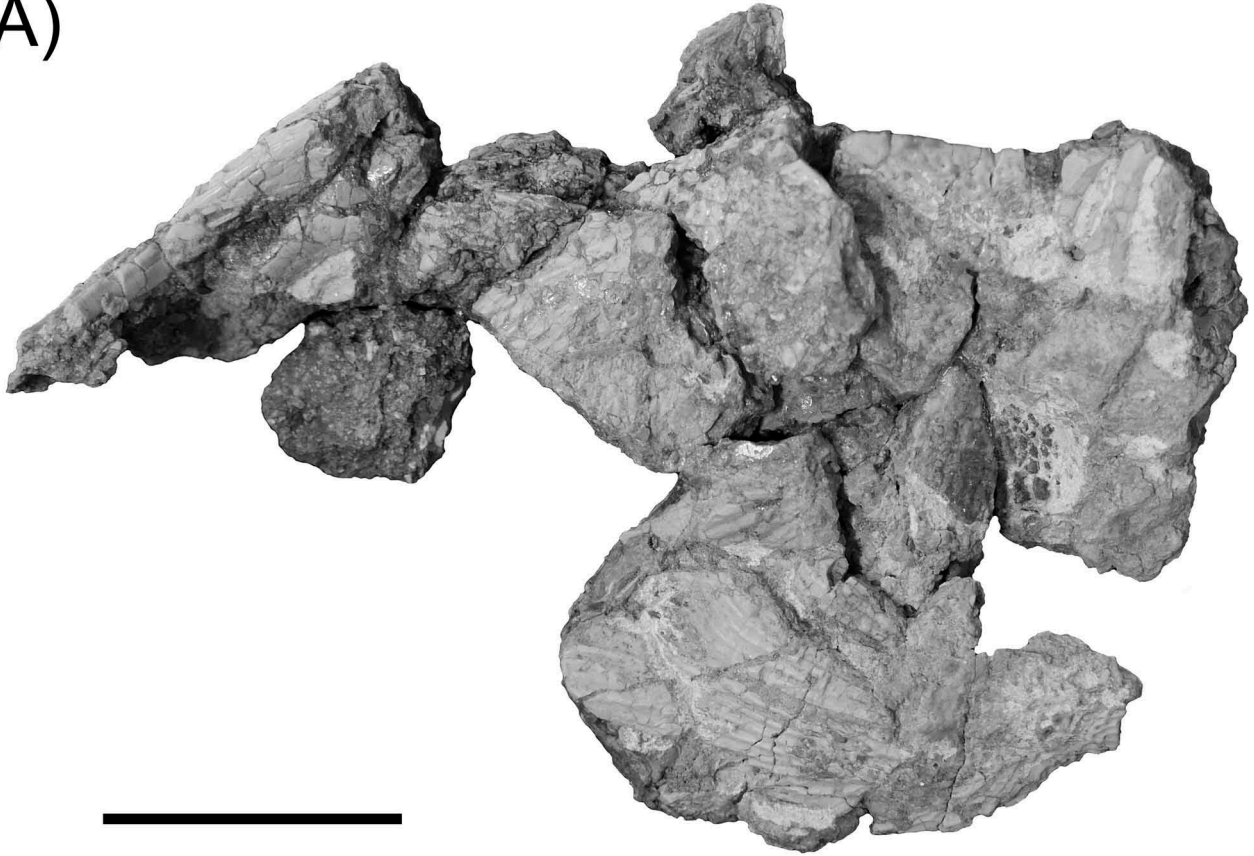

Figure 5. Mandibles of PEFO 16759. (A) partial left mandible articulated with skull roof in lateral profile (arrow points anteriorly); (B) mandibular fragment in dorsal profile; (C) same fragment in lateral profile. Abbreviations: ang, angular; d, dentary; ps, postsplenial. Scale bars equal 1 cm.
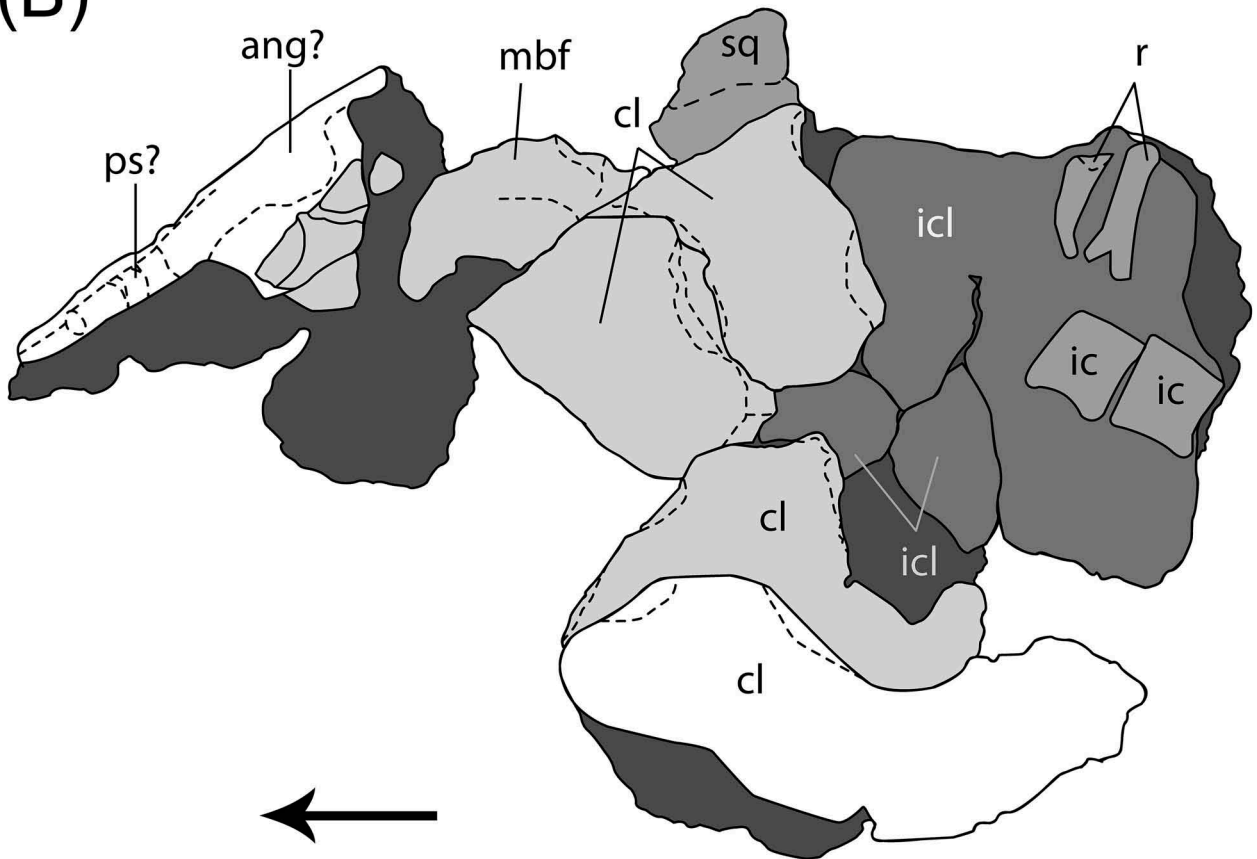
Figure 6. Ventral profile of PEFO 16759. (A) photograph; (B) outline drawing. Darkest grey represents sediment-infilled areas. Arrow points anteriorly. The two intercentra of the specimen, from left (anterior) to right (posterior) are respectively 'J' and 'K' of Table 2. Abbreviations: ang, angular; cl, clavicle; ic, intercentrum; icl, interclavicle; mbf, mass of bone fragments; ps, postsplenial; r, rib; sq, squamosal. Scale bar equals 5 cm.

dorsally angled kink. The anteriormost portion of the right mandible is broken off and rotated in position to be roughly perpendicular to the skull. Identifying precise sutural contacts is impossible given the damage sustained to various regions and the presence of overlying elements in some areas. General identification is thus based on the morphological conservation of the metoposaurid mandible in the relative position of elements. The posterior right mandible is relatively well-preserved and intact; features such as the retroarticular process and the chorda tympanic foramen can be tentatively identified (Figure 7).

Postcrania

Pectoral girdle

A nearly complete interclavicle and both clavicles are present in association with the skull of PEFO 16759 (Figure 6). The interclavicle is preserved posteroventral to the skull and with the ornamented surface facing ventrally in the proper anatomical position. Only a small portion of the left anterolateral region has been lost. The smooth dorsal surface is mostly exposed, but various elements obscure much of the ventral surface. A small posterior region features the typical elongate grooves toward the periphery. The interclavicle of PEFO 40023 (Figure 7) is broken into several pieces but is identified by its flat morphology (in contrast to the dorsal curvature of the posterior clavicle), the transition from circular pitting to elongate grooves, and the relative thickness and contour of the posterior base. In all regards, the interclavicles described here are identical to those of other metoposaurids. The only source of variation pertains to the size of the central region of circular pitting, but this cannot be exposed in PEFO 16759. The fragmentation of the interclavicle of PEFO 40023 prevents a confident characterization. The preserved region contains a portion of circular pitting, but its relative extent is uncertain.

The clavicles of PEFO 16759 are preserved anterior to the interclavicle and ventral to the skull (Figure 6). The right clavicle is essentially complete save for minor loss along the posterior margin and the blade-like dorsal process. It is closely adhered to the skull roof and underlies a flat plate with elongate grooves that is probably the anterior portion of the left clavicle. The posterior left clavicle is adjacent to its counterpart and is similarly closely adhered to the skull roof. It is also relatively complete, but is broken at about the mid-length, with the more anterior fragment displaced between the interclavicle and the right clavicle. The clavicles of PEFO 40023 are only complete posteriorly and lie ventral and slightly posterior to the skull (Figure 7). The right clavicle is well-exposed where it underlies the interclavicle; the left clavicle is exposed both ventrally and dorsally. They feature no differences with those of PEFO 16759 beyond a larger size. The anterior end of the right clavicle of PEFO 16759 is rounded, which does not appear to be the result of weathering at the margin. This condition is more comparable to the clavicles of *Metoposaurus krasiejowensis* (e.g. Sulej 2007, figure 43) than to *Koskinonodon perfectus* (Lucas et al. 2016, figures 53–61) or to *Dutuitosaurus* (Dutuit 1976, plate 22). The ornamentation of the clavicles is also consistent with that of

other metoposaurids in comprising small, circular pits at the posteroventrolateral base that radiate outward into elongate grooves.

Vertebral material

Nineteen intercentra are catalogued under PEFO 16759 (Figures 6 and 8; Table 3). Whether they were closely associated with the skull during collection is unknown, but they are of an appropriate and consistent size for the skull. Two can be more confidently associated with the skull based on their position ventral to the interclavicle that is also associated with the skull. Seven of the intercentra, including an atlas, are isolated. The remainder are divided among five blocks (including the interclavicle block), none of which could be pieced back together. Many of the intercentra are weathered, thereby complicating a determination of their axial position. They are of the elongate proportions formerly referable to *Apachesaurus* (Hunt 1993), being of subequal anteroposterior length and transverse width. Precise axial determination is somewhat complicated by the fact that the parapophyses are less developed than in large metoposaurids (e.g. Sulej 2007). Changes in the shape and position of the parapophyses along the column are considered to be informative for axial determination (Sulej 2007), but little variation is detectable among the sample here. The convexity (or lack thereof) of the anterior articular surface was also considered informative by Sulej, but the intercentra of PEFO 16759 are markedly amphicoelous. This may be a marker of relative immaturity since this morphology is observed in small, histologically immature intercentra (Gee et al. 2017). The intercentra are tentatively identified to the presacral region in the absence of any pelvic material or the more triangular, haemal-arch-bearing caudal vertebrae. The more complete ones (Figure 8(a–f)) appear only to have anterior parapophyses and are tentatively identified as mid-trunk positions.

In PEFO 40023, a total of ten intercentra are associated with the skull (Figures 3, 7, and 9; Table 2). The first three (atlas, axis, third position) intercentra are articulated with the skull (Figures 3 and 7). There is no evidence of the distinct fourth position, and all subsequent intercentra were found jumbled posterior to this region prior to being removed during preparation in order to expose the dorsal surface of the pectoral elements; accordingly, they are assigned a more generic axial position. Similar to PEFO 16759, most of the intercentra pertain to the presacral region. Both the parapophyses and the anterior articular surface are more developed than in PEFO 16759, facilitating their axial determination. The other two intercentra (Figure 8(g-h)) pertain to the perisacral and the caudal region. A similar size, state of preservation, and association with the other elements support their assignment to the specimen. The intercentra of PEFO 40023 are notably larger than those of PEFO 16759, as with the skull, and are proportionately shorter anteroposteriorly than the latter. However, they are still more elongate than those of large-bodied specimens.

The atlas of PEFO 40023 is articulated with the skull roof but is well-exposed in dorsal profile (Figure 9). That of PEFO 16759 is isolated (Figure 8(a)). In their revised diagnosis of *Koskinonodon perfectus*, Lucas et al. (2016) noted differences
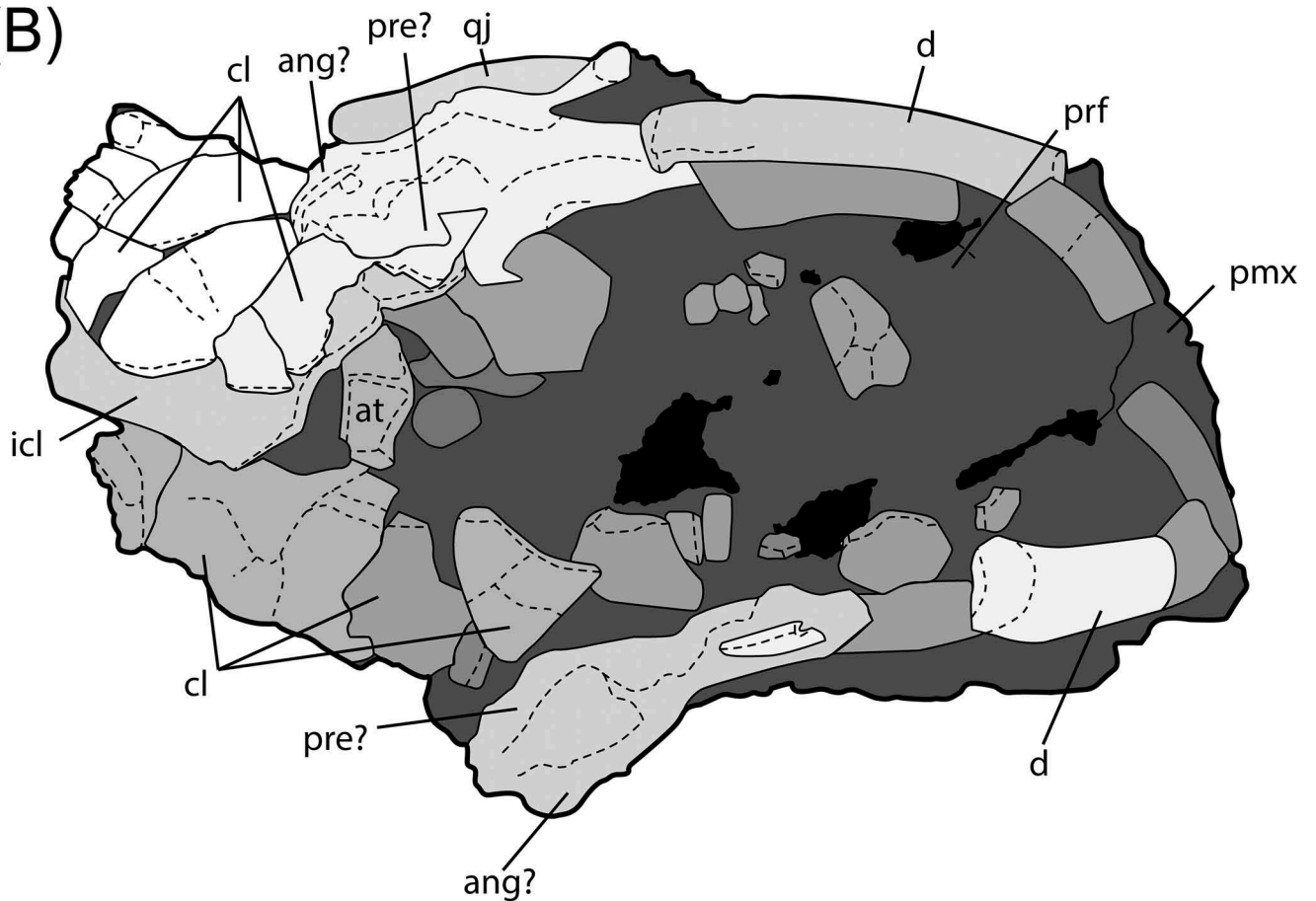
Figure 7. Ventral profile of PEFO 40023. (A) photograph; (B) outline drawing. Darkest grey represents sediment-infilled areas; black represents holes. Abbreviations: ang, angular; at, atlas; cl, clavicle; d, dentary; icl, interclavicle; pf, prefrontal; pmx, premaxilla; qj, quadratojugal. Scale bar equals 5 cm.
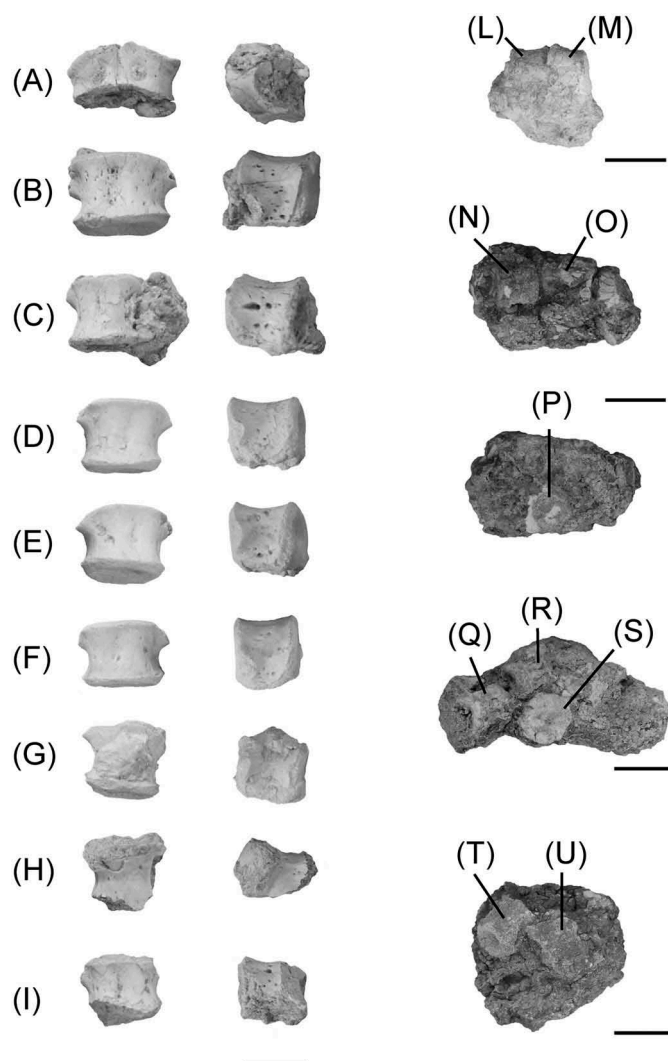
Figure 8. Photographs of intercentra of PEFO 16759 in dorsal and lateral profiles. All subletters correspond to the listings of Table 3. Scale bars equal 1 cm.

between the atlases of *K. perfectus, M. krasiejowensis* (referred to as *M. diagnosticus* in the publication), and *Dutuitosaurus*. The atlas of *K. perfectus* (e.g. WT 3144, Lucas et al. 2016, figure 38) features shallow articular surfaces that are not separated by a cleft. Conversely, the referred atlas of *Apachesaurus* (e.g. NMMNH P-22487, Spielmann and Lucas 2012, figure 22A-D) features a separation between the articular surfaces; it is not nearly as deep of a cleft as in *M. krasiejowensis* (e.g. ZPAL AbIII/1702, Sulej 2007, figure 22B), but the gap is notably larger. In both PEFO 16759 and PEFO 40023, the atlas is characterised by a very slight contact of the articular surfaces and without a cleft. The degree of contact is lesser than in *K. perfectus*.

Other postcrania

Two ribs are found in articulation with the two intercentra found on the ventral surface of the interclavicle in PEFO 16759 (Figure 6). Fragmentary rib material is also catalogued under the same specimen number, but it is too incomplete to be referable to a temnospondyl. In addition, a large number of other fragmentary metoposaurid elements were collected

from nearby localities (termed RAP Hill West and RAP Hill North [PFV 277]). This evidently occurred around the same time as PEFO 16759 based on their collection numbers (comprising a non-continuous range from PEFO 19502 to PEFO 19514). The coloration, quality of preservation, general size of material, and nature of encrusting minerals is identical to that of elements recovered from RAP Hill (PFV 216), and the series of localities probably represents a single depositional environment. No fits or confident association between this material and that assigned to PEFO 16759 were found. Some of the other elements include dentulous cranial and mandibular elements with teeth and 'tusks' that would belong to individuals of a comparable size to PEFO 16759 (Figure 5(b, c)). Isolated, partial clavicular and interclavicular material and smaller intercentra are also present.

Isolated postcranial elements are also associated with PEFO 40023, including fragmentary ribs, a small, partial clavicle (Figure 10(a,b)), and a partial ilium complete proximally (Figure 10(c,d)). This material was collected as float in close proximity to the skull, so it can be reasonably associated with the individual. A feature shared with ilia referred to
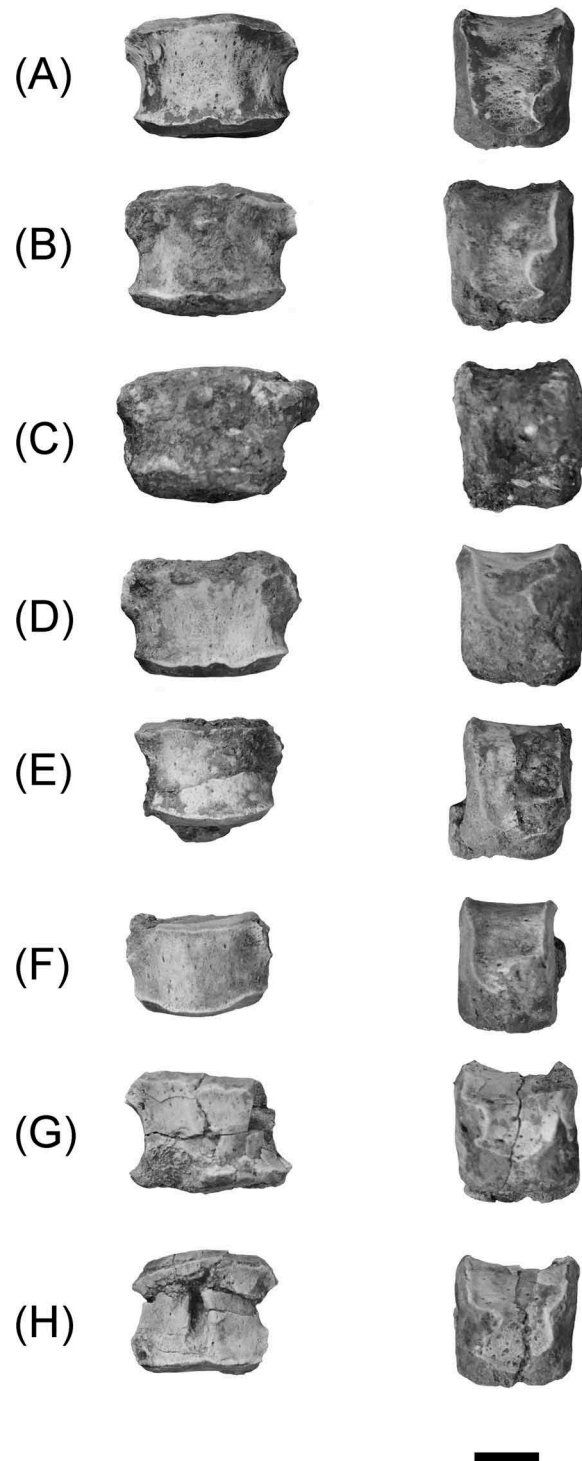
Figure 9. Photographs of intercentra of PEFO 40023 in dorsal and lateral profiles. All subletters correspond to the listings of Table 3. Note that specimens 'J' and 'K' are found in close association with the skull (see Figure 6) and are not figured here. Scale bar equals 1 cm.

Apachesaurus (e.g. NMMNH P-17040, Spielmann and Lucas 2012, figure 27) is a narrow groove is found at the anterior margin of the acetabulum adjacent to a shallow ridge that marks this margin. This is not explicitly reported or figured in other metoposaurids, but the ilium is also a relatively rare element. One feature of note is the presence of a protuberance dorsal to the anterior margin of the acetabulum (Figure 10(c, d)). This is not seen in the two referred specimens of
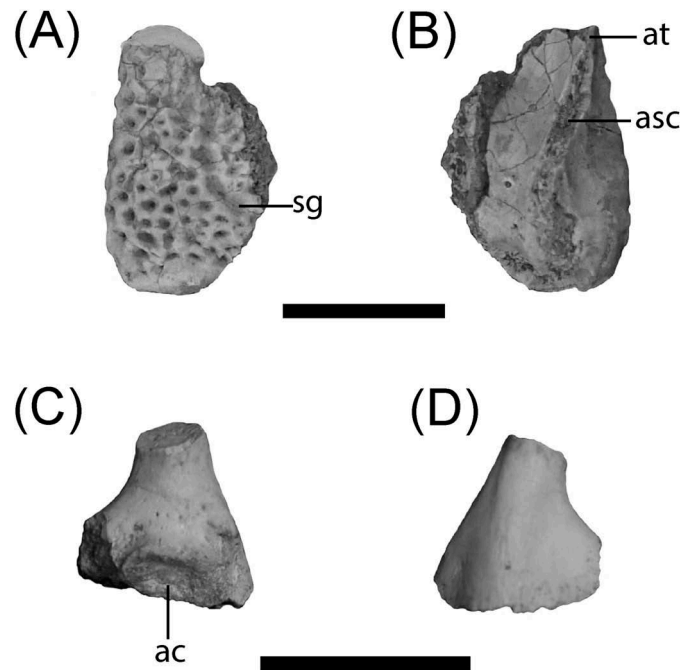
Figure 10. Photographs of postcrania assigned to PEFO 16759 and PEFO 40023. (A) ventral profile of a small partial clavicle (PEFO 16759); (B) dorsal profile of the same clavicle; (C) lateral profile of a partial ilium (PEFO 40023); (D) medial profile of the same ilium. Abbreviations: ac, acetabulum; asc, ascending crest; at, anterior torus; sg, sensory groove. Scale bars equal 2 cm.

Figure 11. Microanatomy of intercentra of PEFO 16759 and PEFO 40023 in sagittal sections. (A) PEFO 16759 under plane-polarized light; (B) the same section under cross-polarized light; (C) PEFO 40023 under plane-polarized light; (D) the same section under cross-polarized light. The boundary between the endochondral and the periosteal domains is marked by a dashed white line in (A) and (C). Abbreviations: en, endochondral domain; pe, periosteal domain. Scale bars equal 5 mm.

Apachesaurus (NMMNH P-17040, UCMP 65309 [Spielmann and Lucas 2012]) or in any other metoposaurid, and whether it is pathological or a natural condition is unclear.

Intercentra histology

Two trunk intercentra of each specimen were sampled (Figures 8(e, f), 9(a-d); Table 3). These elements could either be reasonably associated with the skull (PEFO 40023) or are more tentatively associated but of identical size and proportions to others associated with the skull (PEFO 16759). The preservation of the intercentra of PEFO 16759 is relatively poor but permits a number of broad microanatomical characterizations and identification of some informative histological features. As detailed descriptions of metoposaurid intercentra have been provided by a number of workers (Konietzko-Meier et al. 2013, 2014; Danto et al. 2016; Gee et al. 2017), the following description presents only a brief

characterization with an emphasis on ontogenetically relevant features.

Microanatomy

The metoposaurid intercentrum consists of endochondral and periosteal domains (Figure 11–12). The periosteal domain comprises an ordered region of parallel layers in the ventral region of the intercentrum that also extends up the lateral surfaces in transverse profile. The endochondral domain, made of a semi-organized trabecular network, forms most of the intercentrum. In sagittal profile (along the midline anteroposteriorly), the periosteal bone is confined to a sub-triangular region at the ventral portion of the intercentrum (Figures 11 and 12). In PEFO 16759, a more pronounced concavity of the ventral margin of the element results in a more dorsally concave ventral and dorsal contour (Figure 11(a,b)). This differs from PEFO 40023 in which the periosteal region narrows to a discrete apex (Figure 11(c,d)). PEFO 40023 is similar in this regard to similarly sized and
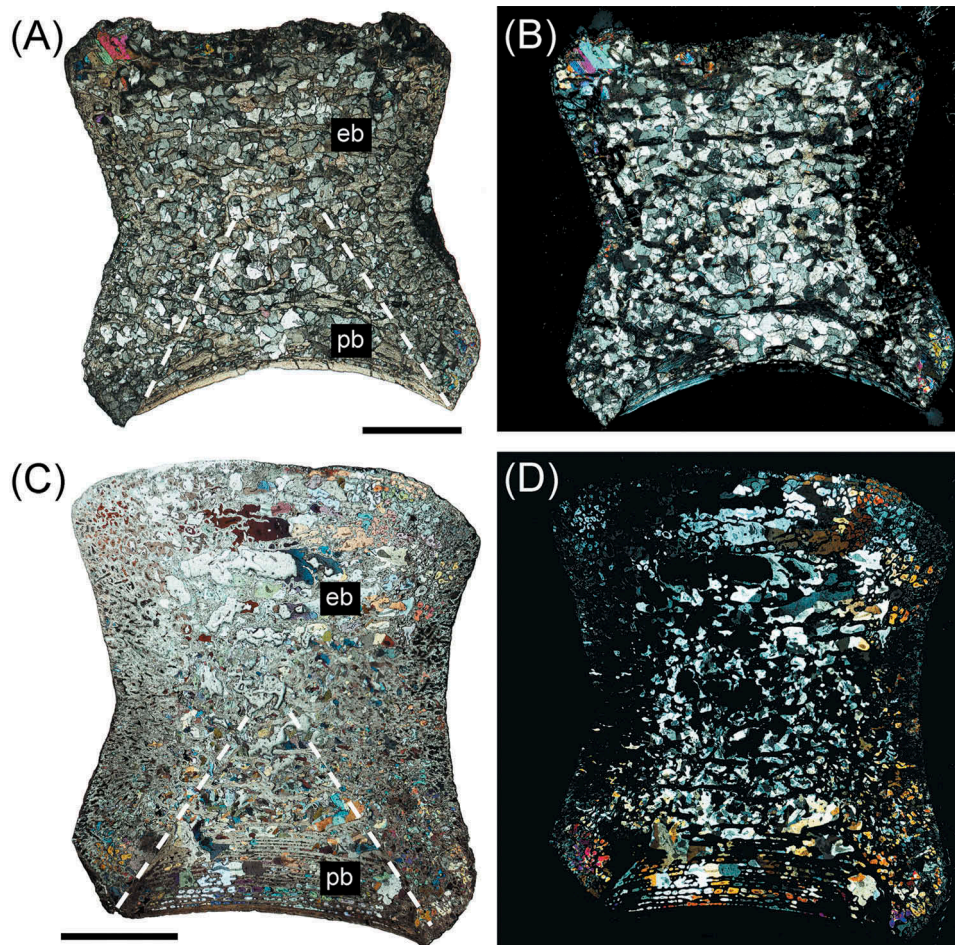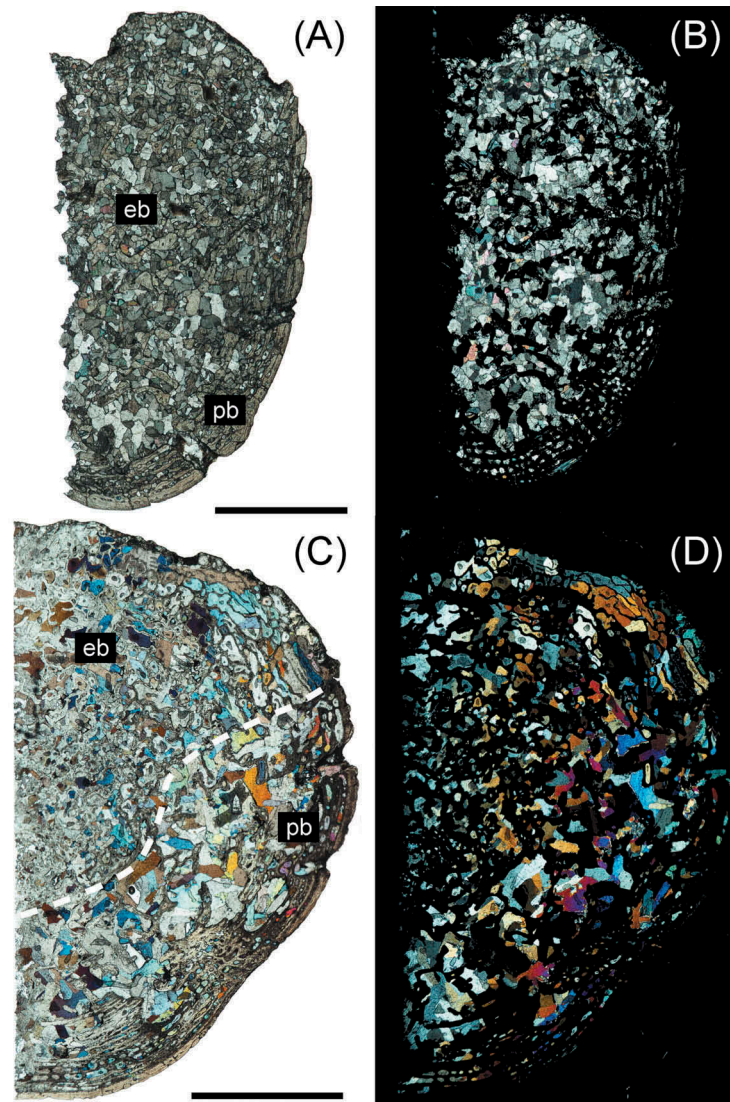

Figure 12. Microanatomy of intercentra of PEFO 16759 and PEFO 40023 in half-transverse sections. (A) PEFO 16759 under plane-polarized light; (B) the same section under cross-polarized light; (C) PEFO 40023 under plane-polarized light; (D) the same section under cross-polarized light. The boundary between the endochondral and the periosteal domains is marked by a dashed white line in (C); the damage to the internal trabecular network prevents a confident demarcation in (A). Abbreviations: en, endochondral domain; pe, periosteal domain. Scale bars equal 5 mm.
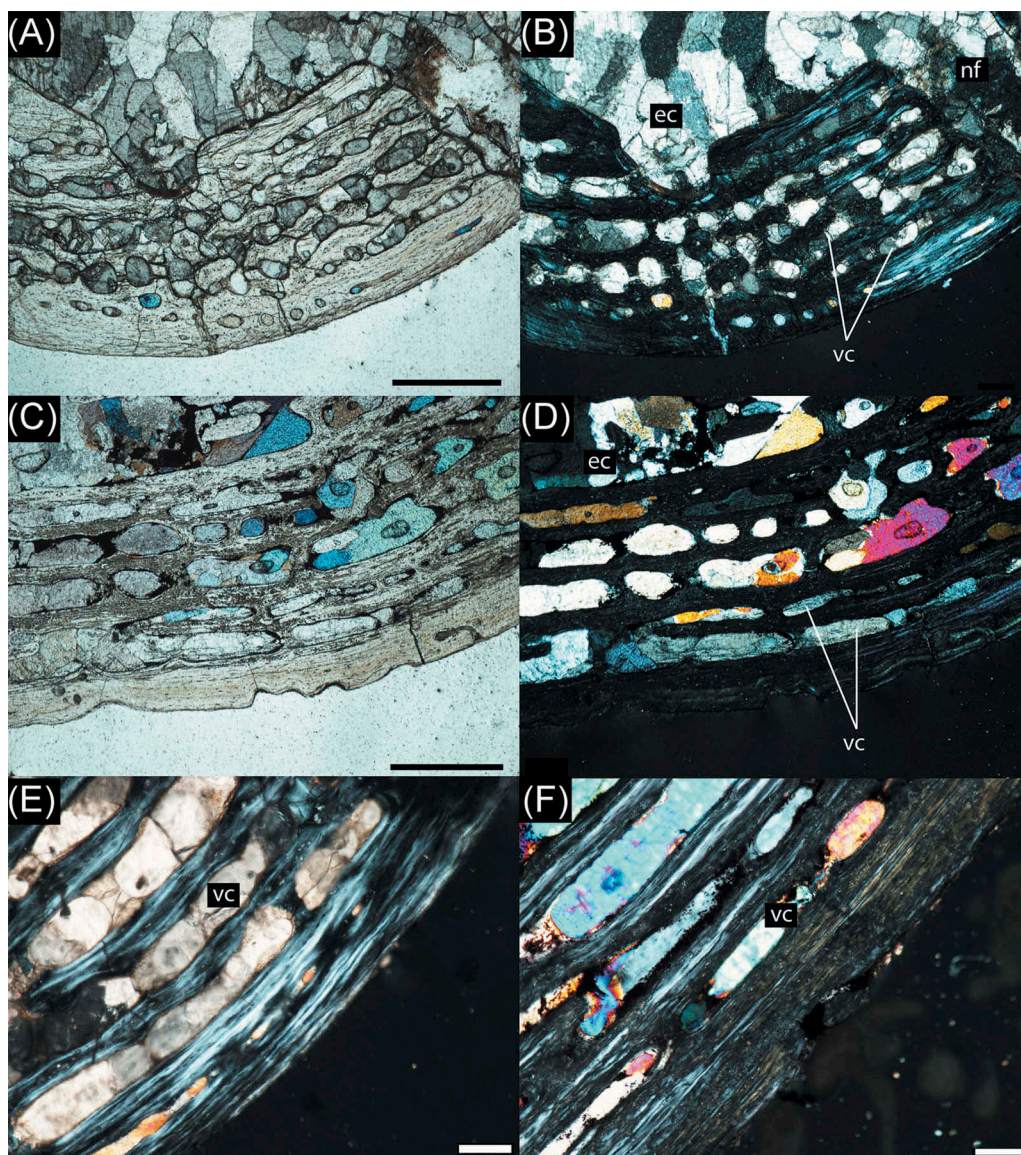
Figure 13. Comparison of the external periosteal cortex of PEFO 16759 and PEFO 40023 in transverse section. (A) vascularized external periosteal cortex of PEFO 16759 under plane-polarized light; (B) same section under cross-polarized light; (C) vascularized external cortex of PEFO 40023 under plane-polarized light; (D) the same section under cross-polarized light; (E) close-up of the cortex of PEFO 16759 in cross-polarized light showing primary lamellar deposition within the vascular canals; (F) close-up of the cortex of PEFO 40023 showing primary lamellar deposition within the vascular canals. Abbreviations: ec, erosion cavity; nf, nutrient foramen; vc, vascular canal. Scale bars equal 300 µm (A-D); 100 µm (E-F).

larger intercentra (e.g. Konietzko-Meier et al. 2013; Gee et al. 2017). In transverse profile, the periosteal region is confined to a small portion along the ventral margin but extends dorsolaterally along the lateral surfaces of the element (Figure 12). In both profiles, the boundary between the periosteal and the endochondral domains is clearly demarcated by obliquely-oriented trabeculae. It is not always continuous, being particularly damaged toward the geometric centre in PEFO 16759 (e.g. Figure 12(b)). Other obliquely oriented trabeculae frame nutrient canals, within the periosteal cortex, that are connected to the external surface. The quality of preservation of PEFO 16759 is relatively poor to those of PEFO 40023 and those previously sampled by Gee et al. (2017); although all of the major features and organization are present, there has been significant loss of much of the endochondral trabecular network; it may be that a combination of poor ossification and larger intertrabecular spacing resulted in increased damage from secondary mineral precipitation. PEFO 40023 is also damaged by secondary carbonates, but most of this is confined to the periosteal region, and the microanatomical features remain readily identifiable.

Histology

Histologically, the metoposaurid intercentrum is formed by highly trabecular bone. Whereas the periosteal cortex is formed by an orderly network of parallel-oriented layers, the endochondral domain is disperse and disorganized. The trabecular networks are fairly loosely spaced in both specimens (more difficult to characterize in PEFO 16759) (Figures 11 and 12). Only at the articular surfaces does the network become densely packed. The periosteal cortex is formed by an

ordered network of parallel layers with vascular canals oriented anteroposteriorly. Toward the geometric centre, there often are large erosion cavities (Figure 13). The trabecular network also becomes more disorganized toward the centre; this may have contributed to the greater extent of damage seen in the dorsal region of the periosteal domain (e.g. Figure 13(b)). The cortex is well-vascularized throughout in both specimens (Figure 11–13). Primary lamellar deposition is visible in the vascular canals of the periosteal cortex and is relatively thin (Figure 13). In neither specimen is a thickened, poorly vascularized annulus observed, and no lines of arrested growth (LAGs) were identified.

Calcified cartilage is widespread throughout the element, especially at the articular surfaces (Figure 14(e,f)) and near the dorsal margin. In places where remodelling has begun, the cartilage is greatly reduced in abundance, but it often remains present between trabeculae (Figure 14 (c,d)). Remodelling is most apparent near the geometric centre of the element (e.g. Figure 14(c)) and at the boundary separating the endochondral and periosteal domains (e.g. Figure 14(a,b)). A few sections captured a small circular (semi-circular in half-transverse section) region at the centre of both specimens that likely represents the closure of the notochordal canal. This region is still characterized by an abundance of primary trabeculae and calcified cartilage, as in previously sampled specimens (Gee et al. 2017, figure 8(c,d)). The abundance of calcified cartilage is difficult to assess in PEFO 16759 because much of the trabecular network has been destroyed by secondary mineralization. Nonetheless, remodelling, appears more abundant in PEFO 16759. In PEFO 40023, slight occurrences of remodelling are always correspondent with a greater abundance of cartilage.

Discussion

Taxonomic identity of PEFO 16759 and PEFO 40023

An assignment of PEFO 16759 to *Apachesaurus gregorii* is supported by one autapomorphy of the revised diagnosis: a symmetrical, pentagonal squamosal with an anterior process that is not transversely deflected. None of the other anatomical features are incompatible with this taxonomic assignment. The taxonomic assignment of PEFO 40023 is more complicated. The specimen possesses a squamosal with a medially deflected anterior process, which is distinct from *Apachesaurus* under the diagnosis of the taxon. However, incorporating features that were considered differential but not formalised as diagnostic by Spielmann and Lucas (2012) complicates the matter. The more abrupt posterior tapering of the frontals and the groove on the anterior margin of the acetabulum are features suggested to be unique to *Apachesaurus*. Elongation of the intercentra is reiterated to be an uninformative feature. As a result of the conflicting anatomical features and a lack of assignable apomorphies, we assign PEFO 40023 to Metoposauridae indet.

Morphological determination of ontogenetic maturity

The principle challenge in determining the ontogenetic maturity of specimens based on their morphological features alone is the low sample size of small-bodied taxa of a reasonably good preservation and completeness. In North American deposits, the potential presence of a diminutive taxon (*Apachesaurus*) in co-existence with large-bodied taxa (*Koskinonodon*, '*Metoposaurus*' *bakeri*) complicates the identification of small-bodied specimens that would be useful as morphological reference points. Furthermore, the small sample of small-bodied taxa from other geographic regions is of limited utility because of uncertainty regarding the morphological distinctions between juveniles of given taxa. The potential for intraspecific variation (and interspecific variation of intraspecific variation) due to ontogeny, developmental plasticity, size-based sexual dimorphism, and other ecological variables (e.g. Steyer 2000) only further complicates the issue. The high degree of morphological conservation among metoposaurids and the subsequent challenges of resolving their taxonomy similarly represent ongoing challenges. Based strictly on a superficial correlation of size and morphological features (again, semi-unreliable without good constraints on variation), the otic notch of small-bodied North American specimens (PEFO 16759, 35392, 40023) appears to deepen in larger individuals (Gee and Parker 2017; this study). Similarly, the temporal lobe, formed primarily by the squamosal and the quadratojugal, appears to broaden such that the lateral margins become concave. Comparisons with closely related taxa offer one means of circumventing the low sample size of small-bodied metoposaurids, but many trematosauroids are similarly poorly known (but see discussion of Schoch 2006, for example). However, the unique cranial morphology of the metoposaurids relative to other trematosauroids (typically with elongate snouts and posteriorly positioned orbits) presents some complications in inferring patterns of cranial ontogeny. More metoposaurid specimens are necessary to confidently characterize developmental trends, which emphasizes the importance of alternative methods for ontogenetic determination.

Histological determination of ontogenetic maturity

A number of microanatomical and histological features were identified by Konietzko-Meier et al. (2013) and corroborated by Gee et al. (2017) that inform the relative maturity of metoposaurid intercentra. Microanatomical structures include: (1) the sagittal profile and height of the periosteal region; (2) the density of the endochondral trabecular network at the articular surfaces; (3) the vascularization of the periosteal cortex; and (4) the presence of lines of arrested growth (LAGs) in a thickened annulus (Figures 11 and 12). Histological features include: (1) the relative abundance of calcified cartilage to secondarily remodelled trabeculae; (2) the presence of secondary osteons; and (3) the amount of lamellar deposition with vascular canals of the periosteal cortex.

From the microanatomical perspective, both specimens are relatively immature. The periosteal cortex remains well-
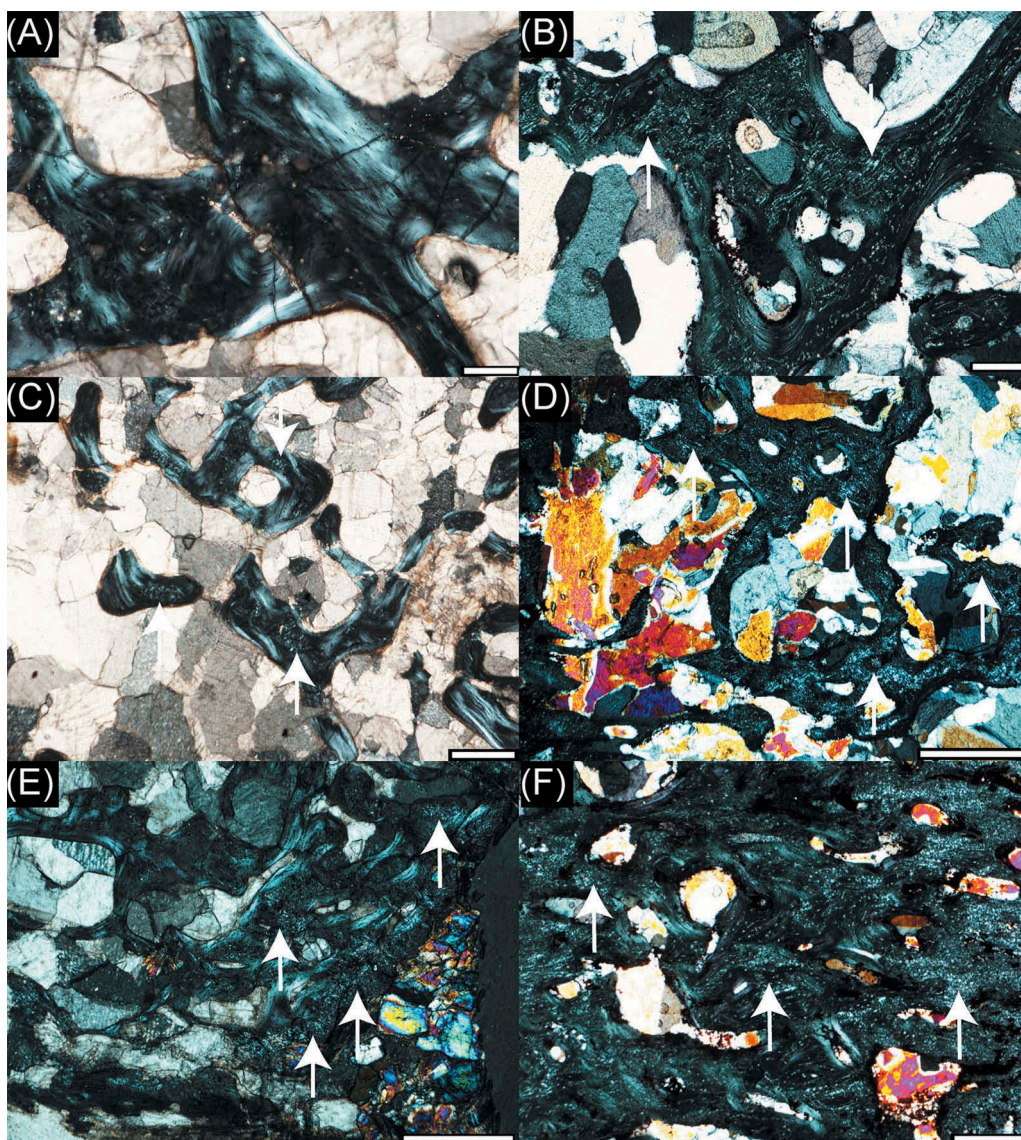
Figure 14. Comparison of remodelling and calcified cartilage in cross-polarized light of PEFO 16759 and PEFO 40023. (A) remodelling at the endochondral-periosteal domain boundary in PEFO 16759; (B) remodelling and calcified cartilage at the endochondral-periosteal domain boundary in PEFO 40023; (C) calcified cartilage and slight remodelling near the geometric centre of PEFO 16759; (D) calcified cartilage near the geometric centre of PEFO 40023; (E) calcified cartilage at the articular surface of PEFO 16759; (F) calcified cartilage at the articular surface of PEFO 40023. Arrows indicate cartilaginous regions (grainy texture). Scale bars equal 100 μm (A-B, E-F); 300 μm (C-D).

vascularized throughout, including at the ventral margin of the intercentra. There is no disproportionately thickened, poorly vascularized annulus that records the LAGs in larger specimens (Konietzko-Meier et al. 2013, figure 4(e,f); Gee et al. 2017, figure 11(g,h)). The periosteal cortex forms a triangular cortex in sagittal profile in both specimens, so they are certainly more mature than the smallest sampled intercentra from North American taxa (Gee et al. 2017, figure 9). The apex is around the mid-height of the intercentrum in both specimens, although that of PEFO 16759 is difficult to confidently identify. The notochordal canal is fully closed, although there may be some remnants of the closure at the geometric centre. Based on their size and their microanatomical features, both specimens conform favourably to that general ontogenetic trends of North American taxa identified by Gee et al. (2017).

The histological perspective is a bit more complicated. PEFO 40023 is straightforward and conforms to the histological patterns identified by Gee et al. (2017). Calcified cartilage is in extreme abundance in relation to larger intercentra, and remodelling is rare. In isolation, the presence or absence of cartilage is not informative, as it persists late in ontogeny (likely due to paedomorphism) (Konietzko-Meier et al. 2013, 2014). However, by comparison to previously sampled specimens whose ontogenetic maturity can be identified based on other features, the relative abundance is informative. For example, PEFO 40023 is similar to a previously sampled, comparably sized specimen (PEFO 35392) in this regard (and other histological aspects) (Gee et al. 2017). It is also notably less histologically mature than the largest sampled intercentrum of a North American taxon (PEFO 38726) in which cartilage is rare and remodelling is abundant. Where remodelling occurs in PEFO 40023 (e.g.

endochondral-periosteal boundary), it is rare and surrounded by calcified cartilage. Secondary osteons are not identified. Conversely, PEFO 16759 is more difficult to characterize, in part because of the damage to the trabecular network. Calcified cartilage is present and in greater abundance than most other previously sampled intercentra of a larger size. However, it is noticeably less abundant in this specimen than in PEFO 40023. Remodelling is conversely more abundant, although it is still less remodelled than most larger intercentra. This suggests a relatively mature individual, but other aspects of the histology and microanatomy are in conflict with this interpretation. For example, the well-vascularized cortex contains only primary lamellar deposition of a relative thinness within the vascular canals (e.g. Figure 13(e)). As noted above, there is no evidence of a highly compact and poorly vascularized external cortex or LAGs that would similarly be expected in a mature individual. Secondary osteons are also not identified. A number of explanations to reconcile these observations may be suggested.

The first possible explanation is that variability in the ontogeny of a taxon can contribute to a range of variation in size such that two individuals of the same size may not be of the same skeletal maturity (e.g. Brochu 1992; Griffin and Nesbitt 2016). This could result from a number of factors, including natural intraspecific variation, sexual dimorphism, or developmental plasticity. It bears reiterating that these individuals are definitively time-separated (Figure 1). Possible sexual dimorphism has been suggested in *Metoposaurus krasiejowensis* by Teschner et al. (2018) based on the identification of two distinct histotypes in humeri of the taxon. Divergent histotypes ascribed to developmental plasticity and variable habitat occupation have also been documented in humeri of the plagiosaurid *Gerrothorax* by Sanchez and Schoch (2013). Under this hypothesis, PEFO 16759 could be both slightly more mature than PEFO 40023 and relatively immature in the broader context of sampled intercentra. This possibility awaits additional work to better characterize the ontogenetic and intraspecific variability of the external and histological features of the skeleton within metoposaurids. The second consideration is that taphonomic damage to the trabecular network contributed to an exaggerated perception of the relative abundance of remodelling and calcified cartilage. Of the sampled North American intercentra, PEFO 16759 certainly features the most extensive secondary mineral precipitation within the intercentra. If calcified cartilage were less likely to be preserved based on some structural property, this might explain why it seems sparser in PEFO 16759. However, this would require additional work to better characterize taphonomic biases at the histological level.

Konietzko-Meier et al. (2013) erected histological ontogenetic stage (HOS) designations for the intercentra of *Metoposaurus krasiejowensis* that were applied in the study by Gee et al. (2017). We repeat this approach here and designate both specimens as HOS 2 based on the presence of a well-vascularized periosteal cortex. This is the same conclusion that we arrived at based on a more general comparison of histological features with previously sampled North American metoposaurid intercentra (Gee et al. 2017).

It is not possible to fully reconcile the anomalous proportions of calcified cartilage and remodelling in PEFO 16759 without additional sampling to test the various hypotheses proposed above. However, we emphasize that the specimen is certainly not mature, either in absolute terms of the presence/absence of features (e.g. LAGs) or by comparison of the relative development to previously sampled specimens (e.g. the degree of remodelling in PEFO 38726 [Gee et al. 2017, figure 12(e,f)]). The other features of the histology and the microanatomy are in agreement with similarly sized intercentra. Similarly, aspects of the external anatomy, such as the amphicoelous articular surfaces and poorly developed parapophyses, further suggest relative immaturity.

These specimens are now the second and third to be identified as juvenile individuals on the basis of histology when they would traditionally have been referred to *Apachesaurus* under the original interpretation as a diminutive metoposaurid on the basis of either size or a few morphological features (e.g. shallow otic notch). This highlights the importance of a multi-faceted approach to determining the ontogenetic maturity of specimens in order to avoid circular logic (e.g. recognizing morphological changes in specimens inferred to be juvenile through their morphology). Several considerations bear reiterating for future work. The absence of articulated vertebral columns for most metoposaurid taxa creates challenges in defining the precise axial position for isolated material. In general, it is easy to identify general positions (e.g. anterior trunk, caudal), but more precise determination that would allow for more direct control in histological studies remains challenging. This is particularly salient for small-bodied metoposaurids, regardless of the interpretation of ontogenetic maturity, because the current characterization of the variability along the axial column is derived from the large-bodied *Dutuitosaurus*. The identifications made for PEFO 16759 in particular (Table 3) are more tentative because the parapophyses, a key criterion used by Sulej (2007) to identify the axial positions in *Metoposaurus krasiejowensis*, are underdeveloped. The amphicoelous nature of small metoposaurid intercentra, a remnant of the early closure of the notochordal canal, prevents the use of the anterior articular surface to differentiate positions. The intercentra of PEFO 40023 are of a more comparable development to large-bodied metoposaurids in these regards.

Additionally, histological work on temnospondyl intercentra is relatively recent and thus limited. Some studies have extensive taxonomic coverage in sampling and have established a strong baseline for comparison of a large number of taxa (e.g. Konietzko-Meier et al. 2014; Danto et al. 2016). However, most of these studies are limited in the ontogenetic information that can be derived for a given taxon because they lack a wide intra-taxon sampling of variably sized (and presumably variably mature) specimens. Thus, even conclusions about intraspecific ontogenetic patterns remain somewhat unresolved, let along interspecific comparisons. Various histological differences between the North American and the European metoposaurid intercentra were noted by Gee et al. (2017). The relative elongation seen only in the North American taxa suggests that there may be proportionately greater expansion of the periosteal domain to result in a proportionately anteroposteriorly short intercentrum in more mature individuals. Such differences likely indicate differences in various aspects of ontogeny (e.g.

growth rate) that could in turn reflect different environmental conditions, for example. However, this requires further work with tight controls for axial position and size to better characterize differences in the developmental trajectories of the axial column among the various metoposaurid taxa. This would also improve the understanding of how the HOS designations that were created for *M. krasiejowensis* apply to North American metoposaurids. A final area that requires additional work is the proposal that the general histological immaturity of stereospondyls may reflect paedomorphism (e.g. Konietzko-Meier et al. 2013; Danto et al. 2016). This is particularly important for considering the interpretation of calcified cartilage, which persists in some amount late into ontogeny (e.g. Konietzko-Meier et al. 2013; Danto et al. 2016).

Implications for metoposaurid ontogeny

The PEFO specimens described here contribute to increased resolution of the earliest stages of ontogeny in large-bodied metoposaurids. PEFO 16759, referable to *Apachesaurus*, is slightly smaller than the holotype (UCMP 63845) (Table 2). PEFO 40023 is larger than the latter but smaller than the specimen described by Gee and Parker (2017), PEFO 35292 (Table 2). Because PEFO 40023 is larger, more histologically mature, and possesses features more typical of large metoposaurids, there is no reason to assume that it is a distinct taxon from PEFO 16759. However, it cannot be referred to *A. gregorii* under either the original or the amended diagnosis. The clear ontogenetic influence on some aspects of the skull (e.g. medial deflection of the anterior process of the squamosal) and the intercentra illustrates the challenges associated with diagnosing unambiguous juvenile forms. The demonstrated immaturity of these specimens, in conjunction with that previously reported by Gee and Parker (2017), indicates that some features previously considered to be autapomorphies of *Apachesaurus* (e.g. shallow otic notch, poorly developed tabular horn) may be markers of ontogenetic immaturity. For example, a comparison of the two specimens presented here with PEFO 35292 (larger than PEFO 16759 and PEFO 40023) shows that a deepening of the otic notch is correlated with increased skull size. Already, elongation in small intercentra has been demonstrated to be a feature associated with immaturity in North American taxa (Gee et al. 2017), findings that are further corroborated by this study. Evidently these features may vary in their ontogenetic trajectories between metoposaurid taxa. For example, a juvenile of *Koskinonodon perfectus* (TMM 31099-12B) that was figured by Hunt (1993, figure 8(a,b)) and the juvenile of '*Metoposaurus*' *bakeri* (YPM VPPU 021742 [Sues and Olsen 2015, figure 12]) are within a comparable size range to the specimens described here and to those referred to *Apachesaurus* but feature well-defined otic notches and tabular horns typical of large-bodied forms. The possibility of interspecific variation in this regard conforms to the observations of Konietzko-Meier et al. (2013), who attributed histological differences in the long bones of the European *M. krasiejowensis* and the Moroccan *Dutuitosaurus* to distinct environments and subsequent paleobiological differences. This may also, for example, explain the difference between

the elongation of small intercentra that is seen in North American taxa. This is suggestive of a taxonomically informative morphological distinction, but whether ontogenetic trajectories could also vary in the timing of major events is unclear given the poor resolution of metoposaurid early ontogeny. It is likely that there is some degree of developmental plasticity that could also produce intraspecific variation in ontogenetic trajectories. Accordingly, two specimens of the same size and taxonomic affinity may not show the exact same development of some ontogenetically linked features (e.g. Brochu 1992; Griffin and Nesbitt 2016). It bears reiterating that it has not been extensively explored whether at least some of the distinct sutural patterns that diagnose *Apachesaurus* are the product of ontogeny. Many of the original and revised characters are qualitative in nature and can easily result from changes in proportions and morphology throughout ontogeny (among other factors). Accordingly, we exercise caution in suggesting changes in the sutural patterns associated with early ontogeny. This is particularly important because sutures are not well-defined in many small, fragmentary metoposaurid specimens.

The findings of this study, which reinforce previous work by the authors on small-bodied metoposaurids (Gee and Parker 2017; Gee et al. 2017), provide further evidence that *Apachesaurus* and other small-bodied metoposaurids from the late Norian are juveniles of a large-bodied taxon. Original arguments presented by Hunt (1993, p. 85) in support of a mature ontogenetic stage are as follows: (1) *Apachesaurus* does not resemble known juveniles of other species (e.g. *Koskinonodon perfectus, Dutuitosaurus ouazzoui*); (2) the elongate intercentra occur in horizons with intercentra of similar diameters but reduced elongation; (3) collections of the NMMNH (at the time) contained no elements of large metoposaurids; and (4) a posterior positioning of the pineal foramen on the parietals. All of these are limited or problematic in their own regard.

Firstly, the sample size of confidently identified juveniles is much sparser than that suggested by Hunt (1993), who noted or figured only four specimens of juvenile metoposaurids, one of *Koskinonodon perfectus* from the Dockum Group (TMM 31099-12B), the only specimen of '*Metoposaurus*' *bakeri* from Nova Scotia (YPM VPPU 021742), and two of *Dutuitosaurus* (Dutuit 1976, plates 34 and 35). At present, only a few juveniles have been described in detail (e.g. Davidow-Henry 1989; Zanno et al. 2002; Gee and Parker 2017). The majority of others are only figured or briefly described as part of a broader description (e.g. TMM 31099-12B [Hunt 1993; Morales 1993]; PEFO 31194, PEFO 33977 [Parker and Irmis 2005]; NMMNH P-37069, UCMP 171591 [Spielmann and Lucas 2012]). We agree with Hunt (1993) that the few known specimens of juvenile *K. perfectus* (e.g. TMM 31099-12B) and the single juvenile of '*M.*' *bakeri* (YPM VPPU 021742) are dissimilar to the holotype of *A. gregorii* and to PEFO 16759. However, an important consideration is that small metoposaurids of the latest Triassic, such as those found in the Petrified Forest Member, may be juveniles of neither species, but rather of a presently unrecognised large metoposaurid. It bears noting that diagnostic cranial material of small metoposaurids is mostly known from horizons of the

upper part of the Chinle Formation and their correlates in the Dockum Group (Bull Canyon and Redonda formations) of New Mexico. The few exceptions include the two specimens described by Zanno et al. (2002) (MNA V8145, UCMP 175145) from the Blue Mesa Member of the Chinle Formation (in which large metoposaurids are extremely abundant) and the now-lost specimen described by Davidow-Henry (1989) (TTU-P09126) from the lower part of the Cooper Canyon Formation (Dockum Group). These specimens are Adamanian in age (Zanno et al. 2002; Martz et al. 2013) in contrast to the Revueltian and Apachean ages of the upper Chinle, Bull Canyon, and Redonda specimens. Based strictly on the known temporal ranges of other stereo-spondyls, it seems unlikely that *K. perfectus* is the only large-bodied metoposaurid found throughout the Chinle Formation because its species lifespan would exceed 10 million years. Metoposaurid succession occurs in Europe, Morocco, and Texas and is thus plausible in the Chinle Formation (Hunt 1993; Milner and Schoch 2004).

Secondly, Hunt (1993) cited the co-occurrence of proportionately short intercentra of a similar size in horizons bearing the elongate intercentra considered diagnostic of *Apachesaurus*. It is important to reiterate that recent histological work has cast doubt on the utility of the elongate intercentra for species discrimination (Gee et al. 2017). Poor constraints on the early ontogeny of metoposaurid postcrania and variation along the axial column that result from a lack of articulated small specimens present additional challenges. For example, the third vertebral position is significantly shorter than the mid-trunk intercentra in PEFO 40023. It is also important to consider that size is not necessarily strongly correlated with ontogenetic maturity at the level of comparing specimens of a nearly identical size. Variables such as developmental plasticity and intraspecific variation can confound interpretations of these observations. A third consideration is that although metoposaurids are the only large-bodied temnospondyls of the Late Triassic of the southwest region of North America, there are several small-bodied, lesser-known stereospondyls from the Late Triassic whose postcrania could plausibly overlap in size with *Apachesaurus*. This includes *Latiscopus disjunctus* Wilson (1948) from the Dockum Group (considered by some to be a *nomen dubium*), *Almasaurus habbazi* Dutuit (1976) from Morocco, *Rileymillerus cosgriffi* Bolt and Chatterjee (2000), also from the Dockum Group, and *Chinlestegophis jenkinsi* Pardo et al. (2017) from the Chinle Formation of Utah. Only postcrania of *Almasaurus* is confidently known; that tentatively associated with *Rileymillerus* is more uncertain. The postcrania of *Chinlestegophis* does not include the intercentra. The presence of these taxa is at least indicative of the presence of possibly coeval, small-bodied non-metoposaurid stereospondyls.

Thirdly, the lack of material of co-occurring large metoposaurids in the Redonda Formation may be associated with a taphonomic bias. Hunt (1993) cited a skew of small to large metoposaurid elements (thousands to none) in the NMMNH collections as evidence for the diminution of body size in *Apachesaurus*. However, the skew is considerably reduced when limiting the comparison to material that can be properly referred to the taxon on the basis of the formal diagnosis of Spielmann and Lucas (2012) and without the discarded

intercentra character: the few skulls. That list is further reduced under our amended diagnosis. The absence of large-bodied forms does not necessarily imply that the existing small-bodied forms are small adult metoposaurids. It can only be concluded that the former are not found in the same environments that frequently preserve the latter. At PEFO, blue paleosol localities with abundant material of small metoposaurids only preserve extremely rare and fragmentary material of large metoposaurids (Parker 2006; Loughney et al. 2011). The presence of articulated specimens and rare taxa (e.g. *Revueltosaurus*) and various sedimentological features indicate a low-energy system with minimal transport. If immature metoposaurids' occupied these environments as an ecological strategy to avoid conspecific predation by larger individuals in high-energy systems that form more typical preservational environments, it would be expected for large metoposaurids to be extremely rare. Taphonomic biases certainly play a role in metoposaurid-bearing horizons considering that juveniles of the various large-bodied taxa are so exceedingly rare, including in the mass death assemblages that comprise dozens of individuals (e.g. Dutuit 1976; Sulej 2007; Lucas et al. 2010, 2016; Brusatte et al. 2015). Biases associated with ecological separation may also have played a role if niche partitioning between life stages was a utilised strategy, which has been previously suggested by various authors (e.g. Rinehart et al. 2009; Lucas et al. 2016; Gee and Parker 2017). Furthermore, although large metoposaurids are extremely rare in the upper portions of the Chinle Formation, they are not entirely absent. Partial material of an indeterminate large metoposaurid taxon is reported from the Petrified Forest Member (Long and Murry 1995; Gee and Parker 2018) and from the Owl Rock Member (Kirby 1989). Thus, material of small-bodied metoposaurids cannot be assumed to pertain to *Apachesaurus* based on size alone.

Lastly, Hunt (1993) made an argument for the utility of the position of the pineal foramen for ontogenetic determination based on the study of *Benthosuchus sushkini* (Bystrow and Efremov 1940). This claim was first made by Davidow-Henry (1987, 1989) on the same basis and primarily based on TTU P-9216, a specimen from the Post Quarry, Texas. It was later reiterated by Zanno et al. (2002, p. 124), who additionally cited the work of Schoch (1995) and Kathe (1999). However, this argument has been propagated primarily on the basis of *Benthosuchus*, which is an Early Triassic trematosaurid from Russia that is phylogenetically and temporally distinct from metoposaurids. It has not been demonstrably proven that the pineal is a useful feature for determining the relative maturity of metoposaurid specimens. Equally distant taxa were studied in the works cited by Zanno et al. (2002). Schoch (1995) and Kathe (1999) focused primarily on Paleozoic rhachitomous forms, with no sampling of basal stereospondyls, let alone derived forms such as metoposaurids. Furthermore, the juvenile specimen of '*M.*' *bakeri* from Nova Scotia (Baird 1986) and a small specimen of *M. diagnosticus* (Milner and Schoch 2004, p. 239–240, figure 2) possess a pineal foramen located in the posterior half of the parietals. *Apachesaurus* is restricted to the southwest of North America, and there is no reason to presume that these specimens are previously unidentified diminutive individuals. Both preserve various features that readily

distinguish them from *Apachesaurus* (e.g. asymmetrical squamosal with curved lateral margin). This does not necessarily imply that the pineal is not a useful feature, but rather that a mid-length position of the foramen may only be useful for identifying the most immature of specimens. If so, the timing of a shift in position must be better constrained through additional recovery of small-bodied specimens.

A total of three small-bodied metoposaurids (PEFO 16759, PEFO 35292, PEFO 40023) of a comparable size to the holotype of *Apachesaurus* (UCMP 63845) have now been sampled and unequivocally demonstrated to be juvenile forms. Conversely, previous arguments and lines of evidence in favour of a notable diminution in adult body size in metoposaurids are here demonstrated to be questionable. Previous histological work (Gee et al. 2017) has demonstrated the presence of a large-bodied metoposaurid in the late Norian based on the relative immaturity of intercentra sampled from this member, irrespective of the validity and status of *Apachesaurus*. This was then directly confirmed by the report of a mandible of a typically large-bodied metoposaurid from Zuni Well Mound (late Norian) (Gee and Parker 2018). It is not a coincidence that small-bodied specimens come from blue paleosol localities (Zuni Well Mound, Dinosaur Hill, RAP Hill) interpreted as lower-energy attritional settings (Therrien and Fastovsky 2000; Loughney et al. 2011). In addition to small metoposaurids, material of otherwise rare taxa (e.g. *Vancleavea campi*, *Postosuchus kirkpatrickorum*, *Coelophysis* sp., *Revueltosaurus callenderi*) also occurs at these sites (Padian 1986; Long and Murry 1995; Parker and Barton 2008), sometimes with a high degree of articulation (Loughney et al. 2011). This is suggestive of a possibility that environments with large metoposaurids are simply not as likely to be preserved. Some counterevidence exists in the form of the aquatic phytosaurs, which typically co-occur with metoposaurids throughout the Late Triassic, including in the blue paleosol localities. However, phytosaurs are extremely rare in these paleosols, and it bears emphasizing that phytosaurs were certainly mobile on land, even if they preferred aquatic environments. The ability for terrestrial locomotion of metoposaurids has been briefly addressed by a number of workers, without much consensus, as part of a broader discussion of metoposaurid dispersal (e.g. Hunt 1993, p. 92; Sulej 2007, p. 120). However, the underdevelopment of the pectoral and pelvic girdles and the lack of well-ossified carpals and tarsals, in comparison to fully terrestrial temnospondyls, suggests that adults in particular were not very efficient at terrestrial locomotion. The proposed partitioning of metoposaurid life stages (e.g. Rinehart et al. 2009) suggests that a certain degree of periodic terrestriality would be necessary in immature individuals to facilitate the dispersal from the environments inhabited primarily by juveniles into those occupied by adults. However, the morphological similarities between small-bodied and large-bodied forms indicates that it remains likely that juveniles spent the majority of the time in the water, as with adults. Additionally, the finite element analysis (FEA) of Fortuny et al. (2017) led to the conclusion that the same feeding strategies were being utilized between the large-bodied *Metoposaurus krasiejowensis* and the small-bodied *Apachesaurus*. Accordingly, phytosaurs were probably less constrained than metoposaurids by the reduction in large, permanent bodies of water. They may thus have faced less of a selective pressure to actively migrate to lower latitudes during periods of aridification. Probably a better proxy taxon would be any of the various fishes that co-occur with tetrapods in the Chinle Formation, but these are often only represented by isolated dental elements (e.g, Heckert 2004; Kligman et al. 2017).

Implications for the taxonomy of *Apachesaurus*

Independent of this study's findings, the diagnosis of *Apachesaurus* sensu Spielmann and Lucas (2012) and the basis for referral of many specimens is already problematic (Appendix 1). Elongation of the intercentra, the sole postcranial character, has been demonstrated as a hallmark of early ontogeny by Gee et al. (2017). The absence of a posteriorly projecting occiput is considered diagnostic, yet this is seen in two previously referred specimens (Spielmann and Lucas 2012, figures 16A–D and 17B). Spielmann and Lucas (2012, p. 15) claim that the second specimen (TTU P-9216) does not feature a posteriorly projecting occiput, but their photograph of this specimen and figures from other authors (e.g. Davidow-Henry 1989, figure 1) clearly indicate a occiput that projects posteriorly beyond the posterior skull margin in dorsal profile in a fashion identical to that of large metoposaurids. The arching of the tabulars is seen in *Koskinonodon perfectus* (Case 1922), and the curvature of the dorsal margin may be a taphonomic artifact or intraspecifically variable based on *Metoposaurus krasiejowensis* (Sulej 2007). Some features, such as the contribution of the postfrontal to the medial orbital margin, are qualitative and somewhat subjective, not to mention that they vary within individuals and intraspecifically. Lastly, the recovery of small-bodied metoposaurids with intercentra that demonstrate marked immaturity raises further questions concerning the status of *Apachesaurus*. A detailed appraisal of the previous diagnosis of *Apachesaurus* is presented in Appendix 1.

This study's findings that support an interpretation of *Apachesaurus* as a juvenile metoposaurid merit further evaluation of its taxonomy. It is fortunate that the best record of juvenile metoposaurid specimens pertains to those of the North American *Koskinonodon perfectus* and '*Metoposaurus*' *bakeri*. Based on comparisons to the few specimens of these taxa, *Apachesaurus* can be readily separated from both at the species level. At the genus level, *Apachesaurus*, which features a lacrimal excluded from the orbital margin cannot be synonymised with *Koskinonodon*, which features a lacrimal entering the orbit. The absence of any documented ontogenetic influence on the lacrimal morphology or position further supports this stance. '*Metoposaurus*' *bakeri* shares a lacrimal excluded from the orbit with *Apachesaurus*, but their synonymy is unsupported because '*M.*' *bakeri* is characterised by several features that are contrary to those of *Apachesaurus* (e.g. asymmetrical squamosal). It should also be noted that the '*M.*' *bakeri* occurs only in the late Carnian (Case 1931, 1932; Lucas 1998) and is thus markedly temporally separated

from *Apachesaurus*. Affinities with a non-North American taxon seem equally unlikely. Metoposaurid taxa are highly endemic, a pattern that would likely have been enhanced throughout the Late Triassic by the rifting of Pangea and that would have separated the North American taxa from the African and European populations. Accordingly, we maintain the taxon but amend the taxonomic diagnosis, as in the systematic palaeontology. The updated diagnosis reflects its status as a juvenile metoposaurid, with the removal of features that can be considered unreliable based on the current understanding of metoposaurid morphology, taxonomy, and ontogeny (e.g. elongation of the intercentra). We reiterate that this diagnosis is unstable given the paucity of juvenile specimens, a poor understanding of metoposaurid ontogeny, and the lack of a known mature end member of the taxon. Some retained features may be ontogenetically influenced (e.g. constriction of the cultriform process), and the diagnosis will likely require additional revision pending further discovery and study of small-bodied metoposaurids. This approach creates complications for the alpha taxonomy of the Metoposauridae, particularly because *Apachesaurus* differs far more morphologically from all other metoposaurids than any other taxon and is only known from specimens that represent immature individuals. It thereby exerts significant influence on the determination of plesiomorphic characters, which has historically been problematic for metoposaurids (Schoch, 2008). Therefore, *Apachesaurus* should be excluded from phylogenetic analyses, both at the family level and in broader temnospondyl analyses, until skeletally mature specimens of the taxon are recovered and characterised.

Conclusions

Here we have presented new morphological and histological data from small-bodied metoposaurids from PEFO that provide important insights into early ontogeny of metoposaurids and the taxonomy of *Apachesaurus*. The most important result of this study is the determination that these specimens belong to immature individuals based on their intercentra histology. Thus, slight morphological differences, such as the development of the otic notch, can be correlated with both increased size and relative maturity. Both the presence of highly immature small-bodied metoposaurids that would traditionally be referred to *Apachesaurus* and the noted morphological changes in turn challenge the traditional interpretation of *Apachesaurus* as a diminutive taxon. A large foundation of histological data from the elongate intercentra now exists through indirect evidence of the presence of large-bodied metoposaurids in the late Norian and dispels the notion that *Apachesaurus* is a mature yet diminutive taxon. The persistent paucity of actual specimens of large-bodied taxa can be plausibly explained by the same ecologically influenced taphonomic bias that results from niche partitioning. This likely contributes to the paucity of juvenile specimens in older strata. It should not be excluded that sampling bias may also contribute to the perceived paucity in part; the abundance of metoposaurid specimens often results in more fragmentary material being overlooked and uncollected.

The relative abundance of metoposaurids, obligately aquatic temnospondyls, in the Late Triassic of western North America has also led them to be utilised for interpretations of the paleoenvironment. Previous workers (e.g. Parker and Martz 2011) have postulated that faunal turnover within the vertebrate assemblage, including from *Koskinonodon* to *Apachesaurus*, may be evidence of ecological responses to noted climate change in the Chinle basin during the late Norian (Atchley et al. 2013; Nordt et al. 2015; Baranyi et al. 2017). The findings of this study suggest that while there is likely to be a faunal turnover of metoposaurids, it is characterised by a typical succession of one large-bodied taxon by another, rather than by a trend toward smaller body size. There may also be a greater shift in the preservation of different depositional environments rather than a major shift in vertebrate assemblage. The possibility that the turnover between two large-bodied taxa could be partially induced by climatic change remains viable. However, the hypothesis that the clade followed an evolutionary trend of marked size diminution or of increased terrestriality late in its existence should be discarded.

Disclosure statement

No potential conflict of interest was reported by the authors.

ORCID

Bryan M. Gee   http://orcid.org/0000-0003-4517-3290
William G. Parker   http://orcid.org/0000-0002-6005-7098

References

Atchley SC, Nordt LC, Dworkin SI, Ramezani J, Parker WG, Ash SR, Bowring SA. 2013. A linkage among Pangean tectonism, cyclic alluviation, climate change, and biologic turnover in the Late Triassic: the record from the Chinle Formation, southwestern United States. J Sediment Res. 83(12):1147–1161.

Baird D. 1986. Some Upper Triassic reptiles, footprints, and amphibian from New Jersey. The Mosasaur. 3:125–153.

Baranyi V, Reichgelt T, Olsen PE, Parker WG, Kürschner WM. 2017. Norian vegetation history and related environmental changes: new data from the Chinle Formation, Petrified Forest National Park (Arizona, SW USA). Geol Soc Am Bull. 130(5–6):775–795.

Bolt JR, Chatterjee S. 2000. A new temnospondyl amphibian from the Late Triassic of Texas. J Paleontol. 74(4):670–683.

Branson EB, Mehl MG. 1929. Triassic amphibians from the Rocky Mountain region. U Missouri Stud. 4:155–239.

Brochu CA. 1992. Ontogeny of the postcranium in crocodylomorph archosaurs [master's thesis]. Austin (TX): University of Texas at Austin.

Brusatte SL, Butler RJ, Mateus O, Steyer JS. 2015. A new species of *Metoposaurus* from the Late Triassic of Portugal and comments on the systematics and biogeography of metoposaurid temnospondyls. J Vert Paleontol. 35(3):e912988.

Bystrow AP, Efremov JA. 1940. *Benthosuchus sushkini* Efremov - a labyrinthodont from the Eotriassic of the Sharzenga River. Trudy Paleontologicheskogo Instituta. 10:1–152.

Case EC. 1922. New reptiles and stegocephalians from the Upper Triassic of western Texas. Carnegie Int Washington. 321:7–84.

Case EC. 1931. Description of a new species of *Buettneria*, with a discussion of the brain case. Contrib Mus Paleontol, Univ Michigan. 3(11):187–206.

Case EC. 1932. A collection of stegocephalians from Scurry County, Texas. Contrib Mus Paleontol, Univ Michigan. 4:1–56.

Colbert EH, Imbrie J. 1956. Triassic metoposaurid amphibians. Bull Am Mus Nat Hist. 110(6):399–452.

Damiani R. 2008. A giant skull of the temnospondyl *Xenotosuchus africanus* from the Middle Triassic of South Africa and its ontogenetic implications. Acta Palaeontol Pol. 53(1):75–84.

Danto M, Witzmann F, Fröbisch NB. 2016. Vertebral development in Paleozoic and Mesozoic tetrapods revealed by paleohistological data. PLOS ONE. 11(4):e0152586.

Davidow-Henry B. 1987. New metoposaurs from the southwestern United States and their phylogenetic relationships [master's thesis]. Lubbock (TX): Texas Tech University.

Davidow-Henry B. 1989. Small metoposaurid amphibians from the Triassic of western North America and their significance. In: Lucas SG, Hunt AP, editors. Dawn of the Age of Dinosaurs in the American Southwest. Albuquerque: New Mexico Museum of Natural Science and History; p. 278–292.

Dutuit JM. 1976. Introduction à l'étude paléontologique du Trias continental marocain. Description des premiers stegocephales recueillis dans le couloir d'Argana (Atlas occidental). Mem Mus Natl His Nat Paris Series C. 36:1–253.

Fortuny J, Marcé-Nogué J, Konietzko-Meier D. 2017. Feeding biomechanics of Late Triassic metoposaurids (Amphibia: temnospondyli): a 3D finite element analysis approach. J Anat. 230(6):752–765.

Gee BM, Parker WG. 2017. A juvenile *Koskinonodon perfectus* (Temnospondyli, Metoposauridae) from the Upper Triassic of Arizona and its implications for the taxonomy of North American metoposaurids. J Paleontol. 91(5):1047–1059.

Gee BM, Parker WG. 2018. Report of a large-bodied metoposaurid from the late Norian (Chinle Formation) in Petrified Forest National Park (AZ, USA). Neues Jahrb Geol Paläont. 287(1):61–73.

Gee BM, Parker WG, Marsh AD. 2017. Microanatomy and paleohistology of the intercentra of North American metoposaurids from the Upper Triassic of Petrified Forest National Park (Arizona, USA) with implications for the taxonomy and ontogeny of the group. PeerJ. 5:e3183.

Gregory JT. 1980. The otic notch of metoposaurid labyrinthodonts. In: Jacobs LL, editor. Aspects of Vertebrate History. Flagstaff: Museum of Northern Arizona Press Flagstaff; p. 125–136.

Griffin CT, Nesbitt SJ. 2016. The femoral ontogeny and long bone histology of the Middle Triassic (?late Anisian) dinosauriform *Asilisaurus kongwe* and implications for the growth of early dinosaurs. J Vert Paleontol. 36(3):e1111224.

Heckert AB. 2004. Late Triassic microvertebrates of the lower Chinle Group (Otischalkian-Adamanian: carnian), southwestern USA. New Mexico Mus Nat Hist Sci Bull. 27:1–170.

Hunt AP. 1993. A revision of the Metoposauridae (Amphibia: temnospondyli) and description of a new genus from western North America. Mus North Arizona Bull. 59:67–97.

Hunt AP. 1989. Comments on the taxonomy of North American metoposaurids and a preliminary phylogenetic analysis of the Metoposauridae. In: Lucas SG, Hunt AP, editors. Dawn of the Age of Dinosaurs in the American Southwest. Albuquerque: New Mexico Mus Nat Hist Sci Bull.; p. 293–300.

Hunt AP, Wright J. 1999. New discoveries of Late Triassic dinosaurs from Petrified Forest National Park, Arizona. In Santucci VL, McClellan L, (editors). National Park Service Paleontological Technical Report, NPS/NRGRD/GRDTR-99/03. Denver: National Park Service Geological Resources Division; p. 96–99.

Kathe W. 1999. Comparative morphology and functional interpretation of the sutures in the dermal skull roof of temnospondyl amphibians. Zool J Lin Soc. 126(1):1–39.

Kirby RE. 1989. Late Triassic vertebrate localities of the Owl Rock member (Chinle Formation) in the Ward Terrace area of northern Arizona. In: Lucas SG, Hunt AP, editors. Dawn of the Age of Dinosaurs in the American Southwest. Albuquerque: New Mexico Museum of Natural Science and History; p. 12–28.

Kligman BT, Parker WG, Marsh AD. 2017. First record of *Saurichthys* (Actinopterygii) from the Upper Triassic (Chinle Formation, Norian) of western North America. J Vert Paleont. 37(5):e1367304.

Konietzko-Meier D, Bodzioch A, Sander PM. 2013. (for 2012). Histological characteristics of the vertebral intercentra of *Metoposaurus diagnosticus* (Temnospondyli) from the Upper Triassic of Krasiejów (Upper Silesia, Poland). Earth Env Sci T R So. 103(3–4):237–250.

Konietzko-Meier D, Danto M, Gądek K. 2014. The microstructural variability of the intercentra among temnospondyl amphibians. Biol J Linn Soc. 112(4):747–764.

Konietzko-Meier D, Klein N. 2013. Unique growth pattern of *Metoposaurus diagnosticus krasiejowensis* (Amphibia, Temnospondyli) from the Upper Triassic of Krasiejów, Poland. Palaeogeogr Palaeoclimatol Palaeoecol. 370:145–157.

Konietzko-Meier D, Sander PM. 2012. Long bone histology of *Metoposaurus diagnosticus* (Temnospondyli) from the Late Triassic of Krasiejów (Poland) and its paleobiological implications. J Vertebr Paleontol. 33(5):1003–1018.

Leidy J. 1856. Notice of remains of extinct vertebrated animals discovered by Professor E. Emmons Proc Acad Nat Sci Philadelphia. 8:255–257.

Long RA, Murry PA. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. New Mexico Mus Nat Hist Sci Bull. 4:1–254.

Loughney KM, Fastovsky DE, Parker WG. 2011. Vertebrate fossil preservation in blue paleosols from the Petrified Forest National Park, Arizona, with implications for vertebrate biostratigraphy in the Chinle Formation. Palaios. 26(11):700–719.

Lucas SG. 1998. Global Triassic tetrapod biostratigraphy and biochronology. Palaeogeogr Palaeoclimatol Palaeoecol. 143:347–384.

Lucas SG, Rinehart LF, Heckert AB, Hunt AP, Spielmann JA. 2016. Rotten Hill: a Late Triassic bonebed in the Texas Panhandle, USA. New Mexico Mus Nat Hist Sci Bull. 72:1–97.

Lucas SG, Rinehart LF, Krainer K, Spielmann JA, Heckert AB. 2010. Taphonomy of the Lamy amphibian quarry: a Late Triassic bonebed in New Mexico, USA. Palaeogeogr Palaeoclimatol Palaeoecol. 298(3):388–398.

Lucas SG, Rinehart LF, Spielmann JA, Hunt AP. 2007. Case 3420 *Buettneria* Case, 1922 (Amphibia): proposed conservation. Bull Zool Nomencl. 64:4.

Martz JW, Parker WG, Skinner L, Raucci JJ, Umhoefer P, Blakey RC,. 2012. Geologic map of Petrified Forest National Park, Arizona. Arizona Geological Survey Con–tributed Map CM–12–A: 1–18.

Martz JW, Mueller B, Nesbitt SJ, Stocker MR, Parker WG, Atanassov M, Fraser N, Weinbaum J, Lehane JR. 2013. (for 2012). A taxonomic and biostratigraphic re-evaluation of the Post Quarry vertebrate assemblage from the Cooper Canyon Formation (Dockum Group, Upper Triassic) of southern Garza County, western Texas. Earth Env Sci T R So. 103(3–4):339–364.

Martz JW, Parker WG. 2010. Revised lithostratigraphy of the Sonsela Member (Chinle Formation, Upper Triassic) in the southern part of Petrified Forest National Park, Arizona. PLOS ONE. 5(2):e9329.

Milner AR. 1994. Late Triassic and Jurassic amphibians: fossil record and phylogeny. In: Fraser NC, Sues H-D, editors. In the Shadow of

the Dinosaurs: Early Mesozoic Tetrapods. Cambridge: Cambridge University press; p. 5–22.

Milner AR, Schoch RR. 2004. The latest metoposaurid amphibians from Europe. Neues Jahrb Geol Paläontol, Abhandlungen. 232(2–3):231–252.

Morales M. 1993. A small metoposaurid partial skull from the Chinle Formation near St. Johns, Arizona. New Mexico Mus Nat Hist Sci Bull. 3:353.

Nordt L, Atchley S, Dworkin S. 2015. Collapse of the Late Triassic megamonsoon in western equatorial Pangea, present-day American Southwest. Geol Soc Am Bull. 127(11–12):1798–1815.

Padian K. 1986. On the type material of Coelophysis Cope (Saurischia: Theropoda) and a new specimen from the Petrified Forest of Arizona (Late Triassic: Chinle Formation). In: Padian K, editor. The Beginning of the Age of Dinosaurs. Cambridge: Cambridge University Press; p. 45–60.

Pardo JD, Small BJ, Huttenlocker AK. 2017. Stem caecilian from the Triassic of Colorado sheds light on the origins of Lissamphibia. P Natl Acad Sci. 114(27):E5389–E5395.

Parker WG. 2002. Correlation of locality numbers for vertebrate fossil sites in Petrified Forest National Park, Arizona. New Mexico Mus Nat Hist Sci Bull. 21:37–42.

Parker WG. 2006. The stratigraphic distribution of major fossil localities in Petrified Forest National Park, Arizona. Mus North Arizona Bull. 62:46–61.

Parker WG, Barton BJ. 2008. New information on the Upper Triassic archosauriform Vancleavea campi based on new material from the Chinle Formation of Arizona. Palaeontol Elect. 11(3):14A.

Parker WG, Irmis RB. 2005. Advances in Late Triassic vertebrate paleontology based on new material from Petrified Forest National Park, Arizona. New Mexico Mus Nat Hist Sci Bull. 29:45–58.

Parker WG, Martz JW. 2011. (for 2010) The Late Triassic (Norian) Adamanian–Revueltian tetrapod faunal transition in the Chinle Formation of Petrified Forest National Park, Arizona. Earth Env Sci T R So. 101(3–4):231–260.

Ramezani J, Hoke GD, Fastovsky DE, Bowring SA, Therrien F, Dworkin SI, Atchley SC, Nordt LC. 2011. High-precision U-Pb zircon geochronology of the Late Triassic Chinle Formation, Petrified Forest National Park (Arizona, USA): temporal constraints on the early evolution of dinosaurs. Geol Soc Am Bull. 123(11–12):2142–2159.

Rinehart LF, Lucas SG, Heckert AB. 2009. Limb allometry and lateral line groove development indicates terrestrial-to-aquatic lifestyle transition in Metoposauridae (Amphibia: Temnospondyli) [paper no. 96–14]. Geol Soc Am Abstr Progr. 41(7):263.

Romer AS. 1947. Review of the Labyrinthodontia. Bull Mus Comp Zool. 99:1–367.

Sanchez S, Schoch RR. 2013. Bone histology reveals a high environmental and metabolic plasticity as a successful evolutionary strategy in a long-lived homeostatic Triassic temnospondyl. Evol Bio. 40(4):627–647.

Sawin HJ. 1945. Amphibians from the Dockum Triassic of Howard County, Texas. Univ Tex. 401:361–399.

Schoch RR. 2002. The evolution of metamorphosis in temnospondyls. Lethaia. 35(4):309–327.

Schoch RR. 2006. A complete trematosaurid amphibian from the Middle Triassic of Germany. J Vertebr Paleontol. 26(1):29–43.

Schoch RR. 2008. A new stereospondyl from the German Middle Triassic, and the origin of the Metoposauridae. Zool J Linn Soc. 152: 79–113.

Schoch RR. 2013. The evolution of major temnospondyl clades: an inclusive phylogenetic analysis. J Syst Palaeontol. 11(6):673–705.

Schoch RR. 1995. Heterochrony in the development of the amphibian head. In: McNamara KJ, editor. Evolutionary Change and Heterochrony. Hoboken: Wiley; p. 107–124.

Schoch RR, Witzmann F. 2009. Osteology and relationships of the temnospondyl genus Sclerocephalus. Zool J Linn Soc. 157(1):135–168.

Sengupta DP. 2002. Indian metoposaurid amphibians revised. Paleontol Res. 6(1):41–65.

Spielmann JA, Lucas SG. 2012. Tetrapod fauna of the Upper Triassic Redonda Formation east-central New Mexico: the characteristic assemblage of the Apachean land-vertebrate faunachron. New Mexico Mus Nat Hist Sci Bull. 55:1–119.

Steyer JS. 2000. Ontogeny and phylogeny in temnospondyls: a new method of analysis. Zool J Linn Soc. 130:449–467.

Steyer JS. 2003. A revision of the early Triassic "capitosaurs" (Stegocephali, Stereospondyli) from Madagascar, with remarks on their comparative ontogeny. J Vert Paleontol. 23(3):544–555.

Steyer JS, Laurin M, Castanet J, De Ricqlès A. 2004. First histological and skeletochronological data on temnospondyl growth: palaeoecological and palaeoclimatological implications. Palaeogeogr Palaeoecol. 206 (3):193–201.

Sues H-D, Olsen PE. 2015. Stratigraphic and temporal context and faunal diversity of Permian-Jurassic continental tetrapod assemblages from the Fundy rift basin, eastern Canada. Atl Geol. 51(1):139–205.

Sulej T. 2002. Species discrimination of the Late Triassic temnospondyl amphibian Metoposaurus diagnosticus. Acta Palaeontol Pol. 47:535–546.

Sulej T. 2007. Osteology, variability, and evolution of Metoposaurus, a temnospondyl from the Late Triassic of Poland. Palaeontol Polonica. 64:29–139.

Teschner EM, Sander PM, Konietzko-Meier D. 2018. Variability of growth pattern observed in Metoposaurus krasiejowensis humeri and its biological meaning. J Iber Geol. 44(1):99–111.

Therrien F, Fastovsky DE. 2000. Paleoenvironments of early theropods, Chinle Formation (Late Triassic), Petrified Forest National Park, Arizona. Palaios. 15(3):194–211.

Warren AA, Hutchinson MN. 1988. A new capitosaurid amphibian from the Early Triassic of Queensland, and the ontogeny of the capitosaur skull. Palaeontology. 31(3):857–876.

Warren AA, Marsicano C. 2000. A phylogeny of the Brachyopoidea (Temnospondyli, Stereospondyli). J Vertebr Paleontol. 20(3):462–483.

Watson DMS. 1919. The structure, evolution and origin of the Amphibia. The orders Rhachitomi and Stereospondyli. Phil Trans R Soc Lond B. 209:1–73.

Wilson JA. 1948. A small amphibian from the Triassic of Howard County, Texas. J Paleontol. 22(3):359–361.

Witzmann F. 2005. Cranial morphology and ontogeny of the Permo-Carboniferous temnospondyl Archegosaurus decheni Goldfuss, 1847 from the Saar–Nahe Basin, Germany. Earth Env Sci T R So. 96 (2):131–162.

Yates A, Warren AA. 2000. The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. Zool J Linn Soc. 128:77–121.

Zanno LE, Heckert AB, Krzyzanowski SE, Lucas SG. 2002. Diminutive metoposaurid skulls from the Upper Triassic Blue Hills (Adamanian: latest Carnian) of Arizona. New Mexico Mus Nat Hist Sci Bull. 21:121–126.

Zittel KA. 1888. Handbuch der Paläontologie. Abteilung 1. Paläozoologie Band III. Vertebrata (Pisces, Amphibia, Reptilia, Aves). Munich: Oldenbourg.

Appendix 1: Evaluation of the diagnosis of *Apachesaurus gregorii sensu* Spielmann and Lucas (2012)

Evaluation of taxonomic diagnosis

The original diagnosis of *Apachesaurus gregorii* provided by Hunt (1993, p. 81) lists five autapomorphies for the genus and species: (1) lacrimal flexure of the supraorbital canal separated from the lacrimal; (2) a shallow otic notch; (3) an occiput that does not project posteriorly; (4) a narrow cultriform process; (5) elongate intercentra. An additional eight autapomorphies were listed by Spielmann and Lucas (2012, p. 13): (6) a significantly reduced lacrimal; (7) a reduced contribution of the postfrontal to the medial orbital margin; (8) a symmetrical squamosal without significant deflection of the anterior process and with anteroposteriorly-oriented medial and lateral margins; (9) a rounded, trapezoidal foramen magnum (in contrast to a 'keyhole-shaped' foramen in other metoposaurids; (10) moderate arching of the tabulars, resulting

in a curved dorsal margin in occipital profile (shared with *Metoposaurus krasiejowensis*, which is referred to as *M. diagnosticus* in the publication); (11) a less extensive oblique crest of the pterygoid; (12) smaller and more laterally positioned paraquadrate foramen; (13) minimal expression of the accessory paraquadrate foramen. A detailed appraisal of these characters is presented here. Conclusions regarding their validity are reflected in the amended diagnosis.

(1) Lacrimal flexure of supraorbital canal separated from lacrimal: The supraorbital lateral line canal of *Apachesaurus* does not contact the lacrimal in any way. However, the comparative figure of Spielmann and Lucas (2012, figure 19) illustrates *Koskinonodon perfectus* as either having only a very slight contact with the lacrimal or as being cleanly separated from the element (also seen in Case 1922, figure 1); this is suggestive of intraspecific variation. Furthermore, the trajectory of the canal in *Apachesaurus* is not particularly different from large metoposaurids in which the canal is consistent in originating at the anteromedial portion of the premaxilla, curving posterolaterally around the medial narial margin, and then curving posteromedially around the medial orbital margin. The premaxilla of *Apachesaurus* is only known from one specimen, which is presently represented only by a cast, so whether the supraorbital canal originates on the element is unclear. In general, the antorbital region is known only from a few specimens, some of which may not be properly referable to the taxon. The only other difference that may be noted is the precise contour of the lateral curvature of this canal; this is both interspecifically and intraspecifically variable (e.g. Lucas et al. 2016, figure 28) and likely influenced by minor changes to the snout proportions.

The condition of *Apachesaurus* that was identified by Hunt (1993) is thus valid, but it is also complicated by a new character added by Spielmann and Lucas (2012): a reduced lacrimal. The lateral line canal's separation from the lacrimal is not due to a significant deviation in its trajectory but rather due to the reduced size and posterolateral shift in position of the element. Based on illustrations of the holotype (Spielmann and Lucas 2012, figures 10, 19), it becomes apparent that if the lacrimal were of a comparable size and position to large metoposaurids, the canal would more closely approach and perhaps contact the lacrimal. In this regard, these characters are redundant. It seems more parsimonious to maintain the reduced size and altered position of the lacrimal, which does differ significantly from other metoposaurids, rather than the morphology of the canal, which is not different at least in the regard of its lateral extent at the longitudinal point at which it contacts the lacrimal in other taxa. This is different than if the canal's trajectory was significantly altered such that it would not contact the lacrimal if mapped onto a typical large-bodied taxon. Maintaining both characters would be akin to adding an additional (equally redundant) character that the lacrimal does not contact the nasal in *Apachesaurus*, which is also a byproduct of the reduction and the migration of the former. Accordingly, this character should be considered invalid.

(2) Shallow otic notch: A shallow otic notch is a feature that requires careful identification to determine the relative influences of ontogeny, taphonomy, and taxonomy. A deep otic notch with a well-defined tabular horn is present in some small specimens, such as a juvenile '*Metoposaurus*' *bakeri*, YPM PU 21742 (Hunt 1993, figure 6), and a juvenile *Koskinonodon perfectus*, TMM 31099-12B (Hunt 1993, figure 8A–B). However, it cannot be excluded that the element could be broken off in other small-bodied specimens due to its small, flat morphology and protruding angle, or that the broken margin could be more susceptible to weathering. This can be seen in various specimens of large metoposaurids, such as *M. krasiejowensis* (Sulej 2007, figures 4A, 12A, 15A), *Koskinonodon perfectus* (Lucas et al. 2016, figures 28E, 28G, 30C, 30G), *M. algarvensis* (Brusatte et al. 2015, figure 3), '*M.*' *bakeri* (Case 1931, plate 1.1), and *Dutuitosaurus ouazzoui* (Dutuit 1976, plates 31A, 44). This can often reduce the perceived depth of the otic notch. In large metoposaurids, the notch may only appear to remain relatively deep when the tabular horn is broken because of the greater depth achieved in mature forms.

When comparing the three small-bodied specimens from PEFO (PEFO 16759, PEFO 35292, PEFO 40023), increased size and histological maturity are correlated with a development of the otic notch and the tabular horn. Similar ontogenetic trajectories can be seen in various rhachitomous forms (e.g. Schoch 2002), capitosaurids (e.g. Warren and Hutchinson 1988; Steyer 2003) and the stereospondylomorphs *Sclerocephalus* (Schoch and Witzmann 2009) and *Archegosaurus* (Witzmann 2005). The histological data suggest a continuous growth series as represented by these specimens, rather than distinct lineages. Accordingly the shallow otic notch may only be useful for identifying very immature individuals. Additional work is required to characterize changes to the otic notch throughout ontogeny in metoposaurids and timing of these changes across different taxa, but there is sufficient evidence at present to cast doubt on the utility of this feature for taxonomy.

(3) Occiput that does not project posteriorly: An occiput that does not project posteriorly was already a conflicting character because it does project beyond the posterior margin of the postparietals in two of the previously referred specimens via the occipital condyles, NMMNH P-37069 (Spielmann and Lucas 2012, figure 16A–B) and TTUP 9216 (Davidow-Henry 1989, figure 1; Spielmann and Lucas 2012, figure 17B; Martz et al. 2013, figure 4). In neither specimen does the posterior skull margin appear to be weathered in any fashion that would have unnaturally exposed the occiput. These specimens are otherwise identical to the holotype and suggest that the development of more projected condyles may be ontongenetic and intraspecifically variable. It should also be noted that the occipital condyles are very slightly visible in dorsal profile in the holotype (Spielmann and Lucas 2012, figure 9A), although this is typically omitted in line drawings of the specimen. The larger PEFO 40023 features more prominently projecting condyles, though not to the degree of large specimens, which further suggests an ontogenetic influence. The character is maintained here because there is not a clear ontogenetic trajectory in metoposaurids when comparing the smaller TTUP 9216, with markedly projecting condyles, with the holotype of *Apachesaurus*, with barely projecting condyles (if at all).

(4) Narrow cultriform process: The relative width of the cultriform process is one of the more robust characters insofar as a morphology comparable to that of *Apachesaurus* has never been identified in any large metoposaurid taxon. An ontogenetic influence cannot be excluded, particularly if the width of the process significantly influenced some functional aspect of the interpterygoid vacuities, whether in feeding or in respiration. Differences between a semi-terrestrial *Apachesaurus* and all other, fully aquatic taxa would not be unexpected. The broad proportions of the process were considered to be autapomorphic by Hunt (1993), although *Chinlestegophis* and some brachyopoids also feature a broad process (Warren and Marsicano 2000; Pardo et al. 2017). Finite element analyses of *Apachesaurus* and *Metoposaurus krasiejowensis* by Fortuny et al. (2017) suggested that the broad width of the cultriform process in metoposaurids may be an adaptation to accommodate stress given the large interpterygoid vacuities and the relatively thin palatal bones, and that *Apachesaurus* may have possessed a narrower process as a result of its smaller skull size. However, additional specimens with well-preserved palates (absent in both specimens described here) would be necessary to assess this. An ontogenetic transition toward a more constricted cultriform process is seen in some temnospondyls, such as the mastodonsaurid *Xenotosuchus* (Damiani 2008). Whether this transition is phylogenetically informative on a broader scale is unclear and requires additional sampling of ontogenetic trajectories.

(5) Elongate intercentra: Elongation of the intercentra is framed as a apomorphy of *Apachesaurus* despite the fact that Hunt (1993)

noted that similarly elongate intercentra occur in the large-bodied *Dutuitosaurus* from Morocco. The character originally included a metric of a diameter-to-length ratio less than 0.8 to define 'elongate,' but no data or statistical justification have ever been provided to support this. This metric does not appear in the revised diagnosis of Spielmann and Lucas (2012) but reappears briefly in an informal discussion of the taxon in Lucas et al. (2016, p. 14). Recent histological work by Gee et al. (2017) has shown that elongation of small intercentra of metoposaurids from the Chinle Formation is associated with relative immaturity, findings that are supported by this study's results. Even under the interpretation of *Apachesaurus* as a taxonomically distinct, diminutive metoposaurid characterized by elongate intercentra, the feature is not informative for species discrimination because of a lack of features that would distinguish it from the elongate intercentra of very juvenile individuals of large-bodied taxa.

(6) Reduced lacrimal excluded from orbit: The lacrimal has remained a contentious element with regard to metoposaurid taxonomy due to debate over the phylogenetic significance of its position. Earlier workers (e.g. Romer 1947; Colbert and Imbrie 1956) argued that the lacrimal did not enter the orbital margin in *Metoposaurus diagnosticus* (at the time, the genus was monospecific). This was in apparent contrast to the condition in *Koskinonodon*, representing one of the few identifiable differences and the only feature in the original diagnosis of *Koskinonodon*. However, Sulej (2002) reexamined the holotype of *M. diagnosticus*, found a lacrimal that entered the orbit, and subsequently identified the same relationship in the vast majority of specimens of *M. krasiejowensis* (Sulej 2007). Although this has been disputed on several occasions (e.g. Lucas et al. 2007, 2016), there is greater consensus supporting a lacrimal contribution to the orbital margin that is shared between *Metoposaurus* and *Koskinonodon*. The observations of Sulej (2002) were reaffirmed by Brusatte et al. (2015), who further validated the point in their description of *M. algarvensis*. Phylogenetic codings of the genera (e.g. Schoch 2013) also reflect this characterization. The feature is thus of more limited utility in distinguishing the two genera than previously argued, although it can differentiate these metoposaurids from other taxa, such as '*Metoposaurus*' *bakeri*, whose taxonomic affinities have accordingly remained convoluted as it genuinely has a lacrimal excluded from the orbit. Regarding *Apachesaurus*, a reduced lacrimal is an autapomorphy of the taxon. This results from an increase in the posterior extent of the medial incision of the maxilla at its anterior end and a lateral expansion of the prefrontal that relegates the lacrimal to a position nearly fully lateral to the orbit. Subsequently, the lacrimal does not contact the nasal, as in all other metoposaurids, and does not contribute to either the narial or orbital margin. The latter condition is shared with '*Metoposaurus*' *bakeri*. The strength of the character is primarily tied to the absence of significant interspecific or ontogenetic variation in the lacrimal among large metoposaurids.

It should be noted that a previously referred specimen, UCMP V82250/171591, features a proportionately larger lacrimal that is approximately half of the distance between the naris and the orbit. This is greater than that of the holotype and of a comparable degree to large-bodied metoposaurids. Additionally, it is very narrowly separated from the orbit by a minute fragment. Neither the jugal nor the prefrontal is known to narrowly divide the orbit and the lacrimal in any metoposaurid, and it seems most likely that it is in fact a broken fragment of the lacrimal that would thus indicate a contribution of the element to the orbital margin.

(7) Reduced contribution of postfrontal to medial orbital margin: The contribution of the postfrontal to the medial orbital margin appears to be variable within the holotype of *Apachesaurus* itself; the right postfrontal extends to approximately the mid-length of the orbit, whereas that of the left counterpart (with a slightly deformed orbit) is definitively reduced in extent (Spielmann and Lucas 2012, figure 10A). A similar variability is seen in the Rotten Hill population of *Koskinonodon perfectus*. For example, specimens such as WT 3055 (Lucas et al. 2016, figure 30A) feature a comparable contribution to that of the left

postfrontal of the holotype of *Apachesaurus*, whereas most other specimens feature a more typical contribution to that of large metoposaurids and to the right postfrontal. One specimen, WT 3166–1 (Lucas et al. 2016, figure 28A) features an asymmetry similar to the holotype of *Apachesaurus*, with a small contribution of the left postfrontal and a much greater contribution of the right postfrontal. The pattern is present in the holotype of *Metoposaurus algarvensis* (Brusatte et al. 2015, figure 2B) but with the greater contribution on the left side. Any differences in the relative contribution are highly qualitative and relatively minor, lacking any precise threshold. Given the documented variation at all scales, we consider this character to be questionable until more specimens of *Apachesaurus* are recovered.

(8) Symmetrical squamosal with no significant deflection of anterior process and anteroposteriorly oriented lateral and medial margins: This character is considered in the same vein as the cultriform process (character 4) – this morphology has not been identified in large-bodied taxa, and although an ontogenetic influence can be hypothesized, none is evident at present. The primary source of interspecific variation is in the lateral portion of the element, where in large metoposaurids, the margin is convex. This could be associated with an ontogenetic shift toward a transversely expanded posterior skull table that is seen in large-bodied forms with a brachycephalic contour via a lateral expansion of the quadratojugal and the squamosal. This would remove the symmetry of the latter and give the anterior process an appearance of having been deflected medially. A comparison of sub-adult and adult specimens of *Koskinonodon perfectus* (Lucas et al. 2016, figure 30) indicates that such an expansion may characterize the taxon. It should also be noted that there is a weak correlation between increased size and squamosal symmetry across PEFO 16759, PEFO 35292, and PEFO 40023. However, as with the cultriform process, the paucity of small-bodied metoposaurids with clearly defined squamosals limits any broader interpretations.

(9) Rounded, trapezoidal foramen magnum: The significance of the morphology of the foramen magnum is tied to the potential taphonomic influence on the shape of the tabular and the convexity of the posteromedial skull roof in occipital profile (character 10). If the postparietals have been downshifted in any way, they may have altered the upper expansion of the foramen. An extreme case of this is seen in one specimen of *Koskinonodon maleriensis* (Sengupta 2002, figure 5) in which the postparietals have clearly downshifted into the opening such that only the circular ventral portion is exposed. A slightly less deformed foramen magnum is seen in a specimen of *Dutuitosaurus* (Dutuit 1976, plate 47C) in which the opening lacks the bifurcated dorsal expansion and forms a diagonally skewed oval. The foramen magnum of *Apachesaurus* is asymmetrical, and it is noteworthy that the left margin is markedly curved (Spielmann and Lucas 2012, figure 11A–B), a feature seen in other metoposaurids that precedes the dorsal expansion that results in the keyhole-shaped contour. The asymmetry is one line of evidence that some degree of taphonomic deformation has occurred. For example, some variation in the dorsal expansion of the foramen can be seen in *Metoposaurus krasiejowensis* (Sulej 2007, figure 16). This can be correlated with slight damage and deformation to the posteromedial skull roof. The character is maintained here because of the lack of clear evidence for a bifurcated dorsal portion, but caution should be exercised in utilizing this as a diagnostic feature with even slightly deformed specimens.

(10) Moderate arching of the tabular, resulting in a curved profile in occipital view: Based simply on the small sample size of specimens of *Apachesaurus* with a complete tabular, it is difficult to be certain that the convexity created by a slight ventromedial depression of the postparietals and the concavity of the tabulars is not at least partially taphonomic. Spielmann and Lucas (2012) considered this to be similar to the condition of *Metoposaurus krasiejowensis* (referred to as *M. diagnosticus*). However, photographs of multiple specimens of *M. krasiejowensis* in occipital view (Sulej 2007, figure 16) display a range of curvature of the dorsal margin that appears to be correlated with the quality of preservation. What appears to be the best-preserved specimen (Sulej 2007, figure 16A) displays an

essentially flat margin. The generalized reconstruction of the skull of the taxon (Sulej 2007, figure 1D) mirrors this specimen. Conversely, the more poorly-preserved specimens (Sulej 2007, figure 16C–D) feature a prominently concave margin. Figures of the holotype of *Apachesaurus* indicate that it was subject to minor deformation in various regions of the skull, including the occipital region, which is slightly asymmetrical (e.g. Spielmann and Lucas 2012, figure 9). In addition, the postparietals may be slightly down-shifted into the foramen magnum while the tabulars remained articulated. Thus, the former may be slightly angled ventrome-dially, exaggerating the concavity of the margin. Arched tabulars and a concave dorsal margin are present in the holotype of *Koskinonodon perfectus* (Case 1922, figure 1C), and variation in the arching of the tabulars, from minor curvature to a flat margin is seen in '*M.*' *bakeri* (Case 1932, figures 8–9).

(11) Less extensive oblique crest of the pterygoid: This character is considered in the same vein as the reduction of the lacrimal: justifiable insofar as it is not currently known to be particularly variable intraspecifically or throughout ontogeny. It should be noted that the crest of *Dutuitosaurus* (Dutuit 1976; plate 16F; Spielmann and Lucas 2012, figure 11C) is more dorsally oriented than in *Apachesaurus*, but does not appear to significantly differ in size, as is the case with *Metoposaurus krasiejowensis*.

(12) Smaller, more laterally positioned paraquadrate foramina: The variation between the holotype (Spielmann and Lucas 2012, figures 9, 11A–B), in which the foramen is both shorter and narrower than other taxa, and of the previously referred NMMNH P-37069 (Spielmann and Lucas 2012, figure 16C–D), in which it is narrower but far more elongate than in the holotype, is indicative of either intraspecific variation or taphonomic damage to at least one specimen. It also bears noting that the foramina of the holotype of *Koskinonodon perfectus* (Case 1922, figure 1) are of a similar size and proportion to those of the holotype of *Apachesaurus*. Conversely, those of '*Metoposaurus*' *bakeri* (Case 1932, figures 8–10) and *Koskinonodon maleriensis* (Sengupta 2002, figure 5B) are comparable to those of the referred specimen of *Apachesaurus*. It is also unclear how the foramina of *Apachesaurus* are the most laterally positioned when those of *Dutuitosaurus*, although quite distinct in morphology, terminate at about the same point or a bit closer to the lateral skull margin than the former in occipital view (Spielmann and Lucas 2012, figure 11). The documented variation is sufficient to question the utility of this feature for taxonomic differentiation, and the character should be excluded until this can be better resolved.

(13) Minimal expression of accessory paraquadrate foramina: The primary issue with the accessory paraquadrate foramina (also referred to as the paraquadrate accessory foramina) is that they were not identified in metoposaurids until the description of *Metoposaurus krasiejowensis* by Sulej (2007). Since then, only one additional metoposaurid taxon, *M. algarvensis*, has been described, and the posterolateral portions of the occipital region are not preserved in any specimen. The wall separating the primary foramina from the accessory ones is extremely thin (see Sulej 2007, figure 1D). It is thus likely susceptible to taphonomic damage or loss during pre-paration that would render it impossible to confidently determine its presence or absence. Sulej (2007, p. 41) noted that there were no accessory foramina (or no apparent separation) in nearly as many specimens in which the accessory foramina were identified. Where it is identifiable, it is always much smaller than the primary fora-men, and it should not be considered a reliable feature considering its recent discovery and a presumed high susceptibility of the thin dividing wall between the foramina to loss during preservation. Furthermore, it is unclear if the feature identified as the accessory foramina in the holotype of *Apachesaurus* (Spielmann and Lucas 2012, figure 11A–B), the only specimen in which they are identi-fied, is actually the same feature as those described by Sulej (2007). In the former, the foramina are identified as a shallow depression at the ventral margin of the main paraquadrate foramina, which is more of a fossa than a continuous foramen. Quite possibly, the accessory foramina may have been of a more typical size to *Metoposaurus krasiejowensis*, with the dividing wall having been lost. The character is maintained because it cannot be

demonstrably proven to simply be taphonomic, but restudy of existing taxa will be necessary to further characterize this feature and its utility. The foramina may, for example, be preserved but unidentified in a specimen of *Dutuitosaurus* (Dutuit 1976, plate 16F).

The descriptive cranial osteology of Spielmann and Lucas (2012, p. 15–25) notes two features that differ in *Apachesaurus* compared to other metoposaurids but that are not formally included in the diagnosis. These include: (1) reduced premaxilla; (2) minimal dorsal exposure of the quadratojugal.

(1) Reduced premaxilla: A reduced premaxilla is only described in one specimen (TTUP 9216), which is now only known from a cast because of the loss of the original specimen. This condition was suggested to be the result of a more medial position of the nares (Spielmann and Lucas 2012). The same possibility was noted by those authors for a small specimen (MNA V8415) referred to *Koskinonodon perfectus* by Zanno et al. (2002) on the basis of a lacrimal entering the orbital margin. Under previous diagnoses (Hunt 1993; Spielmann and Lucas 2012) and the revised diagnosis presented here, this specimen cannot be referred to the taxon because it features prominently projecting occipital condyles.

(2) Minimal dorsal exposure of the quadratojugal: The reduced dorsal expo-sure of the quadratojugal may be correlated with the formal squamosal character and the considerations raised above with respect to a possible ontogenetic shift toward a transversely broadened posterior skull table via lateral expansion of the quadratojugal and the squamosal. This is seen, for example, in a small specimen of the Rotten Hill population of *Koskinonodon perfectus* (Lucas et al. 2016, figure 30C–D). By compar-ison, the larger specimens from this locality feature proportionately wider quadratojugals (e.g. Lucas et al. 2016, figure 30A–B). It is also possible that relatively broad quadratojugals can be taphonomically influenced. The element typically curves ventrolaterally, but dorsoventral compres-sion could flatten the skull and cause the lateral margin to be artificially flared laterally.

Evaluation of possible autapomorphies

The descriptive postcranial osteology of Spielmann and Lucas (2012, p. 25–30) also notes various features that are suggested to be autapomorphies of *Apachesaurus*. These include: (1) slightly curved anterior margin of the clavicle; (2) shallow, ridge-forming groove on the anterior margin of the acetabulum. These are addressed below, but it should be noted that there is no supported basis for referral of postcranial material to *Apachesaurus* because there are no postcranial autapormophies of the taxon beyond the now-discarded elongation of the intercentra and no apparent association of any referred postcranial specimens with cranial material.

(1) Slightly curved anterior margin of the clavicle: Sulej (2007, figure 43) noted variability in this margin in *Metoposaurus krasiejowensis* but did not explicitly comment on this. Spielmann and Lucas (2012) considered the absence of com-mentary on intraspecific variation, which is frequently com-mented on for other elements in Sulej's description, regarding this specific feature, to be indicative of a tapho-nomic influence. Some variation is also apparent in *Dutuitosaurus*. The majority of illustrated and photographed specimens have a straight margin, but some specimens fea-ture a curved margin that does not appear to be taphonomi-cally altered (e.g. Dutuit 1976, plate 31). The same is true of '*M.*' *bakeri* (e.g. Case 1932, plate 6.2).

(2) Shallow, ridge-forming groove on the anterior margin of the acetabulum: The ilium is an uncommon element in metopo-saurids, being best-known from *Koskinonodon perfectus* (Lucas et al. 2016) and *Metoposaurus krasiejowensis* (Sulej 2007). This particular aspect of the ilium is not seen in any other metoposaurid beyond *Apachesaurus*, but ilia of defini-tively juvenile individuals are unknown, so any potential ontogenetic influence remains undefined.

Appendix 1: Evaluation of the diagnosis of *Apachesaurus gregorii sensu* Spielmann and Lucas (2012)

Evaluation of taxonomic diagnosis

The original diagnosis of *Apachesaurus gregorii* provided by Hunt (1993, p. 81) lists five autapomorphies for the genus and species: (1) lacrimal flexure of the supraorbital canal separated from the lacrimal; (2) a shallow otic notch; (3) an occiput that does not project posteriorly; (4) a narrow cultriform process; (5) elongate intercentra. An additional eight autapomorphies were listed by Spielmann and Lucas (2012, p. 13): (6) a significantly reduced lacrimal; (7) a reduced contribution of the postfrontal to the medial orbital margin; (8) a symmetrical squamosal without significant deflection of the anterior process and with anteroposteriorly-oriented medial and lateral margins; (9) a rounded, trapezoidal foramen magnum (in contrast to a 'keyhole-shaped' foramen in other metoposaurids; (10) moderate arching of the tabulars, resulting in a curved dorsal margin in occipital profile (shared with *Metoposaurus krasiejowensis*, which is referred to as *M. diagnosticus* in the publication); (11) a less extensive oblique crest of the pterygoid; (12) smaller and more laterally positioned paraquadrate foramen; (13) minimal expression of the accessory paraquadrate foramen. A detailed appraisal of these characters is presented here. Conclusions regarding their validity are reflected in the amended diagnosis.

1. Lacrimal flexure of supraorbital canal separated from lacrimal: The supraorbital lateral line canal of *Apachesaurus* does not contact the lacrimal in any way. However, the comparative figure of Spielmann and Lucas (2012, figure 19) illustrates *Koskinonodon perfectus* as either having only a very slight contact with the lacrimal or as being cleanly

separated from the element (also seen in Case 1922, figure 1); this is suggestive of intraspecific variation. Furthermore, the trajectory of the canal in *Apachesaurus* is not particularly different from large metoposaurids in which the canal is consistent in originating at the anteromedial portion of the premaxilla, curving posterolaterally around the medial narial margin, and then curving posteromedially around the medial orbital margin. The premaxilla of *Apachesaurus* is only known from one specimen, which is presently represented only by a cast, so whether the supraorbital canal originates on the element is unclear. In general, the antorbital region is known only from a few specimens, some of which may not be properly referable to the taxon. The only other difference that may be noted is the precise contour of the lateral curvature of this canal; this is both interspecifically and intraspecifically variable (e.g., Lucas et al. 2016, figure 28) and likely influenced by minor changes to the snout proportions.

The condition of *Apachesaurus* that was identified by Hunt (1993) is thus valid, but it is also complicated by a new character added by Spielmann and Lucas (2012): a reduced lacrimal. The lateral line canal's separation from the lacrimal is not due to a significant deviation in its trajectory but rather due to the reduced size and posterolateral shift in position of the element. Based on illustrations of the holotype (Spielmann and Lucas 2012, figures 10, 19), it becomes apparent that if the lacrimal were of a comparable size and position to large metoposaurids, the canal would more closely approach and perhaps contact the lacrimal. In this regard, these characters are redundant. It seems more parsimonious to maintain the reduced size and altered position of the lacrimal, which does differ significantly from other metoposaurids, rather than the morphology of the canal, which is not different at least in the regard of its lateral extent

at the longitudinal point at which it contacts the lacrimal in other taxa. This is different than if the canal's trajectory was significantly altered such that it would not contact the lacrimal if mapped onto a typical large-bodied taxon. Maintaining both characters would be akin to adding an additional (equally redundant) character that the lacrimal does not contact the nasal in *Apachesaurus*, which is also a byproduct of the reduction and the migration of the former. Accordingly, this character should be considered invalid.

2. Shallow otic notch: A shallow otic notch is a feature that requires careful identification to determine the relative influences of ontogeny, taphonomy, and taxonomy. A deep otic notch with a well-defined tabular horn is present in some small specimens, such as a juvenile "*Metoposaurus*" *bakeri*, YPM PU 21742 (Hunt 1993, figure 6), and a juvenile *Koskinonodon perfectus*, TMM 31099-12B (Hunt, 1993, figure 8A–B). However, it cannot be excluded that the element could be broken off in other small-bodied specimens due to its small, flat morphology and protruding angle, or that the broken margin could be more susceptible to weathering. This can be seen in various specimens of large metoposaurids, such as *M. krasiejowensis* (Sulej 2007, figures 4A, 12A, 15A), *Koskinonodon perfectus* (Lucas et al. 2016, figures 28E, 28G, 30C, 30G), *M. algarvensis* (Brusatte et al. 2015, figure 3), "*M.*" *bakeri* (Case 1931, plate 1.1), and *Dutuitosaurus ouazzoui* (Dutuit 1976, plates 31A, 44). This can often reduce the perceived depth of the otic notch. In large metoposaurids, the notch may only appear to remain relatively deep when the tabular horn is broken because of the greater depth achieved in mature forms.

    When comparing the three small-bodied specimens from PEFO (PEFO 16759, PEFO 35392, PEFO 40023), increased size and histological maturity are correlated with a development of the otic notch and the tabular horn. Similar ontogenetic trajectories can

be seen in various rhachitomous forms (e.g., Schoch 2002), capitosaurids (e.g., Warren and Hutchinson 1988; Steyer 2003) and the stereospondylomorphs *Sclerocephalus* (Schoch and Witzmann 2009) and *Archegosaurus* (Witzmann 2005). The histological data suggest a continuous growth series as represented by these specimens, rather than distinct lineages. Accordingly the shallow otic notch may only be useful for identifying very immature individuals. Additional work is required to characterize changes to the otic notch throughout ontogeny in metoposaurids and timing of these changes across different taxa, but there is sufficient evidence at present to cast doubt on the utility of this feature for taxonomy.

3. Occiput that does not project posteriorly: An occiput that does not project posteriorly was already a conflicting character because it does project beyond the posterior margin of the postparietals in two of the previously referred specimens via the occipital condyles, NMMNH P-37069 (Spielmann and Lucas 2012, figure 16A–B) and TTUP 9216 (Davidow-Henry 1989, figure 1; Spielmann and Lucas 2012, figure 17B; Martz et al. 2013, figure 4). In neither specimen does the posterior skull margin appear to be weathered in any fashion that would have unnaturally exposed the occiput. These specimens are otherwise identical to the holotype and suggest that the development of more projected condyles may be ontongenetic and intraspecifically variable. It should also be noted that the occipital condyles are very slightly visible in dorsal profile in the holotype (Spielmann and Lucas 2012, figure 9A), although this is typically omitted in line drawings of the specimen. The larger PEFO 40023 features more prominently projecting condyles, though not to the degree of large specimens, which further suggests an ontogenetic influence. The character is maintained here because there is not a clear

ontogenetic trajectory in metoposaurids when comparing the smaller TTUP 9216, with markedly projecting condyles, with the holotype of *Apachesaurus*, with barely projecting condyles (if at all).

4. Narrow cultriform process: The relative width of the cultriform process is one of the more robust characters insofar as a morphology comparable to that of *Apachesaurus* has never been identified in any large metoposaurid taxon. An ontogenetic influence cannot be excluded, particularly if the width of the process significantly influenced some functional aspect of the interpterygoid vacuities, whether in feeding or in respiration. Differences between a semi-terrestrial *Apachesaurus* and all other, fully aquatic taxa would not be unexpected. The broad proportions of the process were considered to be autapomorphic by Hunt (1993), although *Chinlestegophis* and some brachyopoids also feature a broad process (Warren and Marsicano 2000; Pardo et al. 2017). Finite element analyses of *Apachesaurus* and *Metoposaurus krasiejowensis* by Fortuny et al. (2017) suggested that the broad width of the cultriform process in metoposaurids may be an adaptation to accommodate stress given the large interpterygoid vacuities and the relatively thin palatal bones, and that *Apachesaurus* may have possessed a narrower process as a result of its smaller skull size. However, additional specimens with well-preserved palates (absent in both specimens described here) would be necessary to assess this. An ontogenetic transition toward a more constricted cultriform process is seen in some temnospondyls, such as the mastodonsaurid *Xenotosuchus* (Damiani 2008). Whether this transition is phylogenetically informative on a broader scale is unclear and requires additional sampling of ontogenetic trajectories.

5. Elongate intercentra: Elongation of the intercentra is framed as a apomorphy of *Apachesaurus* despite the fact that Hunt (1993) noted that similarly elongate intercentra occur in the large-bodied *Dutuitosaurus* from Morocco. The character originally included a metric of a diameter-to-length ratio less than 0.8 to define 'elongate,' but no data or statistical justification have ever been provided to support this. This metric does not appear in the revised diagnosis of Spielmann and Lucas (2012) but reappears briefly in an informal discussion of the taxon in Lucas et al. (2016, p. 14). Recent histological work by Gee et al. (2017) has shown that elongation of small intercentra of metoposaurids from the Chinle Formation is associated with relative immaturity, findings that are supported by this study's results. Even under the interpretation of *Apachesaurus* as a taxonomically distinct, diminutive metoposaurid characterized by elongate intercentra, the feature is not informative for species discrimination because of a lack of features that would distinguish it from the elongate intercentra of very juvenile individuals of large-bodied taxa.

6. Reduced lacrimal excluded from orbit: The lacrimal has remained a contentious element with regard to metoposaurid taxonomy due to debate over the phylogenetic significance of its position. Earlier workers (e.g., Romer 1947; Colbert and Imbrie 1956) argued that the lacrimal did not enter the orbital margin in *Metoposaurus diagnosticus* (at the time, the genus was monospecific). This was in apparent contrast to the condition in *Koskinonodon*, representing one of the few identifiable differences and the only feature in the original diagnosis of *Koskinonodon*. However, Sulej (2002) reexamined the holotype of *M. diagnosticus,* found a lacrimal that entered the orbit, and subsequently identified the same relationship in the vast majority of specimens of *M. krasiejowensis*

(Sulej 2007). Although this has been disputed on several occasions (e.g., Lucas et al. 2007, 2016), there is greater consensus supporting a lacrimal contribution to the orbital margin that is shared between *Metoposaurus* and *Koskinonodon*. The observations of Sulej (2002) were reaffirmed by Brusatte et al. (2015), who further validated the point in their description of *M. algarvensis*. Phylogenetic codings of the genera (e.g., Schoch 2013) also reflect this characterization. The feature is thus of more limited utility in distinguishing the two genera than previously argued, although it can differentiate these metoposaurids from other taxa, such as "*Metoposaurus*" *bakeri,* whose taxonomic affinities have accordingly remained convoluted as it genuinely has a lacrimal excluded from the orbit. Regarding *Apachesaurus*, a reduced lacrimal is an autapomorphy of the taxon. This results from an increase in the posterior extent of the medial incision of the maxilla at its anterior end and a lateral expansion of the prefrontal that relegates the lacrimal to a position nearly fully lateral to the orbit. Subsequently, the lacrimal does not contact the nasal, as in all other metoposaurids, and does not contribute to either the narial or orbital margin. The latter condition is shared with "*Metoposaurus*" *bakeri*. The strength of the character is primarily tied to the absence of significant interspecific or ontogenetic variation in the lacrimal among large metoposaurids.

It should be noted that a previously referred specimen, UCMP V82250/171591, features a proportionately larger lacrimal that is approximately half of the distance between the naris and the orbit. This is greater than that of the holotype and of a comparable degree to large-bodied metoposaurids. Additionally, it is very narrowly separated from the orbit by a minute fragment. Neither the jugal nor the prefrontal is known to narrowly divide the orbit and the lacrimal in any metoposaurid, and it seems

most likely that it is in fact a broken fragment of the lacrimal that would thus indicate a contribution of the element to the orbital margin.

7. Reduced contribution of postfrontal to medial orbital margin: The contribution of the postfrontal to the medial orbital margin appears to be variable within the holotype of *Apachesaurus* itself; the right postfrontal extends to approximately the mid-length of the orbit, whereas that of the left counterpart (with a slightly deformed orbit) is definitively reduced in extent (Spielmann and Lucas 2012, figure 10A). A similar variability is seen in the Rotten Hill population of *Koskinonodon perfectus*. For example, specimens such as WT 3055 (Lucas et al. 2016, figure 30A) feature a comparable contribution to that of the left postfrontal of the holotype of *Apachesaurus*, whereas most other specimens feature a more typical contribution to that of large metoposaurids and to the right postfrontal. One specimen, WT 3166-1 (Lucas et al. 2016, figure 28A) features an asymmetry similar to the holotype of *Apachesaurus*, with a small contribution of the left postfrontal and a much greater contribution of the right postfrontal. The pattern is present in the holotype of *Metoposaurus algarvensis* (Brusatte et al. 2015, figure 2B) but with the greater contribution on the left side. Any differences in the relative contribution are highly qualitative and relatively minor, lacking any precise threshold. Given the documented variation at all scales, we consider this character to be questionable until more specimens of *Apachesaurus* are recovered.

8. Symmetrical squamosal with no significant deflection of anterior process and anteroposteriorly oriented lateral and medial margins: This character is considered in the same vein as the cultriform process (character 4) – this morphology has not been identified in large-bodied taxa, and although an ontogenetic influence can be

hypothesized, none is evident at present. The primary source of interspecific variation is in the lateral portion of the element, where in large metoposaurids, the margin is convex. This could be associated with an ontogenetic shift toward a transversely expanded posterior skull table that is seen in large-bodied forms with a brachycephalic contour via a lateral expansion of the quadratojugal and the squamosal. This would remove the symmetry of the latter and give the anterior process an appearance of having been deflected medially. A comparison of sub-adult and adult specimens of *Koskinonodon perfectus* (Lucas et al. 2016, figure 30) indicates that such an expansion may characterize the taxon. It should also be noted that there is a weak correlation between increased size and squamosal symmetry across PEFO 16759, PEFO 35392, and PEFO 40023. However, as with the cultriform process, the paucity of small-bodied metoposaurids with clearly defined squamosals limits any broader interpretations.

9. Rounded, trapezoidal foramen magnum: The significance of the morphology of the foramen magnum is tied to the potential taphonomic influence on the shape of the tabular and the convexity of the posteromedial skull roof in occipital profile (character 10). If the postparietals have been downshifted in any way, they may have altered the upper expansion of the foramen. An extreme case of this is seen in one specimen of *Koskinonodon maleriensis* (Sengupta 2002, figure 5) in which the postparietals have clearly downshifted into the opening such that only the circular ventral portion is exposed. A slightly less deformed foramen magnum is seen in a specimen of *Dutuitosaurus* (Dutuit 1976, plate 47C) in which the opening lacks the bifurcated dorsal expansion and forms a diagonally skewed oval. The foramen magnum of *Apachesaurus* is asymmetrical, and it is noteworthy that the left margin is markedly curved (Spielmann

and Lucas 2012, figure 11A–B), a feature seen in other metoposaurids that precedes the dorsal expansion that results in the keyhole-shaped contour. The asymmetry is one line of evidence that some degree of taphonomic deformation has occurred. For example, some variation in the dorsal expansion of the foramen can be seen in *Metoposaurus krasiejowensis* (Sulej 2007, figure 16). This can be correlated with slight damage and deformation to the posteromedial skull roof. The character is maintained here because of the lack of clear evidence for a bifurcated dorsal portion, but caution should be exercised in utilizing this as a diagnostic feature with even slightly deformed specimens.

10. Moderate arching of the tabular, resulting in a curved profile in occipital view: Based simply on the small sample size of specimens of *Apachesaurus* with a complete tabular, it is difficult to be certain that the convexity created by a slight ventromedial depression of the postparietals and the concavity of the tabulars is not at least partially taphonomic. Spielmann and Lucas (2012) considered this to be similar to the condition of *Metoposaurus krasiejowensis* (referred to as *M. diagnosticus*). However, photographs of multiple specimens of *M. krasiejowensis* in occipital view (Sulej 2007, figure 16) display a range of curvature of the dorsal margin that appears to be correlated with the quality of preservation. What appears to be the best-preserved specimen (Sulej 2007, figure 16A) displays an essentially flat margin. The generalized reconstruction of the skull of the taxon (Sulej 2007, figure 1D) mirrors this specimen. Conversely, the more poorly-preserved specimens (Sulej 2007, figure 16C–D) feature a prominently concave margin. Figures of the holotype of *Apachesaurus* indicate that it was subject to minor deformation in various regions of the skull, including the occipital region, which is slightly asymmetrical (e.g., Spielmann and Lucas 2012, figure 9). In addition, the

postparietals may be slightly downshifted into the foramen magnum while the tabulars remained articulated. Thus, the former may be slightly angled ventromedially, exaggerating the concavity of the margin. Arched tabulars and a concave dorsal margin are present in the holotype of *Koskinonodon perfectus* (Case 1922, figure 1C), and variation in the arching of the tabulars, from minor curvature to a flat margin is seen in "*M.*" *bakeri* (Case 1932, figures 8–9).

11. Less extensive oblique crest of the pterygoid: This character is considered in the same vein as the reduction of the lacrimal: justifiable insofar as it is not currently known to be particularly variable intraspecifically or throughout ontogeny. It should be noted that the crest of *Dutuitosaurus* (Dutuit 1976, plate 16F; Spielmann and Lucas 2012, figure 11C) is more dorsally oriented than in *Apachesaurus*, but does not appear to significantly differ in size, as is the case with *Metoposaurus krasiejowensis*.

12. Smaller, more laterally positioned paraquadrate foramina: The variation between the holotype (Spielmann and Lucas 2012, figures 9, 11A–B), in which the foramen is both shorter and narrower than other taxa, and of the previously referred NMMNH P-37069 (Spielmann and Lucas 2012, figure 16C–D), in which it is narrower but far more elongate than in the holotype, is indicative of either intraspecific variation or taphonomic damage to at least one specimen. It also bears noting that the foramina of the holotype of *Koskinonodon perfectus* (Case 1922, figure 1) are of a similar size and proportion to those of the holotype of *Apachesaurus*. Conversely, those of *"Metoposaurus" bakeri* (Case 1932, figures 8–10) and *Koskinonodon maleriensis* (Sengupta 2002, figure 5B) are comparable to those of the referred specimen of *Apachesaurus*. It is also unclear how the foramina of *Apachesaurus* are the most laterally positioned when those of

Dutuitosaurus, although quite distinct in morphology, terminate at about the same point or a bit closer to the lateral skull margin than the former in occipital view (Spielmann and Lucas 2012, figure 11). The documented variation is sufficient to question the utility of this feature for taxonomic differentiation, and the character should be excluded until this can be better resolved.

13. Minimal expression of accessory paraquadrate foramina: The primary issue with the accessory paraquadrate foramina (also referred to as the paraquadrate accessory foramina) is that they were not identified in metoposaurids until the description of *Metoposaurus krasiejowensis* by Sulej (2007). Since then, only one additional metoposaurid taxon, *M. algarvensis,* has been described, and the posterolateral portions of the occipital region are not preserved in any specimen. The wall separating the primary foramina from the accessory ones is extremely thin (see Sulej 2007, figure 1D). It is thus likely susceptible to taphonomic damage or loss during preparation that would render it impossible to confidently determine its presence or absence. Sulej (2007, p. 41) noted that there were no accessory foramina (or no apparent separation) in nearly as many specimens in which the accessory foramina were identified. Where it is identifiable, it is always much smaller than the primary foramen, and it should not be considered a reliable feature considering its recent discovery and a presumed high susceptibility of the thin dividing wall between the foramina to loss during preservation.

Furthermore, it is unclear if the feature identified as the accessory foramina in the holotype of *Apachesaurus* (Spielmann and Lucas 2012, figure 11A–B), the only specimen in which they are identified, is actually the same feature as those described by Sulej (2007). In the former, the foramina are identified as a shallow depression at the

ventral margin of the main paraquadrate foramina, which is more of a fossa than a

continuous foramen. Quite possibly, the accessory foramina may have been of a more

typical size to *Metoposaurus krasiejowensis,* with the dividing wall having been lost.

The character is maintained because it cannot be demonstrably proven to simply be

taphonomic, but restudy of existing taxa will be necessary to further characterize this

feature and its utility. The foramina may, for example, be preserved but unidentified in a

specimen of *Dutuitosaurus* (Dutuit 1976, plate 16F).

The descriptive cranial osteology of Spielmann and Lucas (2012, p. 15–25) notes two features

that differ in *Apachesaurus* compared to other metoposaurids but that are not formally included

in the diagnosis. These include: (1) reduced premaxilla; (2) minimal dorsal exposure of the

quadratojugal.

1. Reduced premaxilla: A reduced premaxilla is only described in one specimen (TTUP

   9216), which is now only known from a cast because of the loss of the original specimen.

   This condition was suggested to be the result of a more medial position of the nares

   (Spielmann and Lucas 2012). The same possibility was noted by those authors for a small

   specimen (MNA V8415) referred to *Koskinonodon perfectus* by Zanno et al. (2002) on

   the basis of a lacrimal entering the orbital margin. Under previous diagnoses (Hunt 1993;

   Spielmann and Lucas 2012) and the revised diagnosis presented here, this specimen

   cannot be referred to the taxon because it features prominently projecting occipital

   condyles.

2. Minimal dorsal exposure of the quadratojugal: The reduced dorsal exposure of the

   quadratojugal may be correlated with the formal squamosal character and the

considerations raised above with respect to a possible ontogenetic shift toward a

transversely broadened posterior skull table via lateral expansion of the quadratojugal and

the squamosal. This is seen, for example, in a small specimen of the Rotten Hill

population of *Koskinonodon perfectus* (Lucas et al. 2016, figure 30C–D). By comparison,

the larger specimens from this locality feature proportionately wider quadratojugals (e.g.,

Lucas et al. 2016, figure 30A–B). It is also possible that relatively broad quadratojugals

can be taphonomically influenced. The element typically curves ventrolaterally, but

dorsoventral compression could flatten the skull and cause the lateral margin to be

artificially flared laterally.

Evaluation of possible autapomorphies

The descriptive postcranial osteology of Spielmann and Lucas (2012, p. 25–30) also notes

various features that are suggested to be autapomorphies of *Apachesaurus*. These include: (1)

slightly curved anterior margin of the clavicle; (2) shallow, ridge-forming groove on the anterior

margin of the acetabulum. These are addressed below, but it should be noted that there is no

supported basis for referral of postcranial material to *Apachesaurus* because there are no

postcranial autapormophies of the taxon beyond the now-discarded elongation of the intercentra

and no apparent association of any referred postcranial specimens with cranial material.

1. Slightly curved anterior margin of the clavicle: Sulej (2007, figure 43) noted variability in
   this margin in *Metoposaurus krasiejowensis* but did not explicitly comment on this.
   Spielmann and Lucas (2012) considered the absence of commentary on intraspecific
   variation, which is frequently commented on for other elements in Sulej's description,
   regarding this specific feature, to be indicative of a taphonomic influence. Some variation
   is also apparent in *Dutuitosaurus*. The majority of illustrated and photographed

specimens have a straight margin, but some specimens feature a curved margin that does not appear to be taphonomically altered (e.g., Dutuit 1976, plate 31). The same is true of "*M.*" *bakeri* (e.g., Case 1932, plate 6.2).

2. Shallow, ridge-forming groove on the anterior margin of the acetabulum: The ilium is an uncommon element in metoposaurids, being best-known from *Koskinonodon perfectus* (Lucas et al. 2016) and *Metoposaurus krasiejowensis* (Sulej 2007). This particular aspect of the ilium is not seen in any other metoposaurid beyond *Apachesaurus*, but ilia of definitively juvenile individuals are unknown, so any potential ontogenetic influence remains undefined.