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

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Abstract. Metoposaurids are temnospondyl amphibians that are commonly collected from the Chinle Formation deposits of North America. Two species, *Koskinondon perfectus* and *Apachesaurus gregorii* are known from Petrified Forest National Park, AZ, USA. Small, elongate intercentra are the single diagnostic postcranial characteristic of the smaller *A. gregorii.* However, a poor understanding of the earliest life stages of *K. perfectus* and other large metoposaurids makes it unclear whether the proportions of the intercentra are a diagnostic feature for species discrimination or whether they are influenced by ontogeny. Previous work on metoposaurid intercentra has proven that ontogenetic information can be extrapolated from histological analyses. Here we perform a histological analysis of metoposaurid intercentra from Petrified Forest National Park and our results suggest that the elongate intercentra are the consequence of ontogenetic variation rather than speciation. But in discussion you have much more results. Add also here.

Introduction. Metoposaurids are Late Triassic temnospondyl amphibians with a global distribution and are some of the most commonly collected fossils from freshwater depositional settings in the Chinle Formation (Hunt, 1993). There are presently three valid taxa of metoposaurids in North America: two of large size, *Koskinonodon perfectus* and *K. bakeri*, and one of small size, *Apachesaurus gregorii* (Case, 1922, 1931; Branson & Mehl, 1929; Hunt, 1993; Mueller, 2007). Two of these, *K. perfectus* and *A. gregorii* are known from Petrified Forest National Park (PEFO), AZ, USA (Hunt & Lucas, 1993; Long & Murry, 1995; Heckert & Lucas, 2002; Parker & Martz, 2011). The former is common in the lower units within the Chinle Formation (Blue Mesa Member and lower part of the Sonsela Member) and is rare in the upper units (the upper part of the Sonsela Member and the Petrified Forest Member) (Hunt & Lucas, 1993; Heckert & Lucas, 2002; Parker & Martz, 2011). *A. gregorii* demonstrates the opposite pattern of stratigraphic distribution (Parker and Martz, 2011). Although fossils of *A. gregorii* are relatively common, the vast majority of them consist of isolated, elongate intercentra. Additionally, while the diagnosis of *A. gregorii* includes a wide set of cranial traits, only a shallow otic notch can be confirmed by more than one specimen (Spielmann & Lucas, 2012). Finally, while size has frequently been used as an informal characteristic in identifying specimens (*A. gregorii* being significantly smaller than all other metoposaurid taxa), this is not a reliable metric given the role of ontogeny in changing body size (Horner, De Ricqlès & Padian, 1998; Horner & Goodwin, 2009; Werning, 2012). As a result, the diagnosis of *A. gregorii* based on elongate intercentra is tentative in the absence of multiple specimens that can confirm more of the diagnostic cranial features. Because growth series for North American metoposaurids are not well known, particularly among the earliest life stages, it remains unclear whether the diagnostic anatomy of *A. gregorii* is the product of speciation or if it are merely a misinterpretation of features influenced by ontogeny. Such a possibility is rarely considered in determining whether small metoposaurid specimens are skeletally mature individuals of *A. gregorii* or skeletally immature individuals of either *Koskinonodon* species. In this study, we focus on analyzing the single diagnostic postcranial trait of *A. gregorii*, elongate intercentra.

For not-temnospondyl specialists it might be good to introduce short metoposaurids and American taxa with the specification of the problem about the position of Apachesaurs, including both hypothesis and arguments pro and against (juvenile Koskinodon vs adult dwarf). Now it is not clear if you are speaking about problems with diagnose only for this particular locality or if it is a general problem with the *A. gregorii*. In my opinion the short chapter about the diagnostic characters (localities, most important skull characters) of both taxa might help to understand the problem with the ontogenetic or/and taxonomic variety. Also may you short list, what kind of other bones (diagnostic or not) suspected to be an Apachesaurus, have you got in Petrified Forest National Park (not only to give the citations – again for not temnospondyl researcher will be easier to have all information in one place and not to search for specific sources).

Bone histology is a common method used to study ontogeny in a variety of extinct taxa, often by comparison to extant members of these clades (Padian, 2013). Although the majority of paleohistological inquiries have centered on amniotes, several workers have previously performed histological analyses on temnospondyls (e.g., Steyer et al., 2004; Witzmann & Soler-Gijon, 2010; Sanchez & Schoch, 2013). Most of these analyses have examined long bones, as is conventional for other tetrapods (e.g. Konietzko-Meier & Sander, 2013). Histology of temnospondyl intercentra has been performed only a handful of times (e.g., Enlow & Brown (1956; Mukherjee, Ray & Sengupta, 2010; Konietzko-Meier, Bodzioch & Sander, 2013; Konietzko-Meier, Danto & Gąadek, 2014; Danto, Witzmann & Fröbisch, 2016), and the only previous examination of metoposaurid intercentra was conducted on the European taxon *Metoposaurus krasiejowensis* (Konietzko-Meier, Bodzioch & Sander, 2012). Metoposaurid

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Kommentar [DK1]: There are thousands of papers about this… So, maybe to point that it is a review book you can add: **summarized in** Padian, 2013.

Kommentar [DK2]: Why did you selected these papers as examples? Two are about long bones, and one about osteoderms. There is a lot more articles about temnospondyl bone-histology.

Kommentar [DK3]: Again, you should use more citations. Here the both from previous sentence are also valid…

Formatiert: Englisch (USA)

Kommentar [DK4]: Special character: "a" with coma

Kommentar [DK5]: Literally it was published very unusually as: 2013 (for 2012)… The paper version with the final article was publish in 2013, thus I prefer to use the date 2013.

intercentra spanning a wide size range are commonly recovered elements at PEFO, making them more accessible for histology than the relatively rare limb elements. This study seeks to provide an alternative approach to comparisons of external morphology in order to evaluate the potential for metoposaurid intercentra proportions to be influenced by ontogeny rather than speciation.

This chapter you should change a little bit to add some more citations about the history of the histological temnospondyl studies, especially based on long bones. Now you have cited only three papers about long bones, but there is no clear why have you selected these three as examples (all are interesting, but not more important then others). Try to rewrite this paragraph to make it more general.

Keywords: paleohistology, ontogeny, metoposaurid

Institutional Abbreviations: NMMNH: New Mexico Museum of Natural History and Science, Albuquerque, NM, USA; PEFO: Petrified Forest National Park, AZ, USA; UOPB, University of Opole, Department of Biosystematics, Opole, Poland.

Materials and Methods.

Selection of specimens

All material referenced here was collected from the Late Triassic sedimentary rocks of the Chinle Formation at Petrified Forest National Park, AZ, USA (Fig. 1). Metoposaurids are found throughout three commonly occurring units of the Chinle (the Blue Mesa Member, Sonsela Member, and Petrified Forest Member), but there are disparate relative abundances of large and small metoposaurids throughout the stratigraphic column (Fig. 2). Eight of the ten elements were selected with the goal of sampling an intercentrum of shortened proportions normally referred to *K. perfectus* and an intercentrum of elongate proportions normally referred to *A. gregorii* from the same stratigraphic horizon, if not the same locality (Table 1, Fig. 3). PEFO 4826 and PEFO 38726 are from locality PFV 122 in the Blue Mesa Member (Fig. 1-2). PEFO 38645 is from PFV 040 in the Petrified Forest Member (Fig. 1-2). PEFO 36874 and PEFO 16696 (two and three intercentra, respectively) are from a locality (PFV 215) in the Petrified Forest Member (Fig. 1-2). Elements are assigned to the same specimen number on the basis of physical proximity during collection and general taxonomic identity and should not be interpreted to mean that the elements

Kommentar [DK6]: From figure and table it is not clear which one it is.

are from the same individual. The final two intercentra, belonging to PEFO 35392 (also from PFV 215), were selected because of their association with a skull of a small metoposaurid that was interpreted to be a juvenile *K. perfectus* (B.M. Gee & W.G. Parker, unpublished data). Specimens were measured using the same standards as Konietzko-Meier, Bodzioch & Sander (2012). The overall size range of the elements sampled in this study (mediolateral width between 9.81 mm and 55.32 mm) is similar to that sampled by the motivational study (mediolateral width between 20.1 mm and 71 mm; Konietzko-Meier, Bodzioch & Sander, 2012).

Kommentar [DK7]: Rather not use the unpublished data…

Kommentar [DK8]: There are results, not method

Classification of specimens' axial position

Because North American metoposaurids, especially those from PEFO, are rarely articulated, determining the exact serial position of the studied vertebrae remains difficult. Vertebrae are placed using previously-outlined criteria (Sulej, 2007), but it should be noted that these criteria were used in the description of *Metoposaurus krasiejowensis* and it remains unknown what differences may exist in the vertebral column between the European and North American taxa, especially in the absence of preserved neural or haemal arches. Additionally, intraspecific variation in North American metoposaurids is poorly known; thus the serial position of smaller intercentra is the most tentative.

Kommentar [DK9]: To be accurate, in Poland the material is also not articulated. The very first and only articulated (and used by Sulej) is *Dutuitosaurus* described by Dutuit, 1976.

Thin section preparation and imaging

The intercentra were first cleaned using a toothbrush and water to remove excess matrix before being consolidated with Paraloid B-72 (Rohm and Haas) dissolved in acetone. All specimens were molded and casted according to PEFO museum standards, with Carbowax (molecular weight 4000; Dow) added to stabilize cracks and other fragile areas. After creating two-part molds using (I need to send you latex info), the Carbowax was removed using a brush and warm water. All specimens were impregnated in a polyester resin mixture of Castolite™ AC and hardener (Eager Polymers) at a ratio of 1 oz of Castolite™ to 12 drops of hardener. The specimens were placed in a vacuum chamber to evacuate gas from the resin and then allowed to cure for a minimum of 24 hours. Because the primary focus of the study was to assess the ontogenetic stage of various intercentra to determine whether small, elongate intercentra ascribed to *A. gregorii* belonged to juveniles of *K. perfectus*, we decided to focus on sagittal cuts (down the midline in the anteroposterior axis) based on the amount of ontogenetic information that

Kommentar [DK10]: You should ;).

could be derived from the different planes in the analysis of Konietzko-Meier, Bodzioch & Sander (2012). All specimens were cut using an automated IsoMet 1000 Precision Saw (Buehler). The cut surface of the desired block and its respective thin section were prepared by polishing each with a 600-mesh silicon carbide on (include make, model, rpm with parent company in parentheses). Both surfaces were rinsed with ethanol and then attached to plexiglass slides using Scotch-Weld Instant Adhesive (CA40; 3M). The sections were allowed to dry for a minimum of 1 hour. All specimens except PEFO 38726 were cut to a height of 0.7 mm using the IsoMet 1000 Precision Saw. PEFO 38726 was too large to be cut by the automatic saw, so it was cut manually by hand with a larger saw fitting for the IsoMet. All specimens were polished in the following sequence: Hillquist 1010 grinding cup, 600-mesh grit, 1000-mesh grit, 1-micron grit. PEFO 38726 was polished on a 600-mesh lap wheel before polishing on the Hillquist to remove uneven surfaces from the manual cut. The thin sections were gradually ground down with repeated examination under a compound microscope to evaluate their optical clarity. All polishing after the Hillquist step was done manually on glass plates. Thin sections were imaged on a Nikon Instruments AZ100 Multizoom microscope fitted with AZ-Plan Apo 0.5x and AZ-Fluor 5x objective lenses, an AZ-RP rotatable polarizer plate, and a DS-Fi2 digital camera mount. NIS-Elements imaging software was used for this study.

Maybe you can make the description shorter, because the methodology of the producing thin-sections is quite well known and described in the methodological publications.
You can add some labeling on the figure 3 to imagine the sectioning planes.

Results.

It is always helpful for readers to have the short morphological description. Maybe you can add the short chapter with the measuring results (which you have now in method description) and the most important morphological characters. I still think that it is important to add here the preliminary taxonomical diagnosis (why do you think that this specimen belongs to… I know that only one belongs to A.g., but proof please why) – then you can discuss the histology with the morphological signal.

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Microanatomy and general histology

Overall, the composition and structure of the intercentra sampled is very similar to those that were described for *Metoposaurus krasiejowensis* (Konietzko-Meier, Bodzioch & Sander, 2012). At peripheral surfaces that were preserved, endochondral bone is found on the anterior and posterior faces and at the dorsal surface where the intercentrum would have been attached to the neural spine (Fig. 4). The ventral surface is formed by endochondral trabecular bone in younger individuals and by an external cortex in more mature individuals (Fig. 4). With the exception of the smallest intercentra that fall outside of the lower size bound of the sampled specimens of *M. krasiejowensis* (Konietzko-Meier, Bodzioch & Sander, 2012), a distinct region of periosteal bone is present in a triangular shape, with the apex ventral to the geometrical center of the element in all but some of the largest intercentra (Fig. 4G-H). This triangular region is separated from the endochondral region by obliquely-oriented trabeculae (Fig. 4). Within the periosteal region, the layers are densely packed and oriented parallel to the ventral surface of the intercentrum in contrast to the random arrangement of endochondral bone (Fig. 4). In some of the larger specimens, the periosteal region lacks the densely packed matrix (Fig. 4B, 4H-I). This does not appear to be ontogenetic in nature because PEFO 38726, the largest specimen, features a densely layered periosteal region in the absence of secondary mineral precipitation that characterizes all specimens with open periosteal regions (Fig. 4J). Additionally, some of the smaller specimens, such as PEFO 36874a, feature reduced secondary mineralization that only damages the local areas of the periosteal region in which it occurs (Fig. 4B).

For this study, we utilize the formal Histological Ontogenetic Stages (HOS) that were created for *M. krasiejowensis* by Konietzko-Meier, Bodzioch,& Sander (2012). The nature of the periosteal bone is used to characterize the ontogenetic stage of an individual; HOS 1 lacks any periosteal ossification, HOS 2 features a wide periosteal bone, HOS 3 features decreased vascularization in the external cortex, and HOS 4 features LAGs in the external cortex (Konietzko-Meier, Bodzioch, & Sander 2012). The ontogenetic assignments are summarized below in Table 2.

PEFO 16696 (Fig. 4B, 4D, 4H, 5C, 6C, 7C, 8C-D): PEFO 16696a is similar to PEFO 4826

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Kommentar [DK11]: It will be helpful to mark the border between domains and add some labeling – again it will help to understand the framework for not-specialist.

Kommentar [DK12]: On the level of microanatomy better use the trabecular domain, or spongious bone. Because without detailed histological description and i.e. remains of calcified cartilage you cannot determine the origin of the structure. I.e. if it is primary and build on the place of cartilage (typical endochondral bone) or it is secondary replacing the primary endochondral bone. Or the trabecular structure might be created as secondary build on the place of "old" periosteal bone).

Kommentar [DK13]: This should be in methods part.

Kommentar [DK14]: The first specimen has to be described without "comparisons" to others. In this point we do not know anything about the PEFO4826. In each next you can use the phrase: similar, like in..., but only refer to these which have already been discrabed in having a fully open notochordal channel filled with secondary minerals (Fig. 5C). The periosteal region is semi-circular as in the smaller intercentra, but the layered matrix is significantly more disperse (Fig. 6C). The presence of secondary mineral precipitates, a feature also seen in the periosteal region of PEFO 35392, PEFO 36874b, PEFO 38645, and PEFO 16696c (Fig. XY), appears to be responsible for the absence of densely layered matrix in the region (Fig. 6C). Additionally, the endochondral bone in the dorsal half of PEFO 16696a is significantly more disperse than in larger specimens sampled here, although the endochondral bone on the articular faces is thicker and more densely packed, as observed in all other intercentra (Fig. 4B, Fig. 7C). Relative to larger intercentra, the marginal endochondral bone appears to be more vascularized. PEFO 16696b and PEFO 16696c share many features with other large intercentra. The periosteal region is triangular in shape and consists of a parallel-layered matrix (Fig. 8D). In PEFO 16696b, the apex that terminates ventral to the mid-height of the element, while in PEFO 16696c, it terminates at or slightly above this point (Fig. 4D, Fig. 4H). In PEFO 16696c, some layers of the periosteal region appear to have been destroyed by precipitation of secondary minerals, a recurring feature in some of the larger intercentra, which makes it difficult to identify the exact point of termination of the apex. The endochondral bone is thickest at the articular surfaces and is more disperse in the internal cavity. There is no evidence of an external cortex in PEFO 16696a and PEFO 16696b. In PEFO 16696c, an external cortex is present, but it is well vascularized and shows no evidence of LAGs (Fig. 8C). We assign PEFO 16696a and PEFO 16696b to HOS 2. PEFO 16696c is assigned to HOS 3 but is considered to be relatively immature in comparison to other specimens of the same assignment.

PEFO 35392 (Fig. 4G, 4I, 8B): Both of these elements are associated with a partial skull that was interpreted as a juvenile *K. perfectus* by B.M. Gee & W.G. Parker (unpublished data). The histological characterization of these intercentra supports this interpretation, as they feature a relatively wide periosteal region and a moderate degree of vascularization in the external cortex region (Fig. 4G, 4I). Both elements are similar to each other and to other intercentra lacking a notochordal channel that were sampled in this study. The periosteal region is triangular in shape with an apex that terminates well below the mid-height of the intercentrum in PEFO 35392a (Fig. 4G) and an apex that terminates around that point in PEFO 35392b (Fig. 4I). The matrix of parallel layers is much less dense and coincides with the presence of secondary carbonate

Kommentar [DK15]: See the comment about endochondral bone

Kommentar [DK16]: The layer of endochondral bone is thicker or the trabeculae are thicker?

Kommentar [DK17]: It is more discussion, when you conclude about the maturity of specimens.

minerals, which likely damaged the region, making it difficult to discern the exact point at which the apex terminates in PEFO 35392b (Fig. 4I). The endochondral bone is relatively intact and is similar to other intercentra in being densest at the articular faces and randomly distributed throughout the internal cavity. A weathered external cortex is preserved in both of the specimens, but appears to still be relatively well vascularized and shows no evidence of LAGs where present (Fig. 8B). We assign both specimens to HOS 3.

Kommentar [DK18]: The bone is not dense or randomly distributed. The trabeculae, which build the bone are randomly distributed. Correct please in whole manuscript.

PEFO 36874 (Fig. 4A, 4F, 5B, 6B, 7B): The smaller of the two elements assigned to this specimen (PEFO 36874a) differs from PEFO 4826 and PEFO 16696a in having a notochordal channel that appears to be in the early stages of ossification. Tissue deposition originates around the geometric center of the element and probably spread outward throughout ossification based on the characterization of the notochordal pits in larger specimens (Fig. 5B). In this specimen, tissue from the two halves appears to have recently connected prior to the death of the individual. The overall shape of the periosteal region of PEFO 36874a is similar to the semi-circular contour of the other small intercentra (Fig. 6B). PEFO 36874b features a typical morphology of the larger intercentra sampled in this study: a triangular periosteal region with an apex terminating ventral to the mid-height of the element, dense endochondral bone on the articular surfaces, and more disperse, vascularized endochondral bone in the internal cavity (Fig. 4F). As in several other intercentra, the periosteal region lacks a densely layered matrix but co-occurs with a similar concentration of secondary carbonate minerals. An external cortex does not appear to be present in PEFO 36874a, and in PEFO 36874b, it is highly vascularized with no evidence of LAGs (Fig. 4A, 4F). We assign PEFO 36784a to HOS 2 and PEFO 36874b to HOS 3.

PEFO 38645 (Fig. 4E, 8A): This specimen shows no evidence of a notochordal channel. The periosteal region is comparable to other specimens in having a parallel-layered matrix and an apex that terminates below the mid-height of the intercentrum (Fig. 4E). The periosteal region lacks a densely layered matrix, as in PEFO 35392 and PEFO 36874b, but also features a high degree of secondary carbonate precipitation that likely damaged the internal structure (Fig. 4E). One articular surface was damaged during preparation of the thin section, but the other shows a dense endochondral bone layer with tighter packing than the elements of PEFO 35392. Similar to PEFO 36874, a posterior protrusion on the dorsal surface that may be a remnant of the neural arch is preserved (Fig. 4E). The remainder of the endochondral bone in the internal cavity is otherwise modestly vascularized and randomly oriented. The external cortex is relatively well preserved and compact, similar to PEFO 38726, but there is no evidence of LAGs or any taphonomic damage that may have erased them (Fig. 8A). We assign this specimen to HOS 3 and note that it is more mature than the elements of PEFO 35392.

PEFO 38726 (Fig. 4J, 8D): This specimen is the largest analyzed in this study and shows no evidence of a notochordal channel. The periosteal region consists of a dense matrix of parallel layers and is triangular in shape with an apex that terminates at or before the mid-height of the element (Fig. 4J). The external cortex of this specimen is relatively well preserved and shows a reduced degree of vascularization compared to the smaller specimens. At least two light-colored bands can be seen in the cortex and run parallel to the ventral surface of the intercentrum (Fig. 8D). They are continuous throughout the well-preserved portion of this area, which leads us to tentatively conclude that these are LAGs. As in other intercentra, the endochondral bone on the articular surfaces is thicker and more densely packed than in the internal cavity. On the dorsal surface, an elevated posterior protrusion may be the remnants of a neural arch that was lost during preservation (Fig. 4J). We assign this specimen to HOS 4.

Kommentar [DK19]: It is more interpretation then description and thus should be in the discussion part. Try maybe to rewrite this.

PEFO 4826 (Fig. 4C, 5A, 6A, 7A): This specimen is the largest of the three intercentra that feature an open notochordal channel. The notochordal channel is obstructed only by secondary matrix; its dorsal and ventral walls are nearly flat (Fig. 5A). The periosteal region is semi-circular, as in the PEFO 16696a and PEFO 36874a, with a dense matrix of parallel layers running in the anterior-posterior axis (Fig. 6A). There is no evidence of taphonomic damage that resulted in the absence of a compact external cortex with LAGs. The endochondral bone in the dorsal portion of the intercentrum shows an intermediate degree of vascularization in being more densely packed than the other two small intercentra and less densely packed than in larger intercentra with a closed notochordal channel (Fig. 7A). Dense endochondral bone also forms the margins on the anterior and posterior articular surfaces. The dorsal margin of the element is slightly damaged, which is common in North American metoposaurids owing to the removal of the neural arches during preservation. We assign this specimen to HOS 2.

Kommentar [DK20]: Not your result or?

This is mostly description of microanatomy, not of the histology. So, you should change the title. But in my opinion the histological description (the organization of the collagen fibers, resorption process, primary or/and secondary osteons/tissue, remains of calcified cartilage, Sharpeys Fibers, etc. are very important for the deduction about the ontogenetic stage).

I would suggest also the other organization of the description of specimens. Maybe you should add here the preliminary taxonomical determination of specimens based on the morphology. And then describe the specimens in two groups, in each from the smallest. I also do not like the "group" specimen numbering. It is a little surprising that you have two or three bones, very different about size (so two/three specimens) with the same number (i.e. Fig 3D- E and Fig. 3H-J). Of course collection numbers are independent and you cannot change these, but maybe you can add to each bone with the same number a letter: A,B,C and then describe each bone separately, as separate specimen (not as a group).

Add also to methodological part the short list of characters typical for each HOS (not only use the citation).

Discussion. The most significant finding of this study is the confirmation that, at least in some instances, small intercentra of proportions referable to *A. gregorii* belong to highly immature individuals. Two prominent features inform the ontogenetic assignment of these specimens: (1) a perforate notochordal channel and (2) a wide, more semi-circular periosteal region (Fig. 5-6). These structures are found in the three smallest intercentra (PEFO 4826, PEFO 16696a, PEFO 36874a) and provide insight into the ontogenetic changes in the internal structure of the axial column in metoposaurids. We are confident that the open notochordal channel is a juvenile feature because its closure is widespread in Triassic temnospondyls, including metoposaurids (Warren & Snell, 1991). The notochordal channel closes and is gradually reduced to a pair of perforations, one on each articular surface, that migrate dorsally and eventually disappear in some species (Warren & Snell, 1991; Danto, Witzmann & Fröbisch, 2016). Based on comparisons to described morphologically or histologically? As your title is histological description you have point clearly when you do your conclusions based on morphology (this is why you need the morphological description in results part) and when on histology. -vertebral series in *M. krasiejowensis, M. bakeri, Dutuitosaurus ouazzoui* and isolated intercentra of *K. perfectus*, this pattern often terminates in an entirely smooth articular surface with no

Kommentar [DK21]: But you have only one intercentrum referable to A.g.

Kommentar [DK22]: I am not sure what do you mean using "wide"

Kommentar [DK23]: Add labelling on figures

Kommentar [DK24]: Again, mark these on figures notochordal perforation in mature individuals (Case, 1932; Dutuit, 1976; Warren & Snell, 1991; Sulej, 2007). Additionally, we can be certain that the notochordal channel does close in smaller individuals with elongate intercentra based on PEFO 36874a, which captures the onset of this ossification and is discussed further below (Fig. 5B). The designation of the three smallest intercentra (numbers) as belonging to juvenile individuals is also supported by the wide periosteal region, which originates near the anteroventral and posteroventral margins, forming a shallow concave depression rather than the distinct triangle seen in larger intercentra of this study and the intercentra of *Metoposaurus* (Konietzko-Meier, Bodzioch & Sander, 2012). In all three of the smallest PEFO specimens, the apex of the periosteal region terminates well before reaching the dorsal surface of the ventral half (Fig. 6). Finally, the small intercentra show other evidence of a relatively immature ontogenetic stage, such as the absence of thick ventral trabeculae near the external surface, the absence of LAGs, and less densely packed endochondral bone in the dorsal portion of the intercentrum in comparison to larger specimens (Fig. 4A-C, Fig. 5-6). As a result, we can be confident that the ossification of the notochordal channel did not occur relatively late in ontogeny and conclude that all three of the small intercentra belong to an early ontogenetic stage of a large metoposaurid rather than to *A. gregorii*.

Kommentar [DK25]: Again clear what do you think here…

I am not convinced. In my opinion you need the classical histological analysis, not only microanatomy. Maybe one of this smallest has ontogenetically old tissue, strongly secondary. How does it look with the remains of calcified cartilage in the "endochondral" domain? Stereospondyli are known for the log preservation of c.c., but the amount of cc. decrease during ontogeny (see the paper about Metoposaurus and Konietzko-Meier et al., 2014). It is not excluded that the one Apachesaurus-like has similar microstructure, but on the histo-level is different. If the apachesaurus is a separate taxon, let´s say dwarf-metoposaurus, the growth should terminate earlier, with the same growth pattern (but then the tissue is older) or be slower. There are a lot of papers about histology of dwarf-amniots.

Larger sampled intercentra also show evidence of relative immaturity up to the largest specimen, PEFO 38726, when LAGs appear in the external cortex (Fig. 8D). Although the material is from a variety of localities and stratigraphic horizons, increased size of the sampled intercentra always produced more ontogenetically mature structures, leading us to conclude that that the sampled material can be compiled into a composite growth series. Because *K. bakeri* has not been identified west of Texas, and its intercentra differ from that of *K. perfectus* with regard to the notochordal channel (discussed below), we tentatively assign this material to *K. perfectus*, with the understanding that future revision may be necessary as more diagnostic material is recovered (Hunt, 1993; Long & Murry, 1995). It is possible that the onset of ossification of the notochordal channel reflects a milestone in the development of *K. perfectus.* In light of the hypothesis suggesting that *Koskinonodon* could have had ecologically separated life stages (Rinehart et al., 2009), the ossification of the intercentra could potentially represent the onset of a more aquatic lifestyle.

Because you discuss a lot of different cases, maybe will be good to add the sub-titles to each paragraph. This study has also produced an unexpected finding that suggests some differences in the ontogenetic trajectory of *K. perfectus* in relation to other metoposaurids with known vertebral columns (citations). In the original description of *K. bakeri*, Case (1932) noted that the presence of a notochordal channel and its persistence as reduced perforations on the articular surfaces in more mature specimens differed from other metoposaurid specimens from Texas, presumably of *K. perfectus*, in that the known material of the latter lacked any sort of perforation. This pattern also appears in the intercentra of *K. perfectus* that are described or figured in other publications (e.g., Colbert & Imbrie, 1956; Hunt, 1993; Long & Murry, 1995; Spielmann & Lucas, 2012). We have also found this same pattern in an informal survey of several dozen metoposaurid intercentra in the collections at PEFO. This suggests that with regards to timing, the ossification of the notochordal canal occurs much earlier in *K. perfectus.* We also note that the smallest specimen analyzed by Konietzko-Meier, Bodzioch & Sander (2012), an early juvenile (UOPB 00117), is larger than two of the three small intercentra sampled here (PEFO 16696a, PEFO 36874a) but is classified as being more ontogenetically immature (HOS 1) than either due to the absence of periosteal ossification (Fig. 5, Table 2). It may be that *K. perfectus* juveniles experienced a relatively rapid burst of growth and tissue reorganization within the skeleton in comparison to *M. krasiejowensis*, possibly as a result of environmental triggers, but this hypothesis requires additional sampling to test. Finally, only the largest intercentra sampled in our study (PEFO 38726) contains possible LAGs in the external cortex (Fig. 8D). This element is most comparable in size to UOPB 00115, which they classified as a late juvenile (Konietzko-Meier, Bodzioch & Sander, 2012) and in which no LAGs were observed. This suggests that *K.*

Kommentar [DK26]: It is informal information and I not sure if you can use it in this way.

Kommentar [DK27]: You conclude here on the material which is not used in this study or published.

perfectus may have reached maturity slightly faster than *M. krasiejowensis*, but again, additional sampling is required. Variability in ontogenetic trajectories has been previously documented between *D. ouazzoui* and *M. krasiejowensis* as a result of differing environmental conditions (Konietzko-Meier & Klein, 2013). As the Chinle depositional basin was positioned closer to the equator in comparison to the environments in which *D. ouazzoui* and *M. krasiejowensis* are found (Steiner & Lucas, 2000; Rowe et al., 2007; Zeigler & Geissman, 2011; Nordt, Atchley & Dworkin, 2015), it is plausible that the paleoenvironment differed sufficiently from both taxa so as to result in a distinct ontogenetic trajectory in *K. perfectus.* Additional sampling of material, particularly limb elements, is needed for comparative analyses to assess this possibility.

The other unexpected finding of this study was an intercentrum (PEFO 36874a) in the process of undergoing ossification of the notochordal channel (Fig. 4B). This was not evident when examining the external morphology of the specimen, as the notochordal channel or pit is usually filled with secondary minerals. Bone tissue can be clearly seen growing into the channel at the geometric center via deposition of bone on the internal sides of the dorsal and ventral halves (Fig. 4B). The dorsal half appears to be contributing more material through bone deposition, but this requires additional specimens to verify (Fig. 4B). Although this specimen is smaller than the more immature PEFO 4826, this does not contradict our ontogenetic assignment based on examination of the external morphology of other small, elongate intercentra at PEFO. There appears to be some variability in the exact timing of the closure of the notochordal channel, as specimens of similar size and proportion exhibit the full range of conditions, from an open channel to a smooth articular surface lacking any trace of the channel. This could be owing to a number of processes that require additional samples to evaluate, such as the progression of ossification of the vertebral column in the anterior-posterior direction or intraspecific variation in the onset of ossification. If the early stages of vertebral ossification were in some way influenced by environmental factors rather than the size of the animal, developmental plasticity, which occurs in both extant and extinct amphibians, could explain how relatively larger intercentra could sometimes be histologically more immature than smaller ones (Newman, 1992; Schoch, 2014). As previously noted, this may also indicate a relatively fast ossification of the notochordal channel.

These findings also provide support of niche partitioning between life stages of metoposaurids, which has been suggested in *Koskinonodon* (Rinehart et al., 2009) and in *Metoposaurus* (Sulej, 2007). Such partitioning could reasonably have created an associated taphonomic bias, which is well documented in both dense bonebeds and more dispersed localities. All known metoposaurid bonebeds have so far produced only large, relatively mature individuals with no evidence of the earliest ontogenetic stages (Case, 1932; Colbert & Imbrie, 1956; Dutuit, 1976; Hunt, 1993; Sulej, 2007; Lucas et al., 2010; Brusatte et al., 2015). Furthermore, although fossils from mature individuals of *K. perfectus* are common in the middle Norian, material referable to juveniles of the taxon is extremely rare, providing another line of support for niche partitioning; to date, only two partial skulls have been described (Zanno et al., 2002; B.M. Gee & W.G. Parker, unpublished data), with a third figured but not described by Hunt (1993). Material of *A. gregorii* is common in the Redonda Formation in New Mexico but occurs mostly within a single quarry (Gregory's quarry, NMMNH locality 485) (Spielmann and Lucas, 2012). As a result, the relative abundance of *A. gregorii* may not be the result of ecological turnover as postulated by Hunt (1993) but may represent the preservation of depositional environments inhabited by juveniles of *K. perfectus*. As bonebeds of mature metoposaurids have been interpreted as evidence of ecological aggregation prior to death, it is not implausible to infer that juveniles may also have naturally aggregated, creating a preservation potential for dense assemblages (Lucas et al., 2010; Brusatte et al., 2015). Based on the isolated and disarticulated nature of most *Apachesaurus* material, we do not believe these deposits represent mass mortality events, but that they are more likely representative of depositional environments frequented by small metoposaurids over longer durations of time. This hypothesis is supported by a previous study that surveyed blue paleosol localities at PEFO and found that material of many rare taxa, as well as that of *A. gregorii*, are found mostly within these uncommon horizons (Loughney, Fastovsky & Parker, 2011). PFV 040, PFV 215, and potentially PFV 122, the three localities from which specimens for this study were sourced, are all blue paleosol horizons. This lithology is interpreted to have formed in low-energy systems, primarily abandoned channels and ponds adjacent to the main river channel, in contrast to the dominant red floodplain deposits in which fossil material is more fragmentary and isolated (Loughney, Fastovsky & Parker, 2011). The association of *Apachesaurus* material within these blue paleosol localities supports the hypothesis that deposits that are disproportionately skewed toward fossils of small metoposaurids (exemplified by PFV

Kommentar [DK28]: You have a lot of unpublished data.

040 and PFV 215) form in different geologic settings than deposits that are skewed toward large metoposaurids. This in turn supports the hypothesis of natural ecological separation between life stages of metoposaurids. Additionally, taxa that are primarily associated with blue paleosol horizons may not be as stratigraphically restricted as previously thought, and a perceived faunal turnover may in fact be more closely linked to changes in the relative taphonomic conditions of different depositional settings. It is also worth noting that neither *A. gregorii* nor any other diminutive species of metoposaurid is known outside of North America (Long and Murry, 1995; Spielmann & Lucas, 2012). This is at odds with the conjecture by previous authors that *A. gregorii* is the most terrestrial of metoposaurids based on the intercentra and rare appendicular material (Hunt, 1993; Sulej, 2007; Spielmann & Lucas, 2012). If this were true, it would be reasonable to expect the taxon or other similarly adapted forms to disperse more widely than aquatic relatives, especially if the pronounced aridification of the Late Triassic led to significantly reduced aquatic environments (Parker & Martz, 2011; Atchley et al., 2013; Nordt, Atchley & Dworkin, 2015), but this pattern is not seen.

Conclusions. These findings reiterate the importance of evaluating the potential for morphological variation to be the result of ontogeny, especially when comparing two taxa of vastly different sizes, such as *A. gregorii* and *K. perfectus*. Although fossils of *A. gregorii* are common in late Norian deposits, the vast majority of this material has consisted of elongate intercentra, which we demonstrate here cannot be considered apomorphic. Limited fragmentary pectoral and pelvic material of *A. gregorii* has been described in the literature, but no justification for ascribing it to the taxon has ever been provided (Hunt, 1993; Long & Murry, 1995; Spielmann & Lucas, 2012). Although this material was recovered from the same quarry as cranial and vertebral material, there is no published work suggesting that any of it was found in articulation with any of the diagnostic cranial material (Spielmann & Lucas, 2012). North American metoposaurid specimens are frequently isolated or disarticulated, but this does not negate the importance of reevaluating the taxonomic identity of this material to determine whether they preserve robust diagnostic traits. It is possible that these assignments were made solely on the basis of diminutive size (Hunt, 1993; Long & Murry, 1995; Spielmann & Lucas, 2012), which cannot be utilized as in species discrimination given the role of ontogeny in producing morphological variation associated with different size bins (Steyer, 2000; Horner and

Goodwin, 2009; Witzmann, Scholz & Ruta, 2009). Similarly, although a large number of diagnostic cranial characters have been identified for *A. gregorii*, only a single character, the shallow otic notch, can be confirmed in any specimens beyond the holotype (Spielmann & Lucas, 2012). The potential for these cranial landmarks to be ontogenetically influenced has not been sufficiently addressed by past workers, in spite of the widespread documentation of morphological changes associated with ontogeny in both extant and extinct amphibians (Hanken, 1992; Fröbisch et al., 2010; Schoch, 2014). For example, studies of other Triassic temnospondyls have shown that the otic notch, occipital condyles, and cultriform process (by virtue of its relationship with the interpterygoid vacuities) all play a role in bite force mechanics (Fortuny, Marcé-Nogué & Galobart, 2012; Fortuny et al., 2016; Lautenschlager, Witzmann & Werneburg, 2016). Based on these findings, the presence of shallow otic notches, reduced projection of the occipital condyles, and a wider cultriform process (all supposedly diagnostic traits of *A. gregorii*) may in fact be influenced by changing biomechanical demands throughout ontogeny, rather than being the result of speciation. The potential for intraspecific variation to exert an influence on metoposaurid morphology has also not been well studied in North American taxa even though studies of bonebeds of *M. krasiejowensis* and *M. algarvensis* have demonstrated a higher degree of variability in many cranial regions than previously thought (Sulej, 2007; Brusatte et al., 2015).

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Finally, we believe that our results provide one line of evidence that *A. gregorii* is not in fact a distinct species, but rather that it is an early ontogenetic stage of *K. perfectus*. The stratigraphic distribution that is alleged to reflect ecological turnover is actually controlled by taphonomic bias that results from niche partitioning between different life stages of *K. perfectus*. The role of ontogeny and intraspecific variation in producing morphological variation in features such as cranial suture patterns, the basicranium, and the otic notch remain relatively unexplored in North American metoposaurids. Discovery and study of additional juvenile specimens is needed to establish a more robust ontogenetic characterization of the earliest stages of metoposaurid development, but our study has also demonstrated that underutilized methods of analysis such as paleohistology on existing specimens can shed new light on the paleobiology of extinct taxa with implications for taxonomy and ontogeny.

Kommentar [DK29]: You should add more histological facts to support this hypothesis.

My first take based on the title and introduction was that you want to use only histology to confirm (or not) the taxonomical assignment of a long intercentrum and try to estimate some ontogenetic processes. However, the most important histological part seems to be the weakest from the whole chapter (see comments). To proof your taxonomical diagnose you should add more histological details. Maybe on this level the intercentra look different. And for Temnospondylli especially important seems to be the analysis of the structure in polarized light. Some details are visible only in this light and only then you can see “the second face” of histological structures. But in generally in discussion you have a lot of interesting conclusions and hypothesis. Thus you should add some information to the introduction and precise few new goals (because in your introduction there is no well-defined and clear goal).

Acknowledgements. Thanks to Matt Smith (PEFO museum curator) for providing access to specimens for histological analysis and to Brad Traver (PEFO Superintendent) for granting permission to conduct the destructive analyses. Thanks to Cathy Lash (PEFO fossil preparator) for assistance with molding and casting of the specimens and to Yara Haridy (University of Toronto) for instruction and guidance on preparation and imaging of thin sections. This is Petrified Forest National Park Paleontological Contribution no. 49.

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Figure Captions

Generall comment: you need to add much more labelling. Each structure described in the MS should be marked on the figure. See also the comments in text.

Figure 1. Map of PEFO showing localities of sampled specimens. Localities and associated specimens are as follows: PFV 122 (Blue Mesa Member): PEFO 4826 and PEFO 38726; PFV

040 (Petrified Forest Member): PEFO 38645; PFV 215 (Petrified Forest Member): PEFO 36874, PEFO 16696, and PEFO 35392.

Figure 2. Stratigraphic column of PEFO showing position of sampled specimens and localities. Localities and associated specimens are as follows: PFV 122 (Blue Mesa Member): PEFO 4826 and PEFO 38726; PFV 040 (Petrified Forest Member): PEFO 38645; PFV 215 (Petrified Forest Member): PEFO 36874, PEFO 16696, and PEFO 35392.

Figure 3. Photographs of sampled specimens in anterior and lateral profiles. (A) PEFO 38726, (B) PEFO 4826, (C) PEFO 38645, (D-E) PEFO ~~PEFO~~ 36874, (F-G) PEFO 35392, (H-J) PEFO 16696. Order of photographed specimens mirrors their listed order in Table 1.

Figure 4. Microphotographs of the sagittal sections of sampled specimens. (A) PEFO 36874a, (B) PEFO 16696a, (C) PEFO 4826, (D) PEFO 16696b, (E) PEFO 38645, (F) PEFO 36874b (G) PEFO 35392a, (H) PEFO 16696c, (I) PEFO 35392, (J) PEFO 38726. Scale bars equal to 4 mm.

Figure 5. Microphotographs of the notochordal channel in three small specimens. (A) PEFO 4826 (B) PEFO 36874a, (C) PEFO 16696a. Scale bars equal to 1 mm.

Figure 6. Microphotographs of the periosteal region in three small specimens. (A) PEFO 4826 (B) PEFO 36874a, (C) PEFO 16696a, (D) PEFO 16696b. Scale bars equal to 1 mm.

Figure 7. Microphotographs of the dorsal endochondral region in three small specimens. (A) PEFO 4826 (B) PEFO 36874a, (C) PEFO 16696a. Scale bars equal to 1 mm.

Figure 8. Microphotograph of the external cortex in large intercentra. (A) PEFO 38645, (B) PEFO 35392a, (C) PEFO 16696c, (D) PEFO 38726. Arrows indicate the position of the LAGs in PEFO 38726. Scale bars equal to 1 mm.