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The pseudosuchian record in paleohistology: A small review

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Abstract

Archosauria originated around the Earth's largest biotic crisis that severely affected all ecosystems globally, the Permian-Triassic Mass extinction event, and comprises two crown-group lineages: the bird-lineage and the crocodylian lineage. The bird lineage includes the iconic pterosaurs, as well as dinosaurs and birds, whereas the crocodylian lineage includes clades such as aetosaurs, poposaurs, "rauisuchians," as well as Crocodylomorpha; the latter being represented today only by less than 30 extant species of Crocodylia. Despite playing important roles during Mesozoic and Cenozoic ecosystems, both on land and in water, Pseudosuchia received far less attention compared to the bird-lineage, which is also reflected in number and scope of histological studies so far. Lately, the field has seen a shift of focus toward pseudosuchians, however, and the symposium on "Paleohistological Inferences of Paleobiological Traits in Pseudosuchia" held during the International Congress of Vertebrate Morphology 2023 in Cairns, Queensland, Australia, is the latest proof of that. To put these novel aspects of paleohistological and paleobiological research into context, an overview of the non-extant pseudosuchian taxa whose postcranial bones were studied so far is provided here (c. 80 species out of a total of more than 700 extinct species described) and recent trends in pseudosuchian osteohistology are highlighted. In addition, histological studies on cranial and dental material and other potential hard tissues, such as eggshells and otoliths, are briefly reviewed as well.

KEYWORDS

Archosauria, bone histology, bone microstructure, Diapsida, Pseudosuchia

1 | INTRODUCTION

In paleontology, paleohistology comprises the microstructural analysis of mineralized and fossilized tissues, usually of bones and teeth. The paleohistological technique has been established since the second half of the 19th century as a complementary method to classical osteological and anatomical approaches in studying

fossils (de Ricqlès, 2011) and is more and more regularly used also in original descriptions of extinct species (see Paleohistology database on extinct Amniota: Scheyer, 2024). Here, it can provide additional data on biological aspects of the extinct animals that the external morphology of the fossils by itself usually cannot provide, for example pertaining to physiology, metabolism, or life history of these animals. Today, the classical microscopic

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slides can be complemented or even substituted by virtual sections generated by computed-tomography scans (CT) and other novel imaging processes (e.g., Sanchez et al., 2012).

Some of the earliest comparative paleohistological studies (e.g., Owen, 1878; Quekett, 1849) already included fossils of synapsid and diapsid species, the latter being heavily dominated by archosaur reptiles of the avemetatarsalian clade. The avemetatarsalian or bird-lineage archosaurs encompass a few smaller clades (Nesbitt et al., 2017) and the speciose clades of flying reptiles and their kin, Pterosauroomorpha, as well as the iconic dinosaurs and their closest relatives. The latter ultimately also includes over 10,000 extant bird species. The second group, the crocodylian-lineage archosaurs (Figure 1), encompasses the overall lesser studied clades Ornithosuchidae, Aetosauriformes including Aetosauria (sensu Parker et al., 2021), the small Erpetosuchidae (see Lacerda et al., 2018) and Gracilisuchidae clades, and Paracrocodylomorpha; the latter including Popsauroidea and Loricata (Marsh et al., 2020; Parker et al., 2021). Loricata consists of a grade of taxa that were in previous studies considered members of “Rauisuchia,” as well as Crocodylomorpha, a very speciose group throughout most of the Mesozoic and Cenozoic. Today, Crocodylomorpha is represented by less than 30 extant species of alligators and caimans, gharials, and true crocodiles (e.g., Kellner et al., 2014; Payne et al., 2023). Whether the Triassic Phytosauria (=Parasuchia) lie on the crocodylian-lineage or represent the sister group of Archosauria is currently still contested (see discussions and figures in Lacerda et al., 2018; Pradelli et al., 2022; Parker et al., 2021; von

Baczko et al., 2020) but the clade is included here for completeness, and it either serves as ingroup clade and sister taxon to all remaining Pseudosuchia, or is sister taxon to Archosauria (Pseudosuchia + Avemetatarsalia). In both cases Phytosauria play a crucial role for archosaur histocharacter polarization.

2 | RESULTS AND DISCUSSION

Despite high levels of (cranial) disparity and diverse lifestyles throughout most of the evolutionary history, but especially during the Triassic (e.g., Foth et al., 2021), Pseudosuchia generally received less attention compared to the flying reptiles and dinosaurs. This trend is also reflected in the amount of paleohistological studies focusing on or at least including Pseudosuchia (around 80 studies, see Supplementary Table 1; vs. 350+ studies on Avemetatarsalia: Scheyer, 2024). A preliminary survey of studied taxa revealed that only 126 pseudosuchian taxa (Figure 2a) have so far been sampled histologically (including many taxa with open nomenclature), out of a total of more than 700 described extinct species spanning 250 million years of evolution (Payne et al., 2023). More than half of the samples (58%) are from Crocodylomorpha, followed by Aetosauria, Phytosauria, and Loricata, which are also the three most speciose groups of non-crocodylomorph pseudosuchians.

Within Crocodylomorpha, the histology of modern Crocodylia has been studied most extensively, followed by Ziphosuchia/Notosuchia (Figure 2b). It is noteworthy that the latter group is studied histologically only since 2010, while at least a few members of Crocodylia, Thalattosuchia, and Neosuchia were studied already in the 19th century. The high number of recent Ziphosuchia/Notosuchia paleohistological studies appears to be linked with a current focus on this group, as many species have been recently erected including some histological data in the original descriptions. On the other hand, Neosuchia and Thalattosuchia have been treated over longer periods over the whole course of the 20th century, but there are several recent studies as well. In total, of the surveyed taxa sampled, 50 out of 74 (67.6%) were studied only since the year 2000.

Some of the general trends mentioned above are also seen among the eight contributions to the symposium “Paleohistological Inferences of Paleobiological Traits in Pseudosuchia” at ICVM 2023 (ISVM, 2023). Three of the contributions during the symposium dealt with novel descriptions of notosuchian and thalattosuchian histology, two contributions looked into physiological and morphometric aspects in extant crocodylian taxa, and the remaining two contributions focused on classical and

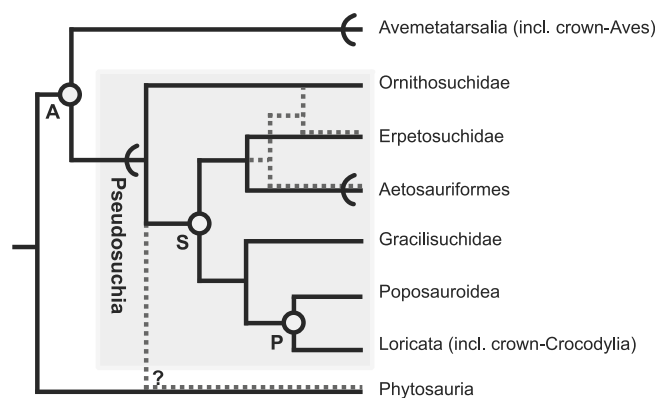
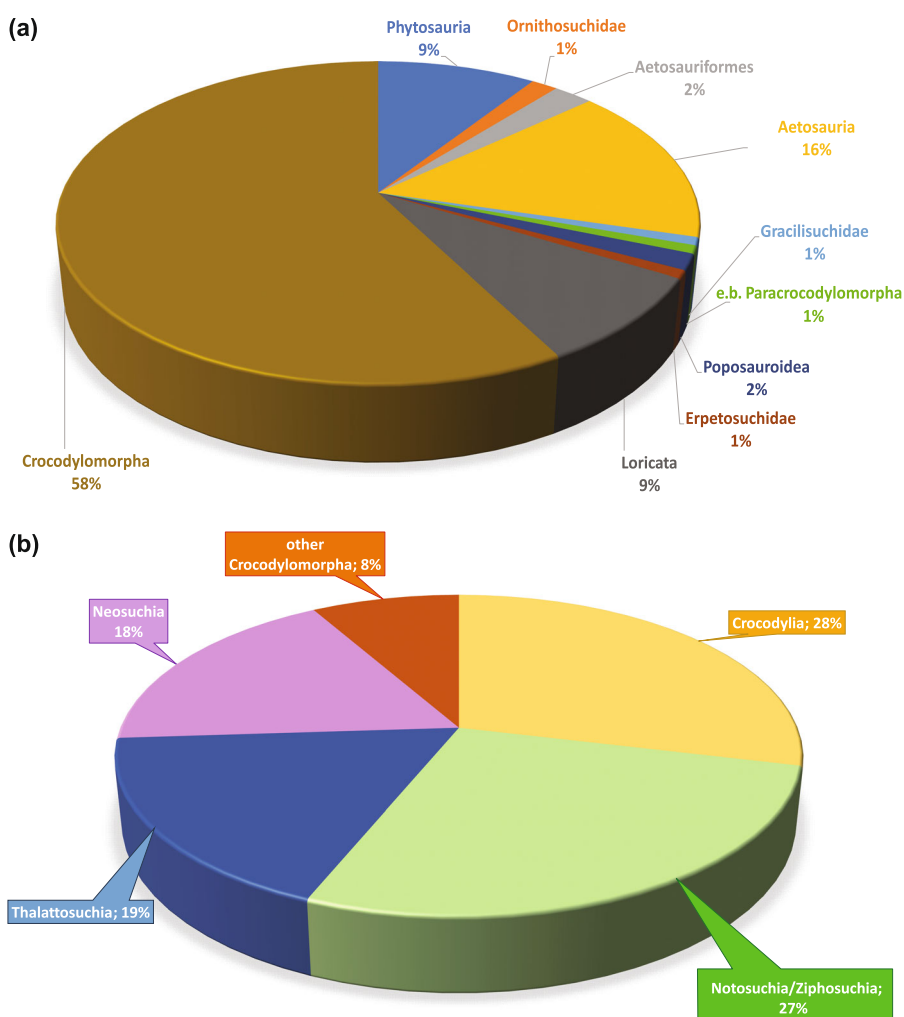


FIGURE 1 Phylogenetic framework of Archosauria. The cladogram is based on Parker et al. (2021) with considerations based also on Lacerda et al. (2018) and von Baczko et al. (2020). The alternative position of Phytosauria as member of Pseudosuchia and tentative position of Erpetosuchidae (i.e., as sister to Ornithosuchidae) are indicated by stippled lines. A, Archosauria; P, Paracrocodylomorpha; S, Suchia.

FIGURE 2 Diagrams showing the distribution of 126 extinct pseudosuchian taxa (a) and the distribution of 74 extinct Crocodylomorpha (b) that were histologically sampled (as listed in Supplementary Table 1; postcranial bones only) at the time of study (Scheyer, 2024). Note that more than half of the studied taxa belong to the clade Crocodylomorpha.



3D-synchrotron based histology of small aetosaurs to assess individuals' ages.

2.1 | General bone histology

The general bone histological aspects of non-crocodylomorph pseudosuchians and that of crocodylomorphs specifically were recently compiled and reviewed in two extensive book chapters in much detail (de Buffrénil et al., 2021; de Ricqlès et al., 2021), for which it is not necessary to elaborate much here, except a few aspects that are highlighted below. Suffice it to say that although many pseudosuchians seem to have grown slower than many of their avemetatarsalian counterparts, especially those on the theropod line leading to modern birds, they show a range of growth strategies and tissue types (Figure 3) from slow forming and weakly vascularized lamellar bone to faster growing, well vascularized parallel-fibered bone and even woven-parallel complex in some cases (e.g., de Buffrénil &

Quilhac, 2021; Fernández Dumont et al., 2021; Lecuona et al., 2020; Scheyer et al., 2014; Scheyer & Desojo, 2011). Furthermore, importantly, the histology of crocodylians is influenced by developmental plasticity (as summarized in Chinsamy, 2023), indicating that environmental factors play a critical role during an individuals' life.

Among extant Crocodylia, the American alligator, *Alligator mississippiensis*, is by far studied most extensively (e.g., Burns et al., 2013; Dacke et al., 2015; Foote, 1911; Greer et al., 2022; Horner et al., 2001; Ikejiri, 2012; Klein et al., 2009; Lee, 2004; Schweitzer et al., 2007; Tumarkin-Deratzian, 2007; Vickaryous & Hall, 2008; Wink et al., 1987; Woodward et al., 2011, 2014), comparable to all remaining Alligatoridae (mostly Caimaninae), Crocodylidae, and Gavialidae together (e.g., Amprino & Godina, 1947; Andrade et al., 2020; de Buffrénil, 1980a, 1980b; de Buffrénil & Amson, 2021; Clarac et al., 2018; Enlow, 1969; Haines, 1938; Hutton, 1986; Mascarenhas-Junior et al., 2021; Peabody, 1961; Quekett, 1850; de

Ricqlès, 1976 and references herein). Extant crocodylians were also part of larger amniote-based studies that addressed the microanatomy of bones for lifestyle inference. As such, crocodylian long bones were studied (de

Buffrénil et al., 2021; Canoville & Laurin, 2010; Krilloff et al., 2008; Laurin et al., 2011), as well as ribs (Canoville et al., 2016) and vertebrae (Houssaye et al., 2014, 2016).

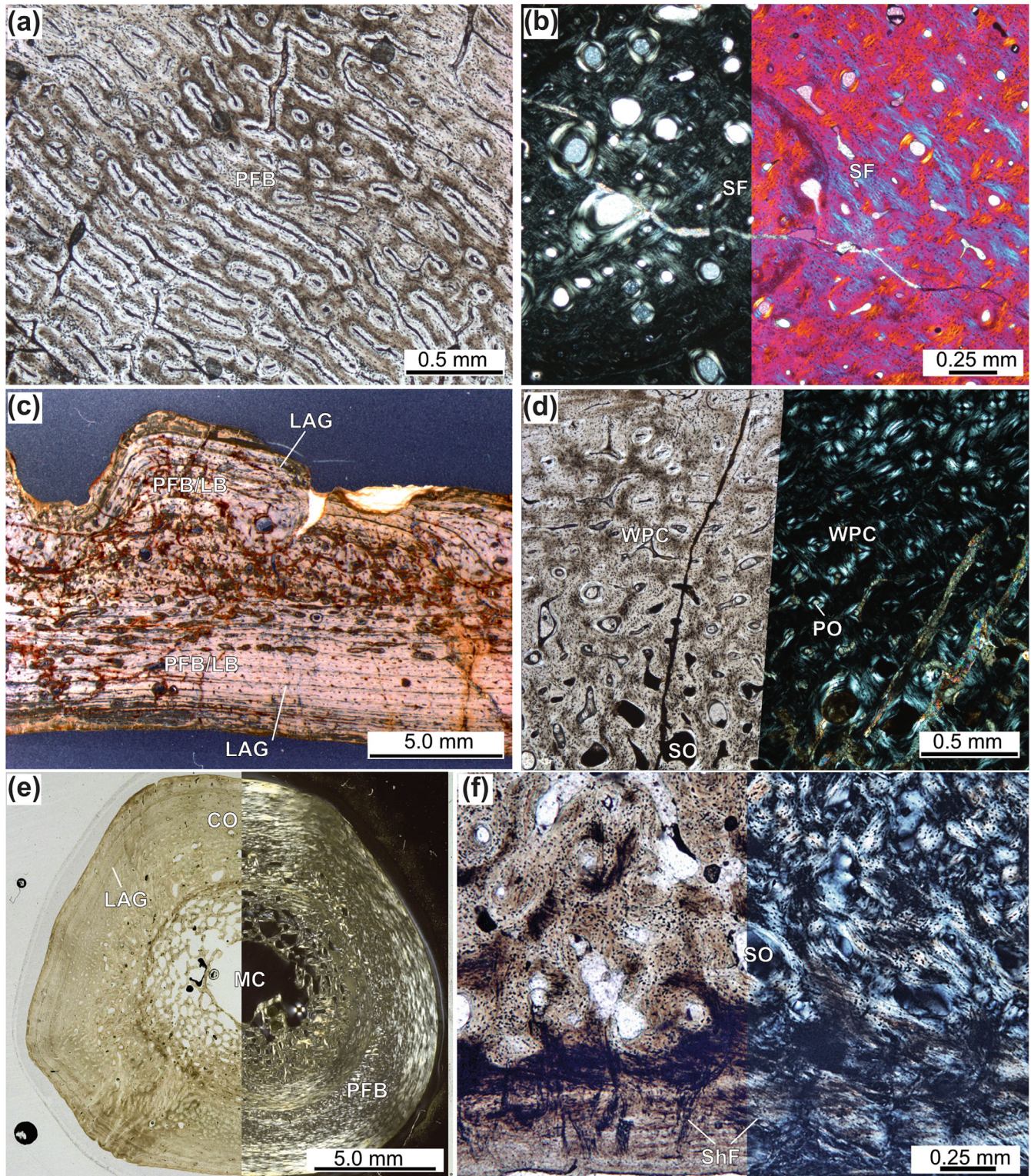


FIGURE 3 Legend on next page.

2.2 | Cell lacunae and genome size

A study of bone cell lacunar size, shape, and density in a broad sample of amniote bones set out to estimate genome sizes of extinct animals (Organ & Shedlock, 2009). While the study focused on animals that evolved active flight, it also included long bones of plesiosaurs (*Rutiodon* sp., Phytosauridae indet.) and the loricatan *Postosuchus kirkpatricki*, and osteoderms of aetosaurs (*Desmatosuchus haplocerus*, *Typhothorax meadei*) and of the alligatorid crocodylian *Leidyosuchus* sp. In their study, support was found for the previously hypothesized correlation between bone cell- and genome size and they indicated that the genome size of the studied pseudosuchians was close to the average genome size of extant crocodylians in their dataset (Organ & Shedlock, 2009), but without going into further details, such as discussing differences or commonalities between sampled endoskeletal or dermal bones. Further, despite listing pseudosuchian taxa, the study is not included in Supplementary Table 1 herein, because no other specific details on the overall histology of the sectioned bones of each taxon were provided. de Ricqlès et al. (2021, p. 482) further discussed the differences in resting metabolic rates in the two archosaur lineages, pointing out that the pseudosuchian signal is more ambiguous than that of bird-lineage and that a differentiation into “endothermic bone (tissues)” versus “ectothermic bone (tissues)” is too simplistic: “Depending on local growth and other circumstances, the basic genetic system controlling bone as a tissue can produce, in time and space, the entire continuum of bone tissue types [...]”

2.3 | Fossilized ontogenies

In 2010, pseudosuchian histology was summarized in a single small paragraph, and—erroneously—it was

pointed out that larger-scale skeletochronology studies in that lineage were at that time restricted to plesiosaurs and rauisuchians (Scheyer et al., 2010). Since then, skeletochronology and cyclical growth was in detail summarized using modern crocodylians such as in the American *Alligator* (e.g., Woodward et al., 2014) and growth aspects are now regularly studied in many other extinct pseudosuchians as well, including aetosaurs (e.g., Teschner et al., 2022), ornithosuchids (von Baczko et al., 2020), and crocodylomorphs (e.g., Pellegrini et al., 2021; Waskow & Mateus, 2017). Contributions on selected non-pseudosuchian tetrapods, however, also raised concerns on correctly estimating ages, even for extant animals of known age, based on the methodology used, and advise further caution when discussing growth and skeletochronology in fossils (Jannello & Chinsamy, 2022; Schucht et al., 2021).

2.4 | Growth rates and resting metabolic rates

When estimating bone growth rates in a broad sample of archosaurs, Padian et al. (2001) discovered a “dichotomy between those archosaurs related to crocodiles and those related to birds and dinosaurs”: in that those taxa on the avemetatarsalian lineage showed histological features indicative of heightened growth rates and linked to that, basal metabolic rates, more aligned with larger extant birds and mammals than the sampled taxa from the pseudosuchian lineage. The pseudosuchians *Rutiodon*, *Desmatosuchus*, *Typhothorax*, *Stagonolepis*, and *Postosuchus* were all indicated to have very low daily bone growth rates (0–2 $\mu\text{m}/\text{day}$), while *Terrestrisuchus* and extant *Alligator* would only be slightly higher (0–5 $\mu\text{m}/\text{day}$). Using a quantitative bone histological approach, Legendre and colleagues later inferred higher resting metabolic rates to be ancestral for archosaurs based on phylogenetic

FIGURE 3 Bone histology of selected pseudosuchian postcranial bones. (a) *Prestosuchus chiniquensis* (SNSB-BSPG_1934_XXV 35; Loricata) right humerus, whose cortex consists of well-vascularized parallel-fibered bone (normal transmitted light). The vascularization shows overall a laminar arrangement. (b) *Batrachotomus kupferzellensis* (SMNS 80317; Loricata) paramedian osteoderm showing a core region of structural fibers (cross-polarized light with lambda filter). (c) *Steneosaurus jugleri* (NMS 7152; Crocodylomorpha) paravertebral osteoderm (slightly thicker section in cross-polarized light). The external and internal cortices consist of weakly vascularized parallel-fibered bone matrix that locally grades into lamellar bone. (d) *Typhothorax* sp. (SMNS 91550; Aetosauria) paramedian osteoderm (normal and cross-polarized light). The deeper regions of the external cortex consist locally of woven-parallel (fibrolamellar) complex. (e, f) *Alligator mississippiensis* (SMNS 10481; Crocodylia) right femur (e) and osteoderm (f) in normal and cross-polarized light. The femur shows high- and low organized layers of cortical parallel-fibered bone and reduced vascularization with increasing age. The osteoderm exhibits large numbers of coarse Sharpey's fibers extending into the internal (basal) cortex and a strongly remodeled core tissue. Institutional abbreviations: NMS, Naturmuseum Solothurn, Solothurn, Switzerland; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; SNSB-BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayerns, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany. Histological abbreviations: CO, cortex; LAG, line of arrested growth; LB, lamellar bone; MC, medullary cavity; PFB, parallel-fibered bone; PO, primary osteon; SF, structural fibers; ShF, Sharpey's fibers; SO, secondary osteon; WPC, woven-parallel complex.

eigenvector maps (Legendre et al., 2016). In addition, the study showed that rates of some pseudosuchians, such as the loricatan *Postosuchus kirkpatricki* and the aetosaur *Calyptosuchus wellsi*, might have been higher even than those of some avemetatarsalian dinosaurs, including the ornithischians *Lesothosaurus diagnosticus* and *Maiasaura peeblesorum* and the sauropodomorph *Thecodontosaurus antiquus*. This is somewhat surprising, given that the hadrosaur *Maiasaura*, for example, was found to have high daily bone apposition rates, especially early in ontogeny, like modern birds (Woodward et al., 2015: 86.4 $\mu\text{m}/\text{day}$ during the first year of life). Expanded datasets which included both, more early branching non-archosauriform taxa and notosuchian crocodylomorphs indicated that higher resting metabolic rates are found basal for crocopodan Archosauromorpha, and that there is a reversal to low metabolic rates only within Crocodylia (Cubo et al., 2020; Cubo & Jalil, 2019). Given the still low numbers of studied taxa per group, it is likely that these general patterns will be revised in the future to present a more differentiated scenario than what is known today.

2.5 | Skull bone and dental histology

In contrast to long bone and osteoderm histology, skull bone and dental histology is often more difficult to standardize, and among Pseudosuchia, thin sections were performed (almost?) exclusively on crocodylomorph taxa, with emphasis on extant and extinct members of Crocodylia. Although cranial shape and dentition seems to be quite similar in the latter, that is, taxa mostly sharing semi-aquatic ambush-predatory lifestyles, the picture gets more complicated when adding the complex cranial shapes, often heterodont dentitions, and various lifestyles of Crocodylomorpha as a whole (e.g., Stubbs et al., 2021; Wilberg et al., 2019; Zanno et al., 2015). Despite this apparent disparity, but likely due to the scarcity of cranial bones compared to more abundant postcranial remains in the fossil record (and likely also because the latter could potentially provide a stronger ecomorphological signal), skull bones have been rarely sampled. In the following, only a brief overview, which is not exhaustive, could be provided (the cited papers also provide a wealth of older studies).

Hua & de Buffr enil (1996) studied sections of Teleosauridae indet. (a dentary fragment), *Metriorhynchus superciliosus*, and *Metriorhynchus* sp., as well as extant *Crocodylus cataphractus*. de Buffr enil & Quilhac (2021) and de Buffr enil et al. (2021) sampled skull bones of *Crocodylus niloticus* and the extinct alligatoroid *Diplocynodon ratelii*. These studies indicate that, although bone

tissue types, vascularization patterns, and also bone remodeling processes can be very similar or the same to long bones, there can in addition be also a strong asymmetry between external and internal cortical bone growth (see de Buffr enil & Quilhac, 2021); an effect that is also often observable in osteoderms. Bailleul & Horner (2016) focused on craniofacial sutures including specimens of the extinct cf. *Brachychampsia* and extant *Alligator mississippiensis*, whereas Lessner et al. (2019) also studied the mandibular symphysis in the latter species. A good example of using CT scan data to study the skull virtual anatomy and histology further can be found in Erb & Turner (2021), who looked at the braincase CT sections of the crocodyliform *Rhabdognathus*. These studies show the complexity and biomechanical and functional importance of the sutural regions between the growing skull bones, using various techniques from micro-CT scanning, wholmount preparation, and ground thin sections to stained serial microtome sections.

Most histological studies, however, deal with tooth histology, the tooth anchoring mechanism in the jaw bones, and patterns of tooth replacement. Like with the other cranial bones, most of the studies again focus on extant and extinct Crocodylomorpha. Using ground sections, Erler (1935) provided one of the first comparative studies on the enamel microstructure of teeth of *Crocodylus porosus* and *C. niloticus*. Peyer (1968) included microtome sections of developing teeth and surrounding tissues in a young crocodile, as well as ground sections of fossil teeth from the Early Cretaceous of Texas. Dauphin (1989) performed element analyses and gave overviews on the presence of both prismatic and non-prismatic enamel in a series of extant and extinct taxa. Using a larger crocodylian dataset and comparison with dinosaur teeth, Dauphin (1991) showed the impact of diagenesis on the element composition, which renders a link to paleo-diet in extinct taxa unreliable. Using scanning electron microscopy (SEM) images, Sander (1999) provided further comparative data on enamel microstructure, schmelzmuster, and tissue distribution in reptile teeth including crocodylians, loricatan “rauisuchians,” and phytosaurs. Dauphin & Williams (2008) reported the chemical composition of teeth of extant *C. porosus* or *Crocodylus siamensis* using SEM and a wavelength-dispersive electron microprobe, noting inhomogeneities in element distribution in the dentine reflecting growth changes, as well as enrichment of Mg in the dentine compared to the enamel. Enax et al. (2013) analyzed the structure and composition of teeth of *C. porosus* using x-ray diffraction and spectroscopy methods, as well as synchrotron x-ray CTs and supporting results of varying degrees in mineral content in the dentine, enamel, and the surrounding cementum tissue. Sellers et al. (2019) addressed the enamel thickness in

extant *Alligator* teeth in relation to the Eocene alligatoroid *Allognathosuchus* and eusuchian *Iharkutosuchus* (and one indeterminate crocodyliform) using micro-CT scans and found (1) an isometric relation between enamel thickness and skull length and (2) that thickness is greater in more caudally positioned teeth compared to more rostral ones. Szweczyk & Stachewicz (2020) analyzed the collagen fiber content using normal light and SEM in shed teeth of extant *Crocodylus rhombifer*. The mechanical characterization and elemental composition of the giant crocodylomorph *Sarcosuchus imperator* teeth were published by Kundanati et al. (2019).

Aspects of tooth replacement in crocodylians (i.e., *Melanosuchus niger*) were already discussed in Owen (1840–1845). Poole (1957, 1961) published on tooth growth and replacement, as well as tooth enamel formation in *C. niloticus*. In the same species, Kieser et al. (1993) argued for a heterodont rather than a homodont dentition based on replacement patterns identified on x-ray images of a series of embryos. Wu et al. (2013) studied tooth renewal and replacement in *Alligator mississippiensis* and Fruchard (2013) in *C. niloticus*. Erickson (1996) estimated tooth replacement in *Alligator mississippiensis* based on daily deposition lines in the dentine using periodic tetracycline staining of the tissue. The study reported mean replacement rate estimates from 83 to 122 days and a decrease of the rate throughout the ontogenetic interval that was studied using various specimens. The similarity of the attachment of crocodylian and mammalian teeth, that is, tooth anchoring in the alveolar bone with cementum and periodontal ligament tissue, has been noted repeatedly. Miller (1968) mentioned that the anterior teeth of *Caiman [sclerops] crocodilus* were held in a thecodont gomphosis, whereas the posterior teeth were said to lay in a bony channel with the interdental bony septa still being in development posteriorly. Berkovitz & Sloan (1979) highlighted commonalities but also differences in the microstructure of the attachment tissues between *Caiman crocodilus* and mammalian teeth. Fong et al. (2016) and LeBlanc et al. (2016) reported on the tooth attachment and tooth histology in *Alligator mississippiensis*, LeBlanc et al. (2017) again on the tooth attachment of *Caiman crocodilus*. LeBlanc et al. (2021, p. 1157) summarized the concept of thecodonty “[...] which is still applied broadly today, was characterized histologically by a three-part tissue attachment system, consisting of root cementum, a periodontal ligament, and the alveolar bone that forms the socket. These three periodontal tissues perform specific functions in mammals and crocodylians [...]” In addition to these extant animals that can be studied using stained microtome or diceCT sections of soft- and hard tissues, there emerged also a recent interest in the teeth microstructures

and attachment in fossil crocodylomorphs from Gondwana. Campbell et al. (2021) studied the teeth of the Plio-Pleistocene genus *Paludirex* from Australia, whereas Augusta & Zaher (2019: *Mariliasuchus amarali*), Ricart et al. (2021: *Mariliasuchus* sp., Baurusuchidae and Sphagesuchidae indet.) and Navarro et al. (2022: *Notosuchus terrestris*) described tooth histology and attachment tissues in notosuchian crocodylomorphs from South America using the conventional paleohistology and SEM analyses.

2.6 | Eggshells and otoliths

So far, there is no fossilized eggshell material of pseudosuchians known outside of Crocodylomorpha. Extant and extinct (e.g., *Krokolithes wilsoni*, Krokolithidae *incertae sedis*) crocodylomorph eggshells have been sectioned in several studies (e.g., Moreno-Azanza et al., 2014; Marzola et al., 2015; Prasad et al., 2015; Prondvai et al., 2017), and special emphasis was given the eggshell thickness (as comparative data usually provided in extensive tables). For *Krokolithes wilsoni*, Moreno-Azanza et al. (2014) described a three-layered microstructure similar to extant eggshells of *C. porosus* and *C. niloticus*.

In non-crocodylian pseudosuchians, to the author's knowledge, no otoliths have so far been found in the fossil record. For extant crocodylians, Schwab et al. (2022) provided a comprehensive overview on saccular otoliths using CT scan data of hatchling, juvenile, and subadult/adult specimens. Although the shape of the otoliths could thus be reconstructed for many extant species, a detailed histological study, either using higher resolution (Synchrotron or micro-) CT or classical sectioning methods, has yet to be conducted.

3 | CONCLUSIONS

In summary, the paleohistological analysis of Pseudosuchia has gained momentum over the past two decades, with many more taxa being included in recent studies and a part on paleohistology is now considered an asset of many new species descriptions. Also, the fact that several clades of pseudosuchians have extensive dermal ossifications overlying their endoskeleton has led to many publications on comparative histology. On the other hand, studies that include both endoskeletal and dermal bones of the same individual are still rare, making comparative studies a challenge. A recent trend to section more cranial, and specifically tooth-bearing elements, can also be seen among pseudosuchian taxa, whereas eggshell and otolith studies in non-crocodylomorph taxa are hampered by lack

of fossils. Bone histology remains a powerful tool to age individual specimens and to identify and study potential growth series, but this implies that not only a few fragments of dubious position on the animal's body are sampled, and in cases, that also more than one or two samples are analyzed per taxon. Furthermore, skeletochronology, growth pattern analyses and thermometabolic regime of giant pseudosuchians, for example, taxa that reach more than 7 to 10 m in body length or even more, remain so far largely unexplored. Following the example of 2023's ICVM symposium, there remain still many aspects of pseudosuchian biology and taxa to be studied, to further close the gap between the equally fascinating groups of bird- and crocodylian lineage archosaurs.

AUTHOR CONTRIBUTIONS

Torsten M. Scheyer: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; validation; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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