**Structure and evolution of the unique pseudosuchian auricular region
from the Late Triassic to the present**

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Abstract

The ear flap in modern crocodilians is poorly understood in function and anatomy. While it generally has been assumed to have evolved in order to protect the tympanic membrane upon submerging underwater, the evolutionary history of this structure is still unknown. In this paper, we seek to discover methods for estimating when the ear flap arose in the fossil record. We accomplish this through comparative descriptions of extant and fossil pseudosuchian skulls via segmentation of computerized tomography (CT) scans, supplemented by a dissection of the outer ear of a juvenile *Alligator mississippiensis* specimen. This has allowed to us to examine previously undescribed features of the crocodilian external ear and elucidate the nature of relationships between soft and hard tissue structures. Thus, we have been able to identify the squamosal, postorbital, quadrate, and quadratojugal bones, as well as the previously unnamed "post-tympanic ridge" more pronounced in juvenile crocodilians, as potential bone-tissue correlates for reconstructing the ear flap in prehistoric pseudosuchians. Using these measures, we find that this structure evolved in terrestrial pseudosuchians: originating in the Late Triassic, fully established in the Late Cretaceous, and remaining mostly unchanged since.

Introduction

An apomorphy of all extant crown crocodilians, the ear flap appears to have a rather straightforward function: upon submerging their heads underwater, the ear flap closes over the canal to the auditory meatus in order to seal off the tympanic membrane from exposure to water (Fleming & Fontenot, 2015). Crocodilian hearing is adapted to receive a wider range of frequencies through air than through water, and the ear flap helps maintain a pocket of air between the aquatic environment and the tympanic membrane (Higgs et al., 2002). Although the skeletal anatomy of crocodilians has been well-studied, research into soft tissue structures have been largely neglected. The earliest papers describing crocodilian skulls remain uncontested in their accurate depictions of the external characteristics of the skull bones, but they do not touch upon the connective tissues that attach to any of them (Miall, 1878; Mook, 1921; Iordansky, 1973).

The first comprehensive study of the soft tissue auricular structures in the temporal skull region is by Shute and Bellairs in 1955. They establish several key features of the ear flap: the superior ear flap, which is operated by the levator auriculae and depressor auriculae muscles believed to be derived from the hyoidean muscle group; the auricular plate, which strengthens

the posterior two-thirds of the ear flap and attaches along the length of the squamosal and the posterior portion of the postorbital; the hinge, described as connecting the auricular plate to the levator and depressor muscles; and the inferior ear flap, which connects to the depressor auriculae inferior muscle found in the orbit through a connective tissue called the ypsilon. Wever (1978) reviews these findings, but rather than adding any morphological information, some features such as the hinge are in fact left out from the recapitulation of the results of Shute and Bellairs. Garrick and Saiff (1974) also propose a link between the ear flap and eyelid musculature in crocodilians, either through nervous reflex or connected musculature, but these results have not been confirmed. Since then, Montefeltro et al. (2016) have published a new comprehensive study of the ear—that is, the middle and inner ear. Montefeltro et al. reestablishes the existence of the auricular plate along the superior ear flap, describing the latter as attaching as a whole along the ventrolateral edge of the squamosal and postorbital; otherwise, their study treats the external ear tissues as perfunctory to the rest of the inner ear.
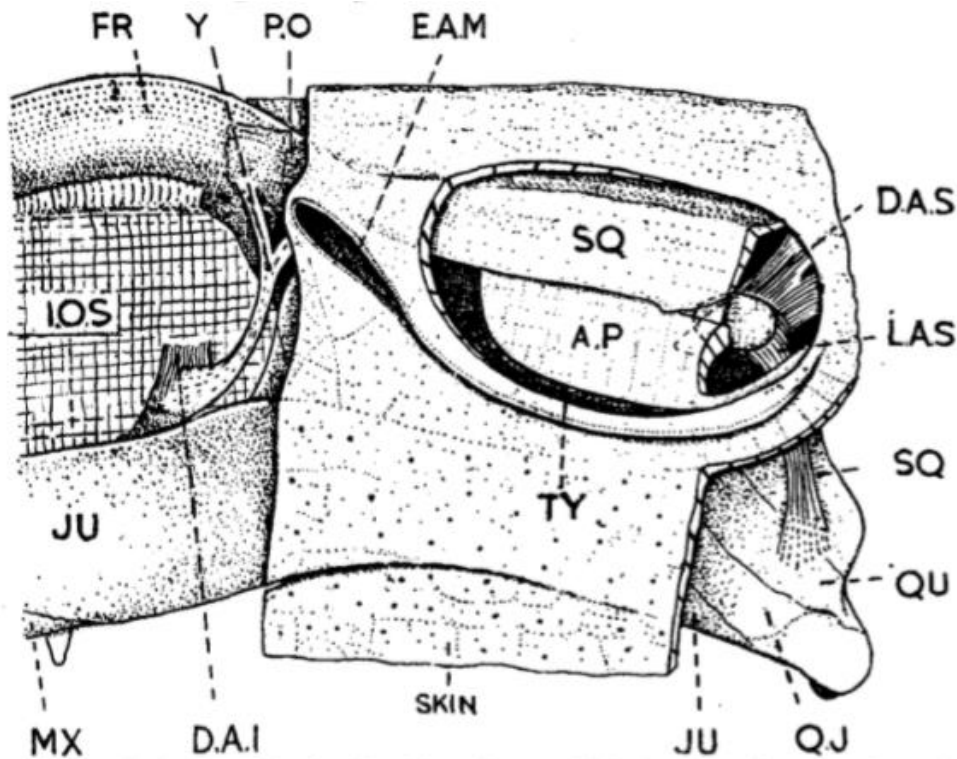

Figure 1. Reproduction of Figure 2, p. 744, from Shute and Bellairs (1955) depicting the lateral view of the superficial ear tissues in *Alligator mississippiensis*.

Text-fig. 2.—Left side of head with skin and superficial tissues partly removed to show attachments of auricular muscles. A window has been cut in the superior ear-flap, and the posterior parts of the squamosal, auricular plate and (unlabelled) plate hinge have been cut away. The outlines of the anterior parts of the levator and depressor auriculae muscles are shown in broken lines. Semi-diagrammatic, based mainly on *Alligator*. (Key to lettering, p. 749.)

Within Reptilia, the presence of superficial ear flaps are unique to crocodilians (Wever, 1978). Within the broader animal kingdom at large, the ability to even open and close the external auricular aperture in order to protect the tympanic membrane upon submerging underwater is otherwise found only in semiaquatic mammals—in particular, pinnipeds and otters. Out of these groups, only sea lions and otters have external flap-like pinnae, but walruses and seals can also occlude their external auditory orifices (Wartzok & Ketten, 1999). Even in birds, the closest living relatives to crocodilians, of those which do submerge their heads underwater, the external ear is protected by a layer of watertight feathers which are each controlled by the individual muscles attached to each feather shaft (Dooling & Therrien, 2012). A study by Sadé et al. (2007) suggests that king penguins (*Aptenodytes patagonicus*) and other deep-diving birds may also be able to close the external ear canal, but it is not confident in concluding so. Even in eutherian mammals, however, the evolution, mechanism, and development of the analogous ear-closing musculature are poorly understood. A dissection of the ear region of a walrus head (*Odobenus rosmarus*) by Kastelein et al. (1996) names seven distinct muscles involved in opening and closing the outer ear canal, but none are homologous to the depressor and levator auriculae muscles of crocodilians as described in Shute and Bellairs (1955), and they also all appear to derive from the temporalis muscle (which are homologous to the adductor muscles in reptiles, from which the crocodilian auriculae muscles are mostly likely not derived).

This paper aims to better understand the anatomy of the ear flap and associated skeletal and muscular tissues, which inevitably requires an understanding of the evolutionary history of these structures. Here, a new mystery arises: the appearance of this structure in the fossil record. In addition to developing contexts based on modern crocodilian anatomy for inferring the presence of external ear structures for the fossilized skulls of crocodilian ancestors, there is another problem to consider: if the ear flap does appear in prehistoric pseudosuchians, what function did it serve, and under what evolutionary pressures did it develop? This issue is further complicated by the fact that stem pseudosuchians, as is the case with likely all early Mesozoic reptiles, were terrestrial creatures. Shute and Bellairs, as well as Gow (2000) and Brochu (2002), suggest that the ear flap may have evolved in pseudosuchians as general protection for the tympanic membrane—but in order to begin to understand the function and structure of the ear flap, we must first determine the approximate time period in which it first appears. Thus, this

paper also aims to roughly discover the initial appearance and subsequent development of the ear flap in pseudosuchians through examining the temporal regions of fossil crocodylomorphs.

Institutional Abbreviations

PVSJ, Division of Vertebrate Paleontology of the Museo de Ciencias Naturales de la Universidad Nacional de San Juan, Argentina; **UA**, Université d'Antananarivo, Antananarivo, Madagascar; **YPM HERR**, Division of Vertebrate Zoology Herpetology Reptile Collection, **YPM VP**, Division of Vertebrate Paleontology Collection, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

Materials and Methods

A juvenile *Alligator mississippiensis* (YPM HERR 13323) was dissected in order to verify previous descriptions of the superficial crocodylian ear (Shute & Bellairs, 1955; Wever, 1978; Montefeltro et al., 2016) and to elucidate the nature of tissue associations seen in the following CT scans of modern crocodylians. It belongs to the collections of the Division of Vertebrate Zoology of the Peabody Museum of Natural History at Yale University. It was obtained from the Rockefeller Wildlife Refuge, Louisiana Department of Wildlife and Fisheries. Its postcranial region has been partially dissected by Tsuihiji (2005) and remains preserved in iodine solution.

Three-dimensional renderings of five pseudosuchian specimens were created using micro-computer tomography (CT) scanning and segmented (i.e. 3D volumes were generated) using the program VGStudio version 3.0: a juvenile *Crocodylus niloticus* (YPM HERR 8722) preserved in phosphomolybdic acid; an embryonic *Alligator mississippiensis*; specimen YPM VP 57103; *Saurosuchus galilei* (PVSJ 32; from Alcober, 2000); and *Simosuchus clarki* (UA 8679, from Kley et al., 2010). The modern taxa were scanned at the Center for Nanoscale Systems at Harvard University, while the fossil taxa were scanned at the High-Resolution X-ray Computer Tomography Facility at the University of Texas at Austin. Files for the latter two were obtained from digimorph.org.

YPM VP 57103 is an undescribed Late Triassic sphenosuchian from the Chinle Formation of Utah. Because it was discovered in the same assemblage as YPM VP 57100, *Poposaurus gracilis* (Gauthier, Nesbitt, Schachner, Bever, & Joyce, 2011), we have nicknamed it "Popobuddy" and will refer to it as such until it is named and fully described.

Results

Dissection of the outer ear of a young *Alligator mississippiensis*

Specimen YPM R 13323 (Crocodylia: Alligatoridae)

The crocodylian ear (IMG 792) is located posterolaterally to the orbit and directly ventral to the lateral shelf of the squamosal. There are two ear flaps asymmetrical in size and shape: the superior ear flap, the larger and more mobile of the two; and the inferior ear flap, which does not have as much associated musculature. The superior ear flap is covered by a layer of thin scales; one of the scales is long and extends ventrally along the squamosal. The ventral end of the ear flap is also covered in a series of laterally aligned scales. The inferior ear flap is much smaller in size and area, and is covered only by one long scale. Deep to the scales, both ear flaps are a cream white color, with some darker superficial pigmentation. The superior ear flap completely covers the tympanic membrane, a circular disc of delicate tissue that marks the first step of transmitting auditory information and obscures the entrance to the interior meatal chamber (Montefeltro et al., 2016). The tympanic membrane is quite tilted relative to the dorsoventral skull axis, facing dorsally at a steep dorsal incline.
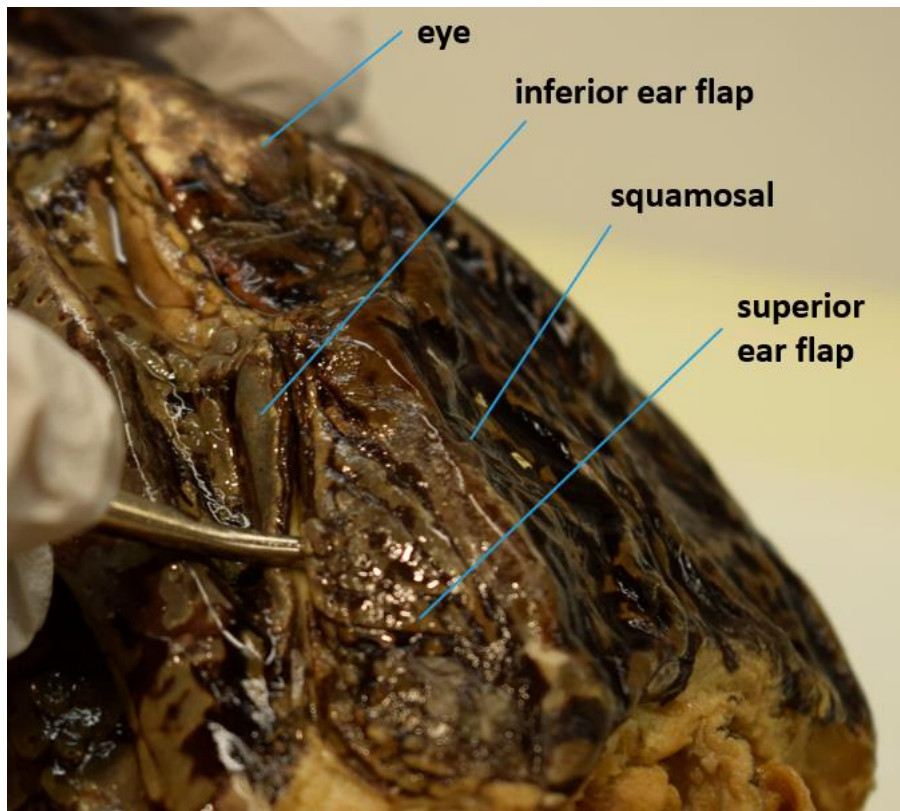

Figure 2. External anatomy of the crocodilian ear.

Continuous with the inner surface of the superior ear flap is a layer of dense, fibrous tissue known as the auricular plate (Shute & Bellairs, 1955). The auricular plate thickens dorsally toward the skull table, forming a disc-like area just superficial to the tympanic membrane, but thins toward the ventralmost base of the flap. This thin ventral margin arcs posterodorsally to the posterior aspect of the squamosal. There are also lateral bands of fibrous tissue connecting the superior ear flap and auricular plate with the paraoccipital process.

Toward the posterior end of the auricular plate is a condensation of thick tissue which may be the "hinge" described in Shute and Bellairs (1955). Attaching to the dorsal and lateral surfaces of the hinge are the depressor auriculae and levator auriculae muscles respectively. The post-tympanic ledge may be the bone correlate of the hinge, as well as possibly the dorsal attachments of both auriculae musles. Additionally, the hinge and surrounding muscles are possibly being innervated by the facial nerve, which courses proximally along the posterior end of the squamosal.
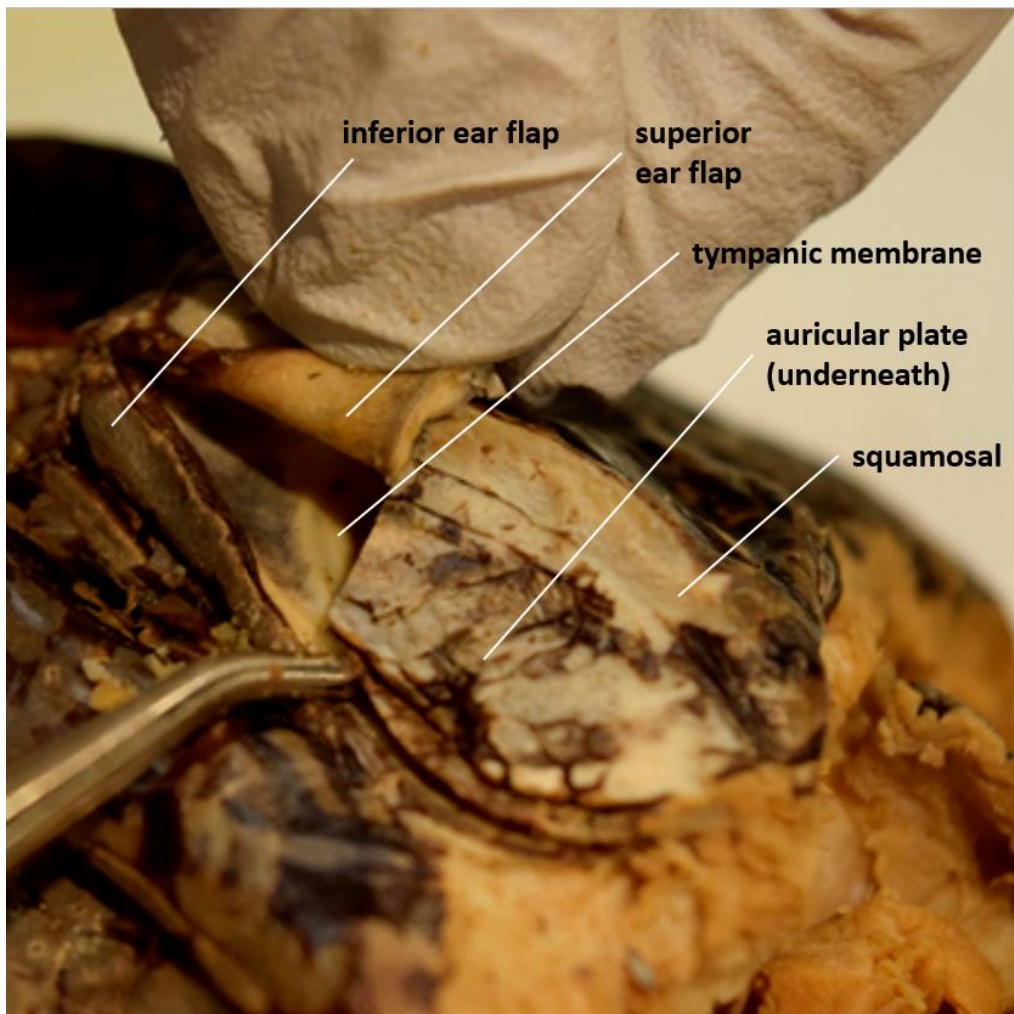

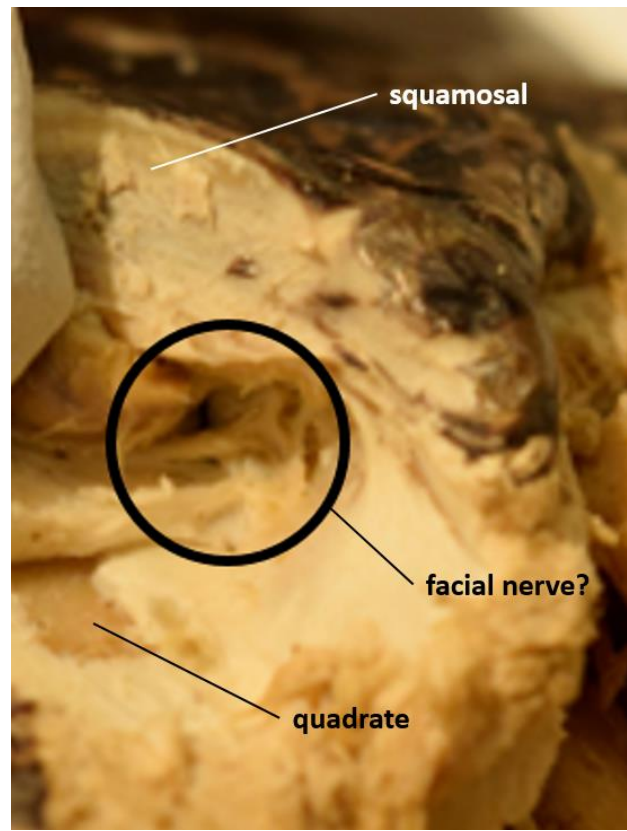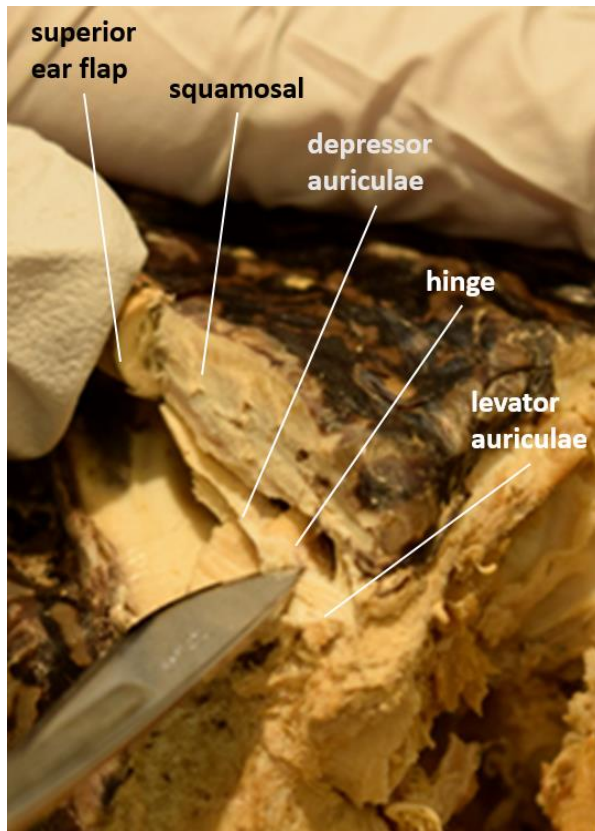Figure 3. Superficial surface of the superior ear flap.

Figure 4 (left). Anatomy deep to the superior ear flap; Figure 5 (right). Nerve, possibly the facial nerve.

The inferior ear flap is also quite fibrous, especially at the anterior end. There is a small gap between the dorsal edge of the inferior ear flap and the ventral edge of the tympanic membrane. A collection of tissues which extends from the posterior end of the postorbital and onto the quadrate, quadratojugal, and jugal bones appears to originate from the base of the inferior ear flap. Most importantly, the inferior ear flap appears to be continuous with the quadratojugal, which could signify a new bone-tissue correlate for inferring the position of the inferior ear flap in fossil pseudosuchians. Since we did not extricate the eyeball or open the orbit, however, we were unable to verify the existence or positioning of the depressor auriculae inferior muscle, nor did we find any connective tissues resembling the ypsilon (Shute and Bellairs, 1955).

Lastly, there is a very thin and tight fibrous tissue stretching across the ventral surface of the squamosal interior to the groove. It is unsure whether it is the "auricular cavernous tissue" in Montefeltro at al. (2016), and the function is not readily apparent.
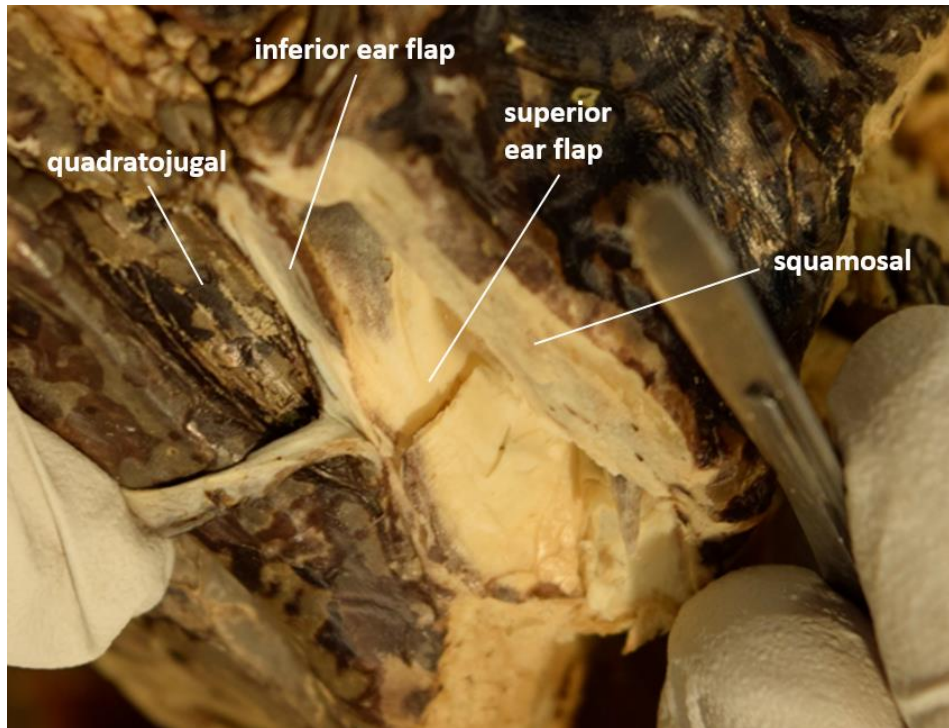
Figure 6. Inferior ear flap with superficial layer separated; superior ear flap is reconstructed.

Description of the temporal region in CT scans of modern crocodilians

A juvenile Nile crocodile (*Crocodylus niloticus*, YPM HERR 8722) and an embryonic alligator (*Alligator mississippiensis*)

The modern crocodilian squamosal has a prominent lateral shelf with a ventral groove running anteroposteriorly. The postorbital inserts neatly into the anterior-most section to extend the horizontal plane. The quadrate contacts the squamosal along the interior shelf and the posterolateral-most shelf, forming the circular otic aperture that marks the medial limit of the meatal chamber. The quadratojugal maintains contact with the lateral shelf of the quadrate and forms a parallel horizontal plane underneath the squamosal-postorbital plane.

The dorsal end of the superior ear flap and auricular plate inserts longitudinally along the lateroventral surface of the squamosal, extending to the postorbital. The tympanic membrane stretches across the otic aperture to form a disc-like plane inserting along the medial projection of the ventral surface of the squamosal. Soft tissues connected to the tympanic membrane extend posterodorsally to the quadratojugal. As they are not connected directly to the superior ear flap, based on the earlier dissection we believe these tissues to form part of the inferior ear flap. The tympanic membrane is tilted at a deep angle facing dorsally, though the ear flap itself maintains

a roughly vertical covering over it. There is an additional piece of bulbous, dense tissue that rests directly underneath the rounded rim of the posterolateral edge of the squamosal. This tissue is most likely the "hinge" mentioned briefly in Shute and Bellairs (1955), but it is unsure whether the rim is equivalent to the "dorsal otic incisure" in Montfeltro et al. (2016). Here, we refer to it as the post-tympanic ridge. The post-tympanic ridge appears to be more pronounced in embryonic and juvenile crocodylians than in adults.
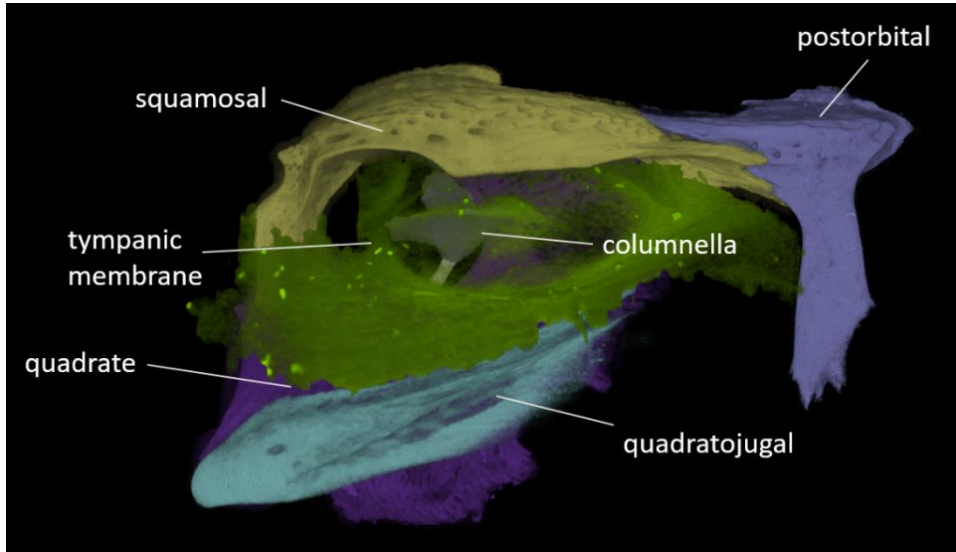

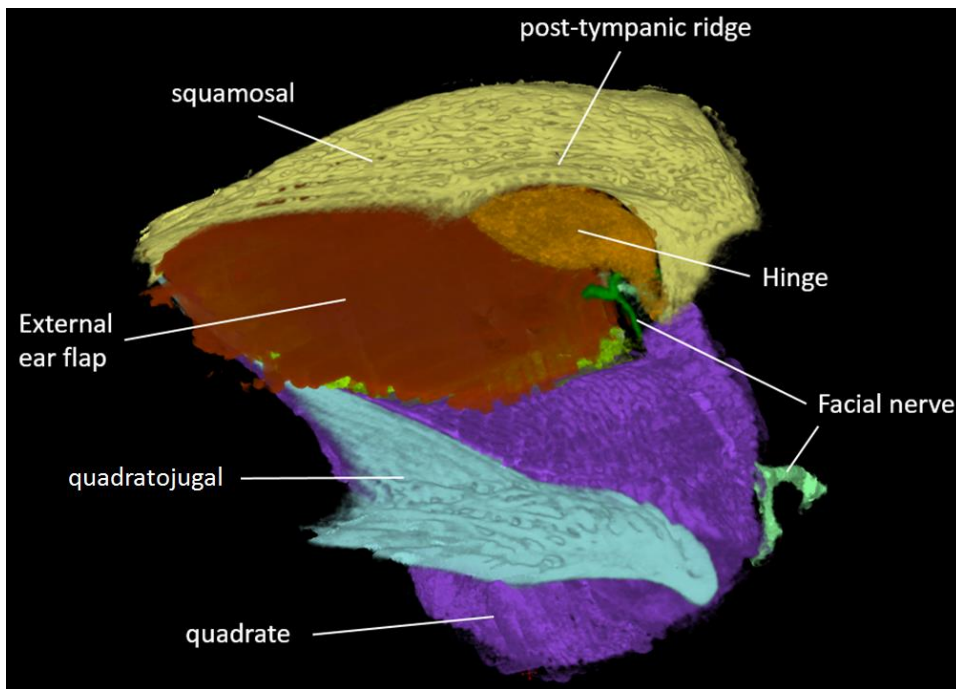Figure 7. CT reconstruction of the temporal region in *Crocodylus niloticus*.

Figure 8. CT reconstruction of the temporal region in *Alligator mississippiensis*.

From the above descriptions from CT scans and a superficial ear dissection of modern crocodylians, we believe that we can identify the groove along the ventral surface of the squamosal posterolateral ridge as the attachment site for the superior ear flap (including the auricular plate); the post-tympanic ledge as location of the hinge tissue that connects the levator and depressor auriculae muscles controlling the superior ear flap; the otic aperture encircled by the squamosal and the quadrate as the area covered by the tympanic membrane; and the quadratojugal as a possible attachment site for the inferior ear flap.

Comparison of the temporal regions in CT scans of Mesozoic fossil pseudosuchians

Saurosuchus galilei (Archosauria: Rauisuchia?)

The squamosal is much shorter in length than those of modern crocodiles and has a much less prominent lateral shelf, though it extends slightly past the posteromedial surface of the skull. The quadrate and quadratojugal are anterodorsally inclined in their attachment to the ventral surface of the squamosal, and the quadrate is much thicker at the anterodorsal end than at the posteroventral end. The quadratojugal is quite short compared to the quadrate and tapers posteroventrally. In the region of the squamosal extending dorsally over the quadrate, there appears to be a deeply convex, almost triangular space, much unlike the disc-like space occupied by the tympanic membrane in modern crocodilians. The post-tympanic ledge appears more as an impression than a deep groove or ridge as in modern crocodylians; therefore, _Saurosuchus_ may not have ear flaps at all, or at least none that were as developed and specialized as in modern crocodylians.
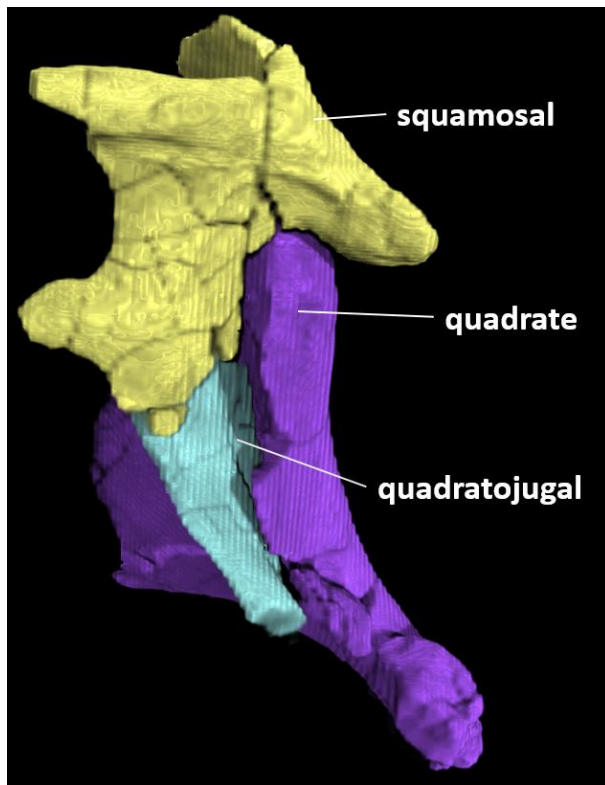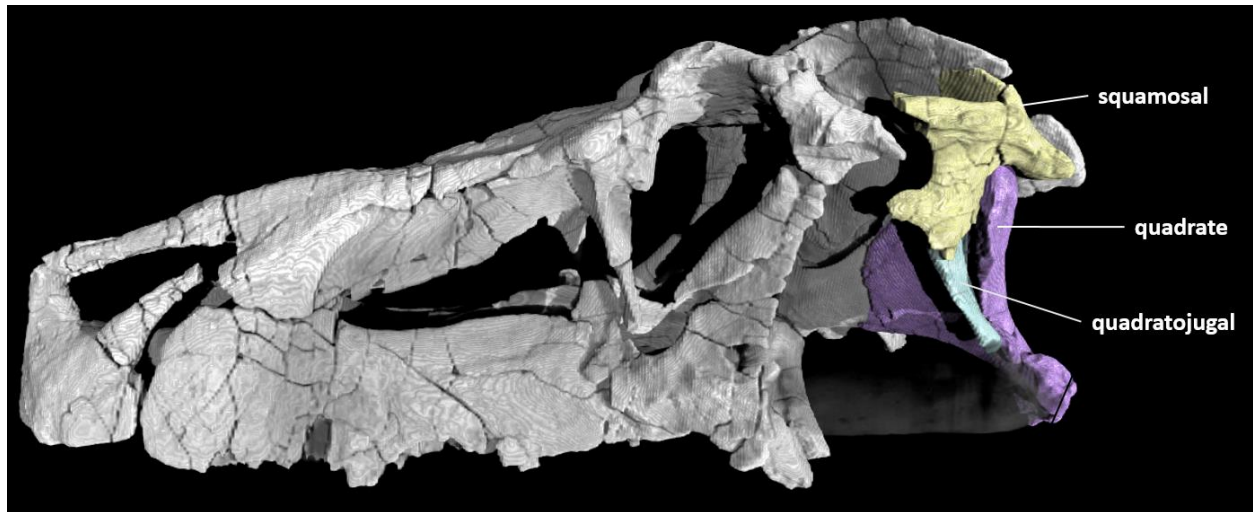
Figure 9 (above). CT scan of *Saurosuchus galilei*, described in Alcober (2000) and retrieved from digimorph.org.

Figure 10 (left). Isolated squamosal, quadrate, and quadratojugal of *Saurosuchus*.

This triangular posterolateral shelf of the squamosal is present in contemporaneous rauisuchians such as *Postosuchus kirkpatricki* (Weinbaum, 2011), *Decuriasuchus quartacolonia* (França, Ferigolo, & Langer, 2011), and *Polonosuchus silesiacus* (formerly *Teratosaurus suevicus*) (Sulej, 2005; Brusatte, Butler, Sulej, & Niedźwiedzki, 2009). While Sterling (2011) places *Saurosuchus* outside of Rauisuchidae in the more basal Loricata, *Saurosuchus* is still considered a rauisuchian by many and will be for the purpose of this study. Weinbaum (2011) proposes that

this may be an apomorphy of all rauisuchians; thus, ear flaps as we understand them may not have been present at all in Rauisuchia.

Specimen YPM 57103, "Popobuddy" (Archosauria: Sphenosuchidae?)

The posteroventral ends of both the squamosal and the quadrate-quadratojugal-jugal complex extend fairly far past the posterior surface of the skull, forming a large cavity in between. The quadrate and quadratojugal are more elongate, thicker at either dorsoventral end. The quadratojugal does not appear to contact the squamosal, but the dorsal end does contact the postorbital. The dorsal end of the quadrate is completely flush with the ventral surface of the squamosal. The post-tympanic ledge is not as unequivocally present as in other pseudosuchians, and the squamosal and quadrate have only one contact point (versus the modern crocodylians and *Simosuchus*, in which two contact points encircle the otic aperture); thus the shape and size of the inferior ear flap and tympanic membrane are uncertain. However, there is a very clear ventrolateral groove along the lateral ridge of the squamosal, which indicates the presence of the superior ear flap.
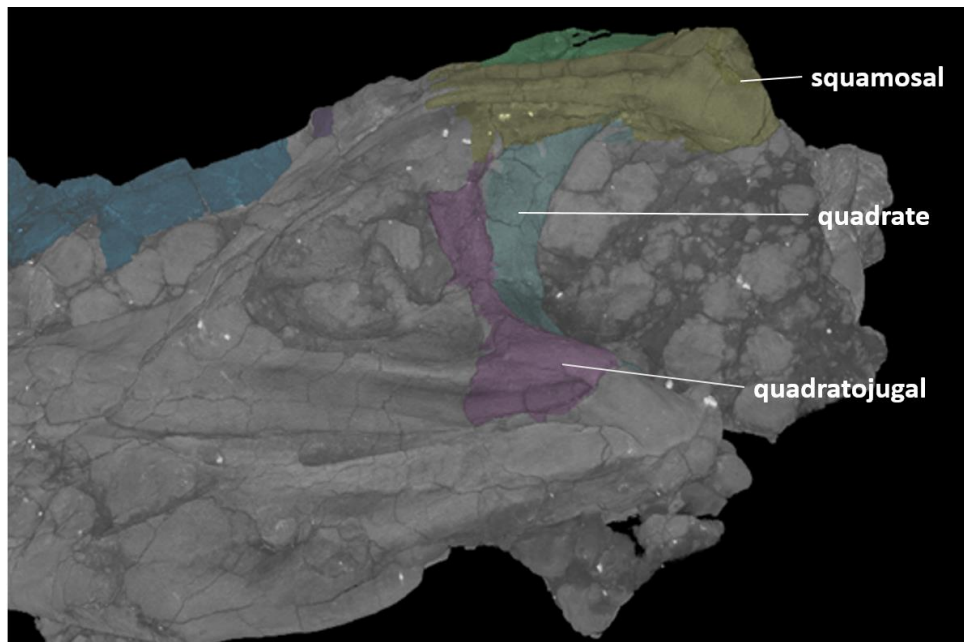

Figure 11. CT scan of "Popobuddy" (YPM 57103).

Other sphenosuchians also appear to have a squamosal overhang forming a spacious cavity, such as in *Sphenosuchus acutus* (Walker, 1990), *Dibothrosuchus elaphros* (Wu & Chatterjee, 1993), and *Terrestrisuchus gracilis* (Sulej, 2005; Brusatte, Butler, Sulej, & Niedźwiedzki, 2009).

Contained within Crocodylomorpha in addition to sphenosuchians are protosuchids, the sister group to Crocodyliformes (Nesbitt, 2011). Protosuchids such as *Orthosuchus stormbergi* (Nash, 1968, 1975) and *Protosuchus haughtoni* (Gow, 2000; Busbey & Gow, 1984) are both noted to have the longitudinal ventral groove of the squamosal as well. Gow (2000) specifically infers the presence of ear flaps in *Protosuchus*, hypothesizing that it may have functioned as physical protection for the tympanic membrane.

Simosuchus clarki (Crocodyliformes: Notosuchia)

The skull of *Simosuchus clarki* is unique amongst pseudosuchians in its downward-oriented snout and overall anteroposterior shortness; relatively speaking, however, the ratio of the size of the temporal bones to the rest of the skull is intermediate between that of *Saurosuchus* and modern crocodilians. The squamosal features a posterolateral extension past the posteromedial surface of the skull like that of *Saurosuchus*, but it also has a much more emphasized ventrolateral groove and post-tympanic ledge. As in modern crocodylians, the squamosal and quadrate make extensive contact with each other and encircle the otic aperture directly ventral to the squamosal groove and post-tympanic ledge. Additionally, the quadratojugal does not contact the squamosal or postorbital at all, but rather tapers anterodorsally ventral to the otic aperture.

As such, *Simosuchus* very likely also had ear flaps, given the deep ventral squamosal groove; a relatively disc-shaped tympanic membrane stretching across the circular otic aperture between the squamosal and quadrate; and an inferior flap inserting onto the quadratojugal, with its laterally sloping position flush against the quadrate. Thus, even though the preorbital portion of the skull of *Simosuchus* is quite derived, the temporal region remains similar in structure to that of modern crocodylians.
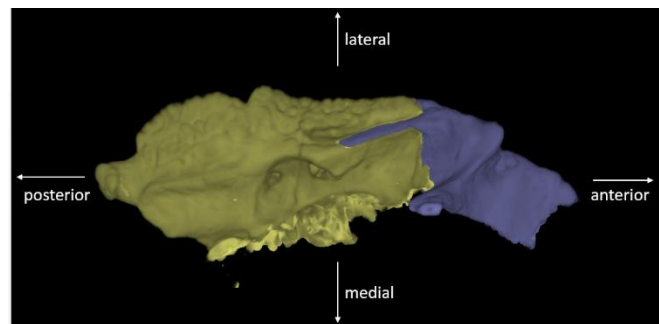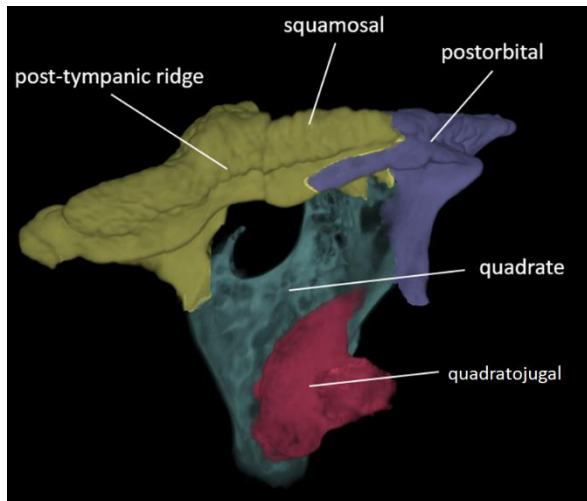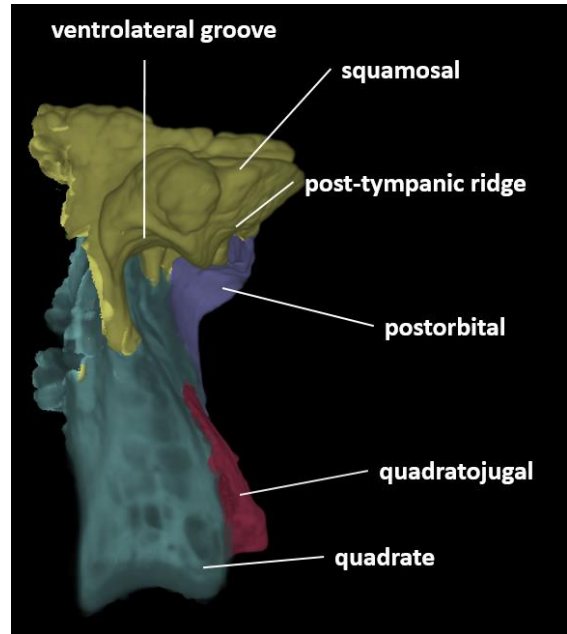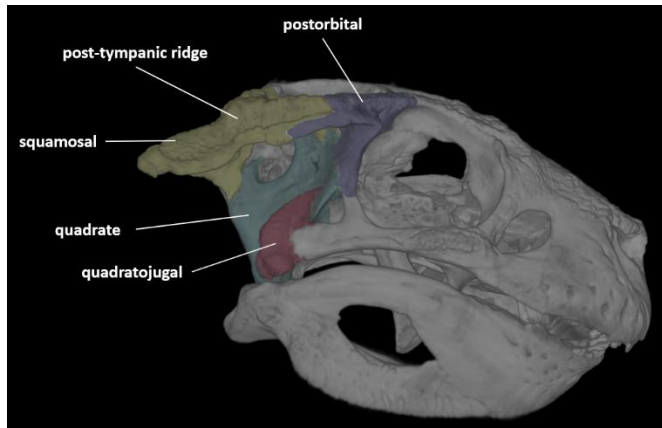
Clockwise from top left:
Figure 12. CT scan of *Simosuchus clarki*, described in Kley et al. (2010); Figure 13. Posterior view of temporal region, showing an unequivocal ventrolateral groove of the squamosal for attachment of the superior ear flap; Figure 14. Ventral view of squamosal and postorbital, showing the depth of the post-tympanic ridge; and Figure 15. Close up of the temporal region of *Simosuchus*.

Contemporaneous with notosuchians such as *Simosuchus* are the neosuchians, which includes modern extant crocodilians; Notosuchia and Neosuchia are both contained within the clade Metasuchia (Bronzati, Montefeltro, & Langer, 2012). It is in Neosuchia that we begin to catch sight of the familiar skull archetype of modern crocodilians: *Sarcosuchus imperator* exhibits the familiar postorbital-parietal-squamosal flattened skull roof with the dorsolaterally-sloping quadrate and quadratojugal bones flush against each other (Sereno et al., 2001); and a specimen of *Rhabdognathus*, which belongs to the sister group Dyrosauridae, specifically is described as having a "long groove for support of the ear-flap muscles" and even preserves a stapes in the otic

recess (Brochu et al. 2002). Both of these specimens are also dated to the Late Cretaceous, but unlike Simosuchus, they are both almost definitely semi-aquatic. The fact that both terrestrial and semi-aquatic crocodylomorphs are exhibiting very similar ear flap-supporting temporal bones at the same time only serves to underline the mystery of the function of ear flaps in terrestrial pseudosuchians.

Thus, we can trace the first appearances of complete ear flaps to the Late Triassic and Early Jurassic in the basal crocodylomorph sphenosuchians, but perhaps not earlier, as evidenced by the skulls of rauisuchians. And at the very least, it appears that the ear flap—or at least, the skeletal structures supporting it—has remained mostly unchanged since at latest the Late Cretaceous with crocodyliformes such as *Simosuchus* and crocodilian-line crocodylomorphs such as *Sarcosuchus*, regardless of other modifications to other skull regions. It is important to note that we are using information from extant crocodilian taxa in the crown clade in order to make extrapolations about soft tissue anatomy in extinct stem pseudosuchians (as opposed to making strictly phylogenetically based inferences); we believe that here, however, the skeletal evidence is robust enough in fossils proximal to the crown clade for us to reach these conclusions (Gauthier, Kluge, & Rowe, 1988; Bryant & Russell, 1992).

Discussion

From the early pseudosuchians of the Late Triassic to modern-day crocodilians, there are a few key trends apparent from this study. Most notably, through time the squamosal shelf elongates anteroposteriorly and deepens medially relative to the rest of the skull, which reflects the structural evolution of the superior ear flap. Additionally, the quadrate and especially the quadratojugal both lengthen and rotate from a vertical to anterodorsally diagonal position, with the quadratojugal nearing the length of the quadrate. This in turn suggests the presence of the inferior ear flap, and it is interesting to consider the evolution of these bones in tandem. There is also the question of whether the two ear flaps co-evolved and occlusion of the flaps was always present, or whether the two flaps evolved separately and came together functionally to protect the tympanic membrane after their initial appearance. Given that the superior ear flap in modern crocodilians is much larger and more mobile in its tissue structure than the inferior ear flap, and

also given that the squamosal is more complex than the quadratojugal throughout pseudosuchian skulls, we tentatively believe that the inferior ear flap evolved secondarily. Quantifying the position of quadratojugal, e.g. its angle relative to the squamosal or its length relative to the quadrate, could be used as a possible test for the presence of the inferior flap in fossil crocodylomorphs. The timing of the appearances of the superior versus the inferior ear flaps may affect implications for the function of ear flaps in terrestrial pseudosuchians, but exactly how is still uncertain.

For future studies, of utmost importance is more broadly applying these bone-tissue correlates to fossil pseudosuchians for a more inclusive survey of skull and ear evolution through time. Specifically, skulls of pseudosuchians found at the transition phase from a terrestrial to aquatic lifestyle should be CT scanned for deeper consideration. Evolving in tandem with the transition to the aquatic lifestyle is the evolution and proliferation of dome pressure receptors along the anterolateral rim of both jaws; as each dome is innervated by the trigeminal nerve (Soares, 2002), there is a corresponding foramen for every dome in the crocodilian skull that can serve as a quantifiable indicator for this transition. It would be interesting to also conduct comparative analyses of the temporal region of crocodylomorphs such as thalattosuchians—although fully aquatic, living in marine environments, and only distantly related to other aquatic crocodilian lineages—and investigate the possibility of homologous or convergently-evolved ear flaps. As fossil material of these Jurassic pseudosuchians is relatively more abundant, there are correspondingly more CT scans available as well as more research into their braincases and sensory anatomy (Pierce, Angielczyk, & Rayfield, 2009; Brusatte et al., 2016; Pierce, Williams, & Benson, 2017). In addition to studying more fossil taxa, more CT scan data of modern crocodilians, especially those of adults, would be useful in studying the ontogeny of these structures in order to better understand tissue and bone growth postnatally.

One avenue of research methods that was not included in this thesis project, but that will be certainly pursued in future studies, is that of observing development and gene expression in crocodilian embryos. Perhaps unsurprisingly, literature concerning crocodilian embryology, never mind that which focuses on the temporal skull region, is also quite sparse. Interestingly, Shute and Bellairs (1955) state that F. H. Edgeworth in 1935 describes the levator and depressor auriculae muscles as being derived from the depressor manibulae muscle. Earlier papers, which mostly focus on the development of the pharyngeal arches, do not make any reference to any of

these muscles, nor do they describe any superficial ear tissues at all; although, the development of the inner ear (e.g. stapedial processes) as well as that of the bones of the temporal region are discussed at some length (Parker, 1883; Meek, 1911).

Decades later, there have been two major overviews of crocodilian development. Peterka et al. (2010) study the development of *Crocodylus niloticus niloticus*, but give no attention to the development of the ear tissues or the bones of the temporal skull region. Iungman, Piña, and Siroski (2008) on the other hand do make some observations of the development of auricular features: they note of the appearance of the external auditory meatus, of its underlying ossification, and then of the growth of the ear flap around it. All of this occurs in roughly the first third of incubation. However, they do not describe the formations, much less the underlying mechanisms behind them, of these structures at all. A related issue concerns the actual innervation of the ear flap muscles: we propose that the nerves found in the dissection and CT scans belong to the facial nerve, but further observation is needed to verify this. Currently the only study of crocodilian skull innervation focuses on the trigeminal nerve (Leitch & Catania, 2012), but perhaps the methodology could be replicated for future experiments to discover the anatomy of the facial nerve in crocodilians. In terms of the genetics of development, a study by Tokita, Chaeychomsri, and Siruntawineti (2013) has identified two genes, *Runx2* and *Msx2*, as key effectors of morphological variation in the ossification of the temporal region of reptilian skulls. While these genes may not play a direct role in the soft tissues, musculature, and innervation associated with the temporal region in crocodilians, still it is important and interesting to understand the underlying bones supporting those structures.

Summary

This thesis investigated the anatomy of the superficial ear flap in modern crocodilians through the dissection of the temporal skull region of a juvenile specimen of *Alligator mississippiensis* in order to elucidate and add to existing literature, as well as using CT scans of young modern crocodilians (*Alligator mississippiensis* and *Crocodylus niloticus*) to reconstruct virtual 3D volumes of the soft and hard tissue structures that were more difficult to visualize in life. From establishing methods to align skeletal with soft tissue structures as described below, we then applied these methods to a handful of fossil pseudosuchian taxa (*Saurosuchus galilei*,

Popobuddy, and *Simosuchus clarki*), using CT scans of their skulls. Thus, we were able to imagine reconstructions of possible ear flap structures, or the lack thereof, in these ancient organisms.

We have identified the following bone-tissue correlates and relationships regarding the structure of pseudosuchian superficial ear flaps: the dorsal end of the superior ear flap (and auricular plate) inserts anteroposteriorly along the length of the ventrolateral groove of the squamosal, extending posteroventrally; the newly-described post-tympanic ridge at the posterolateral rim of the squamosal, which overhangs the hinge, which in turn is directly connected to the depressor and levator auriculae muscles that operate the superior ear flap, as well as the auricular plate itself; the squamosal-quadrate surface contact that supports the correspondingly-shaped tympanic membrane directly dorsal to it; and the quadratojugal with the positioning—although not necessarily the attachment, as in the case of the superior ear flap—of the inferior ear flap relative to the tympanic membrane. We also hypothesize that the superior ear flap is innervated by the facial nerve.

Using the bone-tissue correlates, we believe we can hypothesize the existence or lack of ear flaps in prehistoric pseudosuchians, thereby giving us the ability to approximate the appearance and evolution of this structure in the fossil record. It is clear to us that this structure evolved in terrestrial pseudosuchians, rudimentarily in the Late Triassic and Early Jurassic sphenosuchians and fully recognizable in its modern form by the Late Cretaceous metasuchians. The function of the ear flap and evolutionary pressures acting its formation in terrestrial pseudosuchians, however, remains a mystery that is yet to be solved. Given that the ear flap clearly evolved and persisted in terrestrial pseudosuchians before their secondary return to the water, what is needed, above all, is a reconsideration of existing hypotheses about the precondition of the aquatic habitus in the evolution of the ear flap in modern crocodilians.

References Cited

1. Alcober, O. (2000). Redescription of the skull of *Saurosuchus galilei* (Archosauria: Rauisuchidae). *Journal of Vertebrate Paleontology, 20*(2): 302–316.

2. Brochu, C. A., Bouaré, M. L., Sissoko, F., Roberts, E. M., & O'Leary, M. A. (2002). A dyrosaurid crocodyliform braincase from Mali. *Journal of Paleontology, 76*(6): 1060–1071.

3. Bronzati, M., Montefeltro, F. C., & Langer, M. C. (2012). A species-level supertree of Crocodyliformes. *Historical Biology, 24*(6): 1–9.

4. Brusatte, S. L., Butler, R. J., Sulej, T., & Niedźwiedzki, G. (2009). The taxonomy and anatomy of rauisuchian archosaurs from the late Triassic of Germany and Poland. *Acta Palaeontologica Polonica, 54*(2): 221–230.

5. Brusatte, S. L., Muir, A., Young, M. T., Walsh, S., Steel, L., & Witmer, L. M. (2016). The braincase and neurosensory anatomy of an early Jurassic marine crocodylomorph: Implications for crocodylian sinus evolution and sensory transitions. *The Anatomical Record, 299*(11): 1511–1530.

6. Bryant, H. N. & Russell, A. P. (1992). The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philosophical Transactions of the Royal Society of London B, 337*: 405–418.

7. Busbey, A. B. III & Gow, C. (1984). A new protosuchian crocodile from the Upper Triassic Elliot Formation of South Africa. *Palaeontologia Africana, 25*: 127–149.

8. Dooling, R. J. & Therrien, S. C. (2012). Hearing in birds: What changes from air to water. In A. N. Popper & A. Hawkins (Eds.), *The Effects of Noise on Aquatic Life* (77–82). New York, NY: Springer.

9. França, M. A. G., Ferigolo, J., & Langer, M. C. (2011). Associated skeletons of a new middle Triassic "Rauisuchia" from Brazil. *Naturwissenschaften, 98*: 389–395.

10. Fleming, G. J. & Fontenot, D. K. (2015). Crocodilians (crocodiles, alligators, caiman, gharial). In R. E. Miller & M. E. Fowler (Eds.), *Fowler's Zoo and Wild Animal Medicine, Volume 8* (38–49). St. Louis, Missouri: Saunders, Elsevier Inc.

11. Garrick, L. D. & Saiff, E. I. (1974). Observations on submergence reflexes of *Caiman sclerops*. *Journal of Herpetology, 8*(3): 231–235.

12. Gauthier, J., Kluge, A. G., & Rowe, T. (1988). Amniote phylogeny and the importance of fossils. *Cladistics 4*: 105–209.

13. Gauthier, J. A., Nesbitt, S. J., Schachner, E. R., Bever, G. S., & Joyce, W. G. (2011). The bipedal stem crocodilian *Poposaurus gracilis*: Inferring function in fossils and innovation in archosaur locomotion. *Bulletin of the Peabody Museum of Natural History, 52*(1): 107–126.

14. Gow, C. E. (2000). The skull of *Protosuchus haughtoni*, an early Jurassic crocodyliform from southern Africa. *Journal of Vertebrate Paleontology*, *20*(1): 49–56.

15. Higgs, D., Brittan-Powell, E., Soares, D., Souza, M., Carr, C., Dooling, R., & Popper, A. (2002). Amphibious auditory responses of the American alligator (*Alligator mississipiensis*). *Journal of Comparative Physiology A, 188*(3): 217–223.

16. Iordansky, N. N. (1973). The skull of the Crocodylia. In C. Gans (Ed.), *Biology of the Reptilia, Volume 4, Morphology A* (201–262). London, England, United Kingdom: Academic Press.

17. Iungman, J., Piña, C. I., & Siroski, P. (2008). Embryological development of *Caiman latirostris* (*Crocodylia: Alligatoridae*). *Genesis, 46*(8): 401–417.

18. Kastelein, R. A., Dubbeldam, J. L., de Bakker, M. A. G., & Gerrits, N. M. (1996). The anatomy of the walrus head (*Odobenus rosmarus*). Part 4: The ears and their function in aerial and underwater hearing. *Aquatic Mammals, 22*(2): 95–125.

19. Kley, N. J., Sertich, J. J. W., Turner, A. H., Krause, D. W., O'Connor, P. M., & Georgi, J. A. (2010). Craniofacial morphology of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology, 30*(1): 13–98.

20. Leitch, D. B. & Catania, K. C. (2012). Structure, innervation and response properties of integumentary sensory organs in crocodilians. *Journal of Experimental Biology, 215*: 4217–4230.

21. Meek, A. (2011). On the morphogenesis of the head of the crocodile (*Crocodilus porosus*). *Journal of Anatomy and Physiology, 45*(Pt. 4): 357–377.

22. Miall, L. C. (1878). *The Skull of the Crocodile: A Manual for Students*. London, England, United Kingdom: MacMillan and Co.

23. Montefeltro, F. C., Andrade, D. V., & Larsson, H. C. E. (2016). The evolution of the meatal chamber in crocodyliforms. *Journal of Anatomy, 228*(5): 838–863.

24. Mook, C. C. (1921). Skull characters of recent crocodilia, with notes on the affinities of the recent genera. *Bulletin of the American Museum of Natural History, 44*: 123–268.

25. Nash, D. (1968). A crocodile from the Upper Triassic of Lesotho. *Journal of Zoology, 156*: 163–179.

26. Nash, D. S. (1975). The morphology and relationships of a crocodilian, *Orthosuchus stormbergi*, from the upper Triassic of Lesotho. *Annals of the South African Museum, 67*(7): 227–329.

27. Parker, W. K. (1883). On the structure and development of the skull in the Crocodilia. *Transactions of the Zoological Society, 11*(9): 263–310.

28. Peterka, M., Yves Sire, J., Hovorakova, M., Prochazka, J., Fougeirol, L., Peterkova, R., & Viriot, L. (2010). Prenatal development of *Crocodylus niloticus niloticus*. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution, 314B*: 353–368.

29. Pierce, S. E., Angielczyk, K. D., & Rayfield, E. J. (2009). Shape and mechanics in thalattosuchian (Crocodylomorpha) skulls: Implications for feeding behaviour and niche partitioning. *Journal of Anatomy, 215*: 555–576.

30. Pierce, S. E., Williams, M., & Benson, R. B. J. (2017). Virtual reconstruction of the endocranial anatomy of the early Jurassic marine crocodylomorph *Pelagosaurus typus* (Thalattosuchia). *PeerJ 5*:e3225.

31. Sadé, J., Handrich, Y., Bernheim, J., & Cohen, D. (2009). Pressure equilibrium in the penguin middle ear. *Acta Oto-Layngologica, 128*(1): 18–21.

32. Sereno, P. C., Larsson, H. C. E., Sidor, C. A., & Gado, B. (2001). The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science, 294*: 1516–1519.

33. Shute, C. C. D. & Bellairs, A. d'A. (1955). The external ear in Crocodilia. *Journal of Zoology, 124*(4): 741–749.

34. Soares, D. (2002). Neurology: An ancient sense organ in crocodilians. *Nature, 417*: 241–242.

35. Sterling, N. (2011). The early evolution of archosaurs: Relationships and the origin of major clades. *Bulletin of the American Museum of Natural History, 352*: 1–292.

36. Sulej, T. (2005). A new rauisuchian reptile (Diapsida: Archosauria) from the late Triassic of Poland. *Journal of Vertebrate Paleontology, 25*: 78–86.

37. Tokita, M., Chaeychomsri, W., & Siruntawineti, J. (2013). Skeletal gene expression in the temporal region of the reptilian embryos: Implications for the evolution of reptilian skull morphology. *SpringerPlus, 2*(336): 1–20.

38. Tsuihiji, T. (2005). Homologies of the *transversospinalis* muscles in the anterior presacral region of Sauria (crown Diapsida). *Journal of Morphology, 263*: 151–178.

39. Walker, A. D. (1990). A revision of *Sphenosuchus acutus* Haughton, a crocodylomorph reptile from the Elliot Formation (late Triassic or early Jurassic) of South Africa. *Philosophical Transactions: Biological Sciences, 330*(1256): 1–120.

40. Wartzok, D. & Ketten, D. R. (1999). Marine mammal sensory systems. In J. Reynolds & S. Rommel (Eds.), *Biology of Marine Mammals* (117-175). Washington D.C.: Smithsonian Institution Press.

41. Weinbaum, J. C. (2011). The skull of *Postosuchus kirkpatricki* (Archosauria: Paracrocodyliformes) from the Upper Triassic of the United States. *PaleoBios, 30*(1): 18–44.

42. Wever, E. J. (1978). *The Reptile Ear*. Princeton, NJ: Princeton University Press.

43. Wu, X-C. & Chatterjee, S. (1993). *Dibothrosuchus elaphros*, a crocodylomorph from the Lower Jurassic of China and the phylogeny of the Sphenosuchia. *Journal of Vertebrate Paleontology, 13*(1): 58–89.