

THE BRAINCASE OF *YOUNGINA CAPENSIS* (REPTILIA, DIAPSIDA): NEW INSIGHTS FROM HIGH-RESOLUTION CT SCANNING OF THE HOLOTYPE

Nicholas M. Gardner, Casey M. Holliday, and F. Robin O'Keefe

Nicholas M. Gardner. Department of Biological Sciences, Marshall University, Huntington, West Virginia.
nick.gardner@gmail.com

Casey M. Holliday. Department of Pathology & Anatomical Sciences, University of Missouri, Columbia,
Missouri. hollidayca@health.missouri.edu

F. Robin O'Keefe. Department of Biological Sciences, Marshall University, Huntington, West Virginia.
okeefef@marshall.edu

ABSTRACT

Detailed descriptions of braincase anatomy in early diapsid reptiles have been historically rare given the difficulty of accessing this deep portion of the skull, because of poor preservation of the fossils or the inability to remove the surrounding skull roof. Previous descriptions of the braincase of *Youngina capensis*, a derived stem-diapsid reptile from the Late Permian (250 MYA) of South Africa, have relied on only partially preserved fossils. High resolution X-ray computed tomography (HRXCT) scanning, a new advance in biomedical sciences, has allowed us to examine the reasonably complete braincase of the holotype specimen of *Youngina capensis* for the first time by digitally peering through the sandstone matrix that filled the skull postmortem. We present the first detailed 3D visualizations of the braincase and the vestibular system in a Permian diapsid reptile. This new anatomical description is of great comparative and phylogenetic relevance to the study of the structure, function and evolution of the reptilian head.

KEY WORDS: *Youngina capensis*, diapsid reptiles, CT scanning, 3D models

NOTE IN PROOF

Reisz et al. (2010) find a non-diapsid position for *Apsisaurus* as a varanopid synapsid, but unfortunately, their paper came too late for us to correct Figure 1 by removing it from our tree. We are aware that our placement in the tree for *Apsisaurus* is outdated, this is the unfortu-

nate nature of shifting topologies as new data are incorporated. However, our tree was taken from Müller (2003) who noted that the exclusion of *Apsisaurus* from his data set does not affect the rest of the tree topology in the final analysis.

PE Article Number: 13.3.19A

Copyright: Palaeontological Association November 2010

Submission: 14 September 2009. Acceptance: 8 September 2010

INTRODUCTION

Reptiles first appeared in the fossil record during the Late Carboniferous (320-310 MYA) and rapidly diversified into two different lineages, the parareptiles and the eureptiles (Müller 2003; Figure 1). The earliest known examples are Carboniferous eureptiles such as *Hylonomus* (Carroll 1988a) and *Petrolacosaurus* (Reisz 1977; Reisz 1981). Parareptiles and eureptiles further diversified into numerous clades, of which only the diapsid eureptiles survived past the Triassic and into modern times (archosaurs, lepidosaurs and turtles). The precise relationships among extant reptile clades remain a problem for reptile biologists and paleontologists. For example, turtles have become consensually accepted among reptile paleontologists as being diapsids, but it is uncertain whether or not they are part of the crown-diapsid clade (Gregory 1946; Ivachnenko 1987; Kordikova 2002; Laurin and Reisz 1995; Lee 1997; Lee 2001; Lyson et al. 2010; Werneburg and Sánchez-Villagra 2009), or if they are crown-diapsids, whether or not they are closer to archosaurs (Bhullar and Bever 2009; Evans 2009; Hedges and Poling 1999; Zardoya and Meyer 1998) or lepidosaurs (Bickelmann et al. 2009; deBraga and Rieppel 1997; Li et al. 2008; Müller 2003; Rieppel 2002; Rieppel and deBraga 1996; Rieppel and Reisz 1999). Though conflicting data from molecular studies, soft-tissue morphology and bony morphology provide differing supports for the position of turtles (Lee 2001; Rieppel 2002), a more detailed understanding of the anatomy of early diapsids and other morphologically primitive reptiles would provide much-needed resolution to this disputed portion of the amniote phylogeny, and contribute to a new understanding of the evolutionary history of reptiles and the relationships between extant diapsids (Modesto and Sues 2002).

The Late Permian (250 MYA) diapsid reptile *Youngina capensis* is often regarded as the 'archetypal' basal diapsid (Smith and Evans 1996) and recognized as an "ancestral morphotype" (Carroll 1988b) between more primitive taxa such as parareptiles and captorhinids and modern diapsids (Müller 2003; Figure 1). Its relationships among other diapsids have been disputed. Currie (1981, 1982) posited that *Youngina* shared a closer relationship with *Acerosodontosaurus* (Currie 1980), *Galesphyrus* (Carroll 1976), *Hovasaurus* (Currie 1981), *Kenyasaurus* (Harris and Carroll 1977),

Tangasaurus (Currie 1982), and *Thadeosaurus* (Carroll 1981). These taxa collectively were referred to as the Younginiformes, which were variously allied to lepidosauromorphs (Benton 1985; Evans 1988) or as stem-diapsids (Gaffney 1980; Laurin 1991). Their monophyly was never explicitly tested and recently Bickelmann et al. (2009) published the results of their phylogenetic analysis that suggested that these taxa do not form a monophyletic relationship with each other to the exclusion of other diapsid reptiles, though the relationships between all stem-diapsids were highly unresolved in their topology. *Youngina* is the most derived known stem-diapsid to retain two complete fenestrae in the temporal region, rather than having evolved this condition secondarily (as in derived archosauromorphs and sphenodontids and possibly as in sauropterygians and ichthyopterygians). Thus it appears that the loss of the lower temporal bar occurred in higher stem-diapsids more derived than *Youngina* (Müller 2003). *Youngina* is well known from numerous specimens that were previously described as distinct "younginid" or "younginiform" taxa (Gow 1975). Despite its obviously critical position as a stem-diapsid and the existence of multiple specimens, *Youngina* is in need of a thorough re-description. Formal description of its anatomy is a crucial precursor to understanding: 1) its phylogenetic relationships, 2) its relevance to the interrelationships between other diapsid reptiles and 3) the evolution of the skull in these reptiles (Bickelmann et al. 2009; Modesto and Sues 2002).

The first discussion of the braincase of *Youngina* was carried out by Olsen (1936), who described UC 1528, the holotype of *Youngoides romeri*. He was limited to observations of the superficial anatomy of the skull, and described it largely in palatal and occipital views. Gow (1975) provided a preliminary discussion of the braincase of TM 3603, which was given more attention later by Evans (1987). Evans sawed this specimen in half to gain access to the internal aspects of the neurocranial bones. Her description is currently the only published, detailed treatment of the braincase of *Youngina*.

While all reptiles (and in fact, all amniotes) ossify the caudoventral portion of the braincase cartilages, ossification patterns differ for the rostral cartilages. Archosauriforms (birds, crocodiles and their ancestors) have uniquely ossified the pila antotica as the laterosphenoid, which encloses the

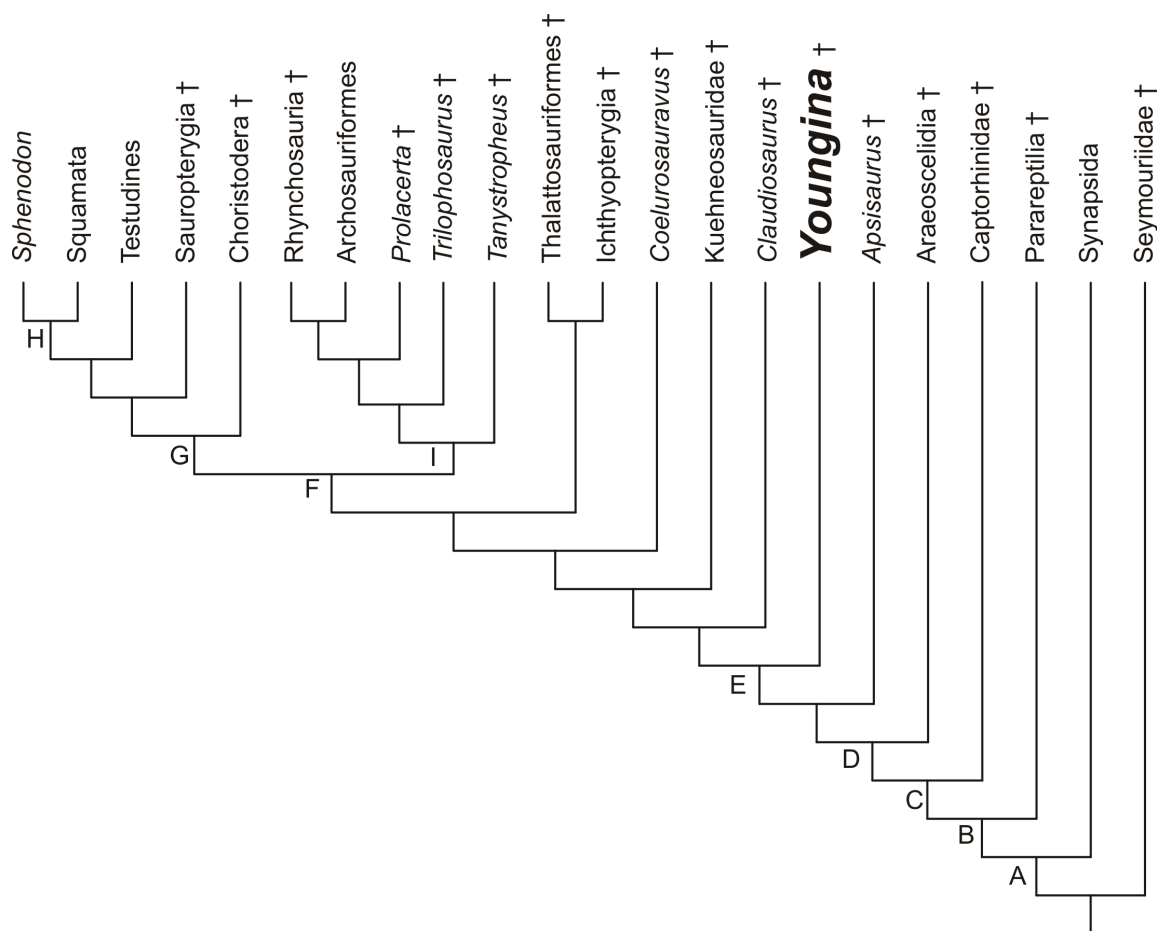


FIGURE 1. Cladogram demonstrating the evolutionary relationships between *Youngina* with other reptile taxa (modified from Müller 2003). Dagger denotes extinct taxa. Nodes: A, Amniota; B, Reptilia; C, Eureptilia; D, Diapsida; E, Neodiapsida; F, Sauria; G, Lepidosauromorpha; H, Lepidosauria; I, Archosauromorpha.

rostral region of the cavum cranii (Clark et al. 1993). Turtles ossify the pila antotica adjoining to the clinoid process of the basisphenoid, similar to the condition found in captorhinids, sauropterygians and many other primitive reptiles, though the clinoid process is much taller in turtles leaving the rostral braincase largely open (Rieppel 1993) and the pila antotica may have also ossified into an archosauriform-like paired “laterosphenoids” primitively in turtles (*Proganochelys*: Bhullar and Bever 2009; *Kayentachelys*: Gaffney and Jenkins 2010), though some parareptiles (pareiasaurs) have a similar ossification (Lee 1997). Some lepidosaurs have a prominently ossified rostral expansion of the prootic (i.e., the alar process) which partially closes the braincase wall rostrally (Rieppel 1993). For taxa in which the cavum cranii is extensively enclosed by bone, it is possible to reconstruct the gross shape of the endocranium and understand

how it relates to the sensory organs and their associated neurology; for poorly ossified taxa, however, such reconstruction is much more difficult (Hopson 1979; Hopson and Radinsky 1980).

Because the braincase of *Youngina* remains buried in matrix, high resolution X-ray computed tomography (HRXCT) provides an excellent tool for imaging this otherwise inaccessible deep cranial region. Several studies have recently shed new light on braincase anatomy using imaging techniques (Clack et al. 2003; Witmer et al. 2008; Holliday and Witmer 2008; Witmer and Ridgely 2009). *Youngina* presents an ideal target for HRXCT scanning and a new description of its skull and braincase anatomy. To that end, the holotype of *Youngina capensis* was successfully scanned, allowing a complete reconstruction of its braincase for the first time.

Institutional Abbreviations. AMNH, American Museum of Natural History, New York; UC, University of Chicago, Illinois; TM, Transvaal Museum, South Africa.

MATERIALS AND METHODS

Youngina Material

All specimens of *Youngina* are known from the Permian *Tropidostoma-Dicynodon* assemblage zones of the Karoo Basin of South Africa. Two of the earliest described specimens are housed in the USA, the holotype of *Y. capensis*, AMNH 5561 (Broom 1914, Broom 1915), and the holotype of *Youngoides romeri*, UC 1528 (Olsen 1936). These specimens were made available on loan to one of the authors (O'Keefe).

HRXCT Scanning and Visualization

Preliminary CT scanning of both specimens in the medical CT scanner at SUNY Stonybrook revealed that only the holotype (AMNH 5561) showed enough differentiation between bone and matrix to justify the expense of HRXCT scanning. The holotype was therefore scanned at Penn State University's Center for Quantitative Imaging on the X-TEK X-ray subsystem (X-ray energy set at 180 kV, 0.500 mA) with a source object distance of 137.771 mm. Within a 43 mm field of reconstruction, 1353, 0.04777 mm thick slices were generated. For each slice, 2400 views were taken with three samples per view. Raw 1024 by 1024 pixel, 16-bit TIFF files were pre-processed using Strip2raw (Nathan Jeffery, University of Liverpool, UK) and then imported into Amira v.4.0 (Visage Imaging, Inc., San Diego) to render 3D images of our HRXCT data and allow segmentation of individual elements as 3D models.

RESULTS AND DESCRIPTION

Figure 2 presents a vortex rendering of the HRXCT scan data. From this rendering it is clear that successful separation between bone and matrix was achieved. However, the skull roof has been extensively damaged during preparation, particularly in the rostrum and mandible. The braincase, however, is preserved in its entirety. It is shown in context in the vortex rendering and is described below.

Anatomy of the Braincase

Supraoccipital. The supraoccipital is a broad, large bone that contacts both the prootic and opisthotic bones on its lateral edges and the exoccipital caudally (Figures 3.1-2, 4). It connects the braincase dorsally to the rest of the skull through contact with the parietals. The supraoccipital bears facets for the postparietals and parietals, but does not show the prominent median or lateral ascending processes that are found in *Captorhinus* (Price 1935) and in placodonts (Rieppel 1995), or the prominent median process found in *Proganochelys* (Gaffney 1990) and *Kayentachelys* (Gaffney and Jenkins 2010). It forms a small portion of the dorsal border of the foramen magnum and covers the caudal portion of the brain dorsally. The right rostralateral portion of the supraoccipital is broken in AMNH 5561, but the supraoccipital is complete UC 1528. Each lateral portion of the supraoccipital encloses a small part of the caudal semicircular canal.

Exoccipital. The exoccipitals form the lateral border of the foramen magnum (Figure 4). Dorsally they extend as triangular processes that approach each other but do not meet medially. The exit for the hypoglossal nerve (CN XII) is present lateral to the foramen magnum within the exoccipital body. The suture between the ventral portion of the exoccipital is distinct from the occipital condyle in UC 1528 and is triangular in shape in dorsocaudal view. There is no distinct suture between the exoccipital and the occipital condyle in AMNH 5561. The exoccipital contributed significantly to the dorsolateral corner of the occipital condyle in *Youngina*.

Basioccipital. The basioccipital forms the ventral border of the foramen magnum, and has a stout main body that supports the brain caudoventrally (Figures 3, 5). The basioccipital has weakly developed basal tubera that lack an extensive bony contact with the parasphenoid caudal processes. The contact between these two elements was likely cartilaginous. The exoccipitals and basioccipital are fused together in AMNH 5561, but a suture is present between the elements in UC 1528. The occipital condyle has a deep notochordal pit.

Basisphenoid. The basisphenoid is an endochondral element that supports the brain ventrally (Romer 1956) (Figures 3.3-4, 4.3-4). In AMNH 5561, the basisphenoid shows no significant differences from the descriptions of TM 3603 made by Evans (1987). The basisphenoid bears small paired foramina for the internal carotid arteries ros-

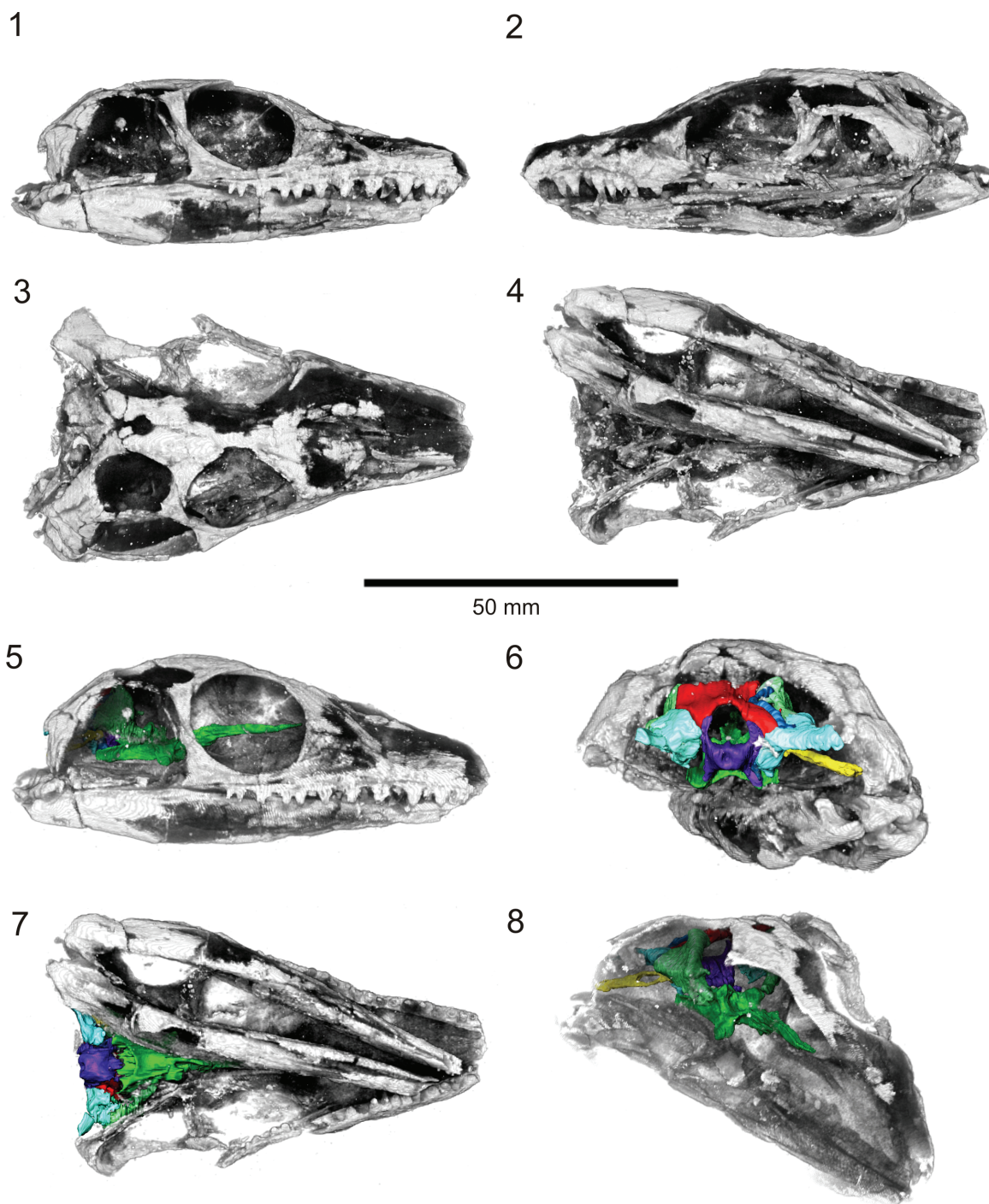


FIGURE 2. Voltex rendering of holotype skull of *Youngina capensis* (AMNH 5561). 1, Right lateral view; 2, Left lateral view; 3, Dorsal view; 4, Ventral View; 5-8, Same respective views with braincase model added. (Abbreviations and color codes in Appendix.)

tral to the sella turcica (or hypophyseal fossa), close to the base of the parasphenoid cultriform process which are not observed in *Hovasaurus* (Currie 1981). The width of the sella turcica is one third that of the rostral portion of the basisphenoid

body. The dorsum sellae separates the sella turcica from the caudal region of the basisphenoid. There is no evidence of an ossified pila antotica, although stout, short clinoid processes are present. The groove for the abducens nerve (CN VI)

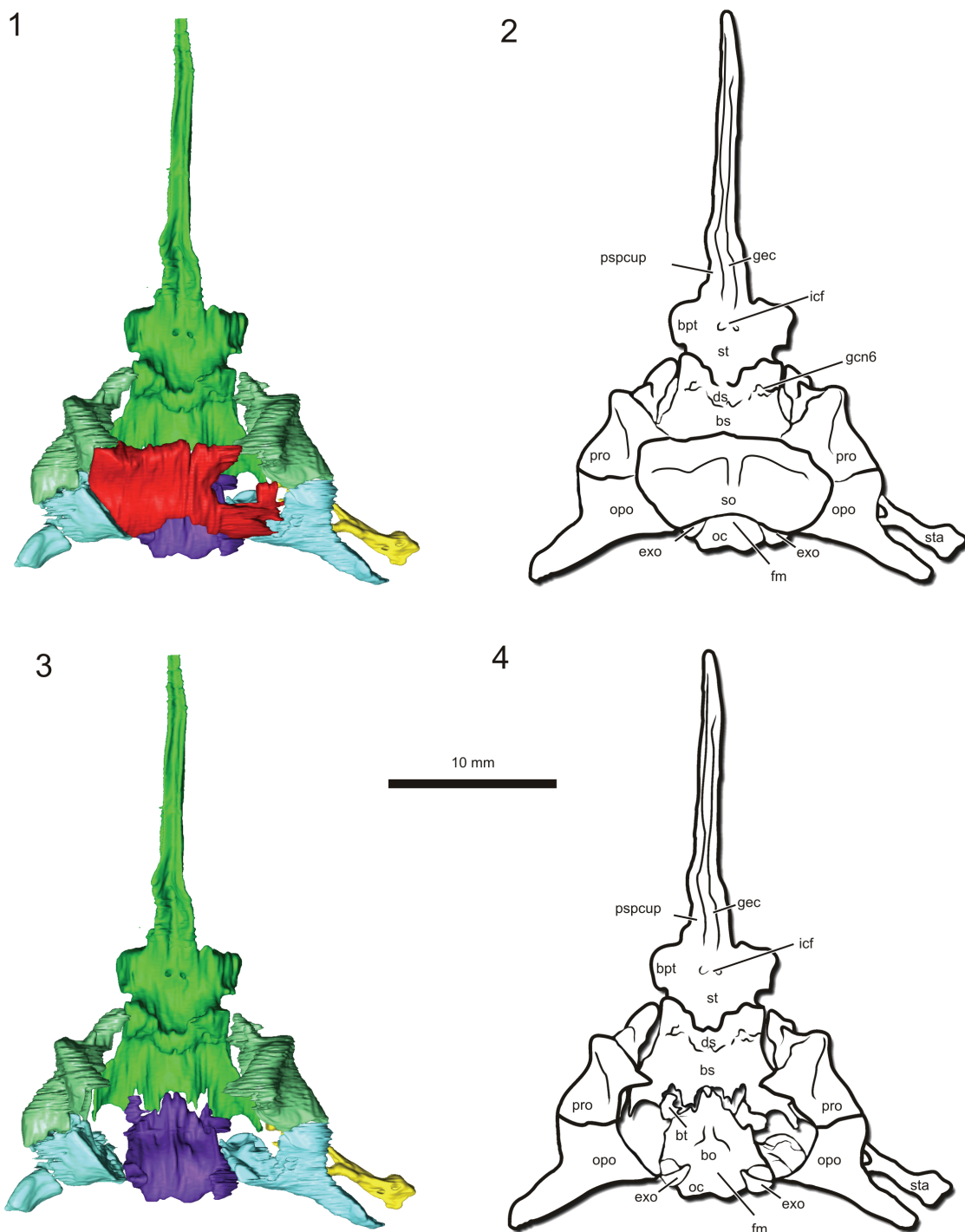


FIGURE 3. Dorsal view of the braincase. 1, Model; 2, Line Drawing; 3-4, Supraoccipital removed to show basicranial floor. (Abbreviations and color codes in Appendix.)

appears to be present on the lateral surface of the dorsum sellae as described by Evans (1987), similar to *Prolacerta* and other early archosauromorphs (Evans 1986). In captorhinids, *Proganochelys* and *Sphenodon*, the abducens nerve pierces the dor-

sum sellae rather than laying in an open groove. Lateral to the dorsum sellae, the clinoid process extends dorsally and contacts the prootic bone ventrally but not the parietal, as in *Proganochelys* (Gaffney 1990). The basiptyergoid has large ros-

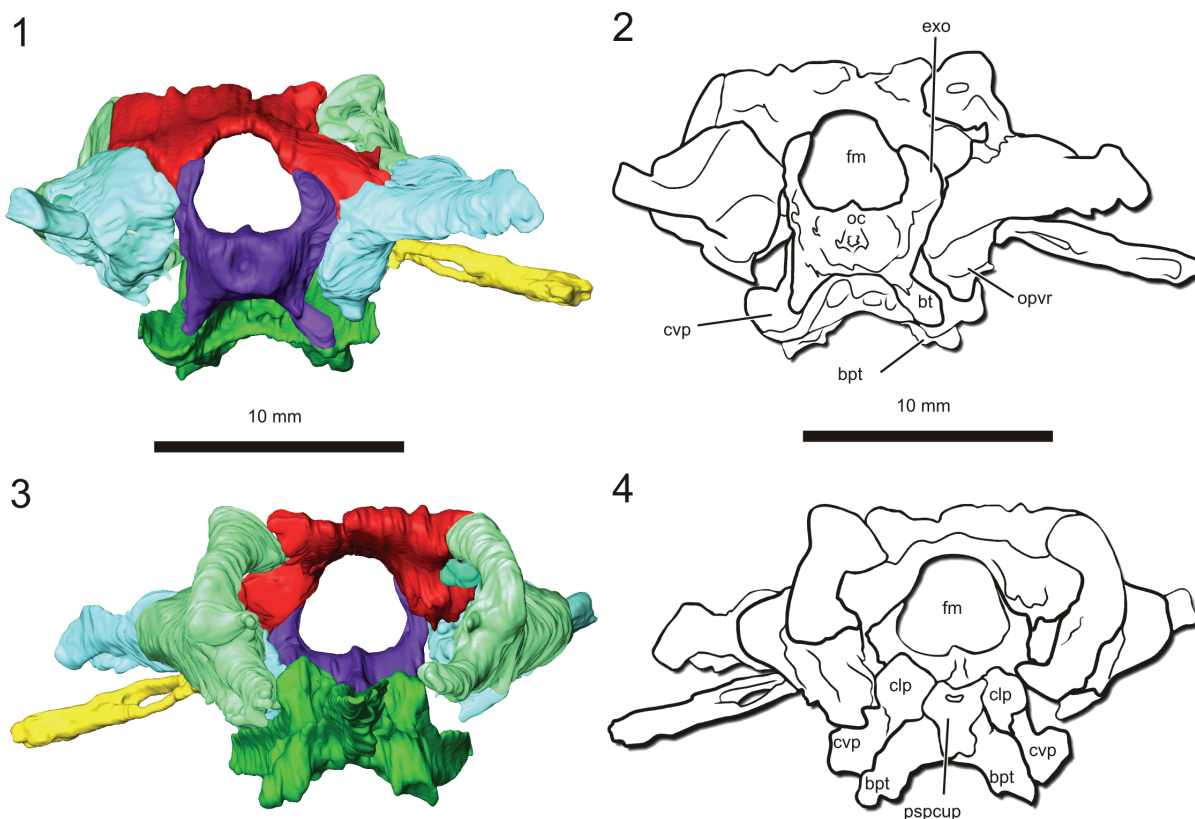


FIGURE 4. Caudal view of the braincase. 1, Model; 2, Line Drawing. Rostral view of the braincase. 3, Model; 4, Line Drawing. (Abbreviations and color codes in Appendix.)

troventral processes (i.e., basiptyergoid processes) that form a broad palatobasal articulation with the pterygoid. These structures are also visible ventrally in UC 1528 (Olsen 1936).

Parasphenoid. The parasphenoid is a dermal element that covers the basisphenoid ventrally and has an elongate cultriform process rostrally that supports ossified trabeculae cranii, producing a V-shaped cross section (Figures 3, 5 and 6). The suture between the parasphenoid and basisphenoid is largely indistinguishable in the HRXCT data, and the two elements have been left the same color in the model. The cultriform process is directed only slightly rostr dorsally, less than 15 degrees from the horizontal plane of the skull. There are small lateral crests on the rostral body of the parasphenoid, which partially enclose the vidian canals (path of the internal carotid artery and palatine ramus of the facial nerve). Evans (1987) reported that the large cultriform process she observed in UC 1528 (as we see in AMNH 5561 via HRXCT data) was not present in TM 3603 despite its large size. She suggested it might not

be ossified, which could imply that its ossification might be variable within *Youngina* as reported for varanids and other lepidosaurs (Bever et al. 2005). The cultriform process extends rostrally to the rostral margin of the orbit as in *Hovasaurus* and *Tangasaurus*. There are no teeth present on the parasphenoid, unlike more primitive reptiles such as *Petrolacosaurus* (Reisz 1981) or kuehneosaurs (Colbert 1970; Evans 2009). The general morphology of the parasphenoid of AMNH 5561 is similar to that of UC 1528 (Evans 1987). The caudal portion of the parasphenoid divides into paired crista ventrolateralis processes (or posterior alar wings) and the caudal margin is deeply concave as in *Petrolacosaurus* (Reisz 1981). These processes do not appear to have contacted the basioccipital tubers through osseous contact; a cartilagenous contact may have been present.

Opisthotic. The opisthotic and prootic enclose most of the vestibular system laterally, but remain unossified medially (Figures 3, 4 and 6). The opisthotic and exoccipitals form the lateral borders of the metotic fissure, the common exit of the jugular

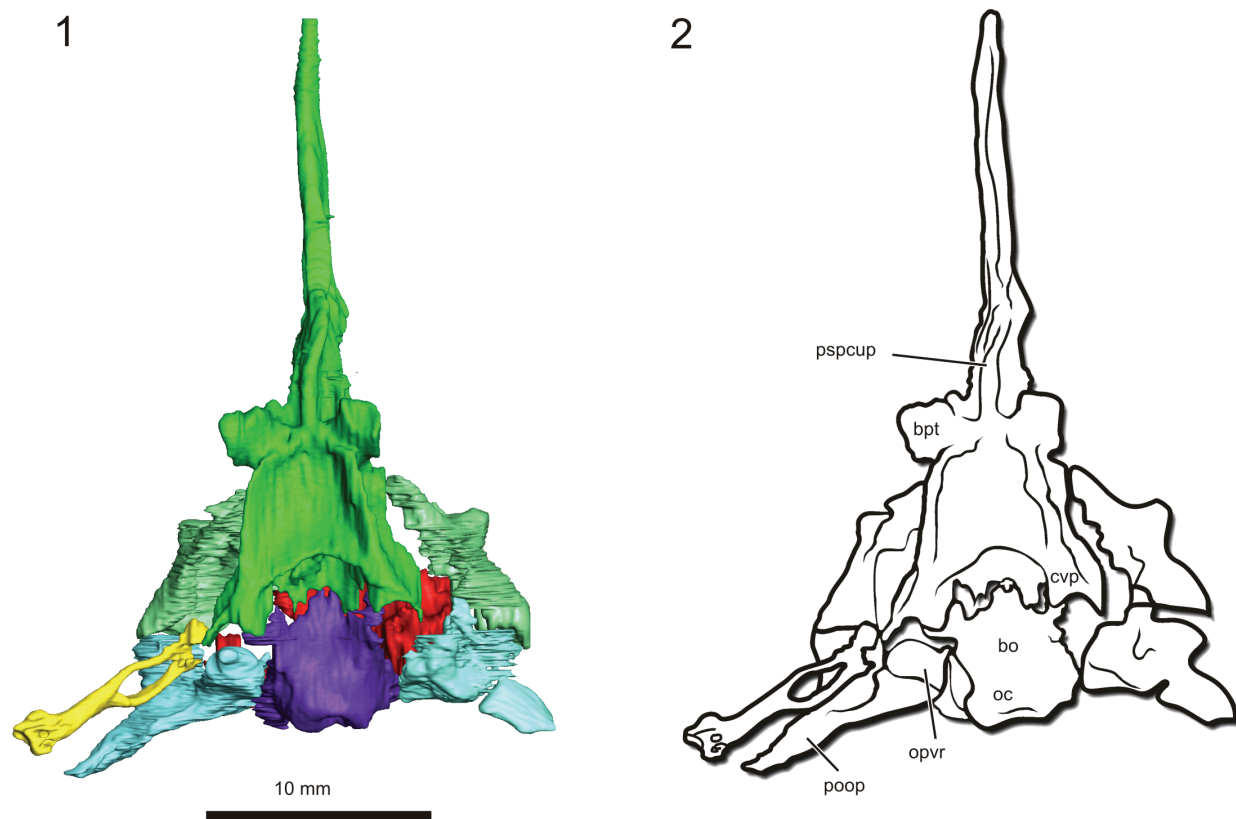


FIGURE 5. Ventral view of the braincase. 1, Model; 2, Line Drawing. (Abbreviations and color codes in Appendix.)

vein, the glossopharyngeal nerve (CN IX) and the vagus nerve (CN X) (Rieppel 1993). The margins of the fenestra ovalis are poorly ossified, with the opisthotic and prootic forming the dorsal portion of the window. Gow (1975) reported that the paroccipital process of the opisthotic articulated with the quadrate in a pocket formed by the supratemporal, similar to the condition in *Proganochelys* (Gaffney 1990). We could not confirm the presence of this pocket; however, the paroccipital processes do contact the quadrate extensively, unlike in some tangasaurids (Evans 1987). The right opisthotic was damaged slightly in its dorsomedial portion by preparation, whereas the left opisthotic is partly damaged by a crack resulting from taphonomic processes. The opisthotic clearly shows a large ventral ramus that contributes to the ossified wall of the braincase.

Prootic. Our HRXCT data confirms many of the characters described by Evans (1987) for the prootic (Figure 3, 4.3-4, 6). On the mediodorsal surface, there is a large subarcuate fossa. However, there does appear to be a small rostral inferior process on the prootic dorsal to rostroventral

contact with the basisphenoid in AMNH 5561. Evans (1987) reported this process as being absent in TM 3603. The dorsal surface of the prootic lacks an extensive contact with the parietal, unlike the condition in turtles. There appears to be a weak ridge ventrally on the rostral ramus contacting the basisphenoid, but there is no prominent expanded crest (as in derived lepidosaurs and archosauromorphs).

Anatomy of the Osseous Labyrinth

Using our HRXCT data, we examined the shape of the osseous labyrinth and stapes in *Youngina* (Figure 7.1-3). It shares a common chamber, with little separation of the tracts of the semicircular canals or the otolithic organs within the prootic and opisthotic. The sacculus likely occupied much of the chamber encased in the opisthotic and prootic, though it is difficult to fully assess the rostral extent of the saccular maculae in the HRXCT data. The caudal portion of chamber is filled by dense metallic precipitates that obscure the precise details of the shape of the saccular maculae. There appears to have been a lagenar (or possibly a postlagenar)

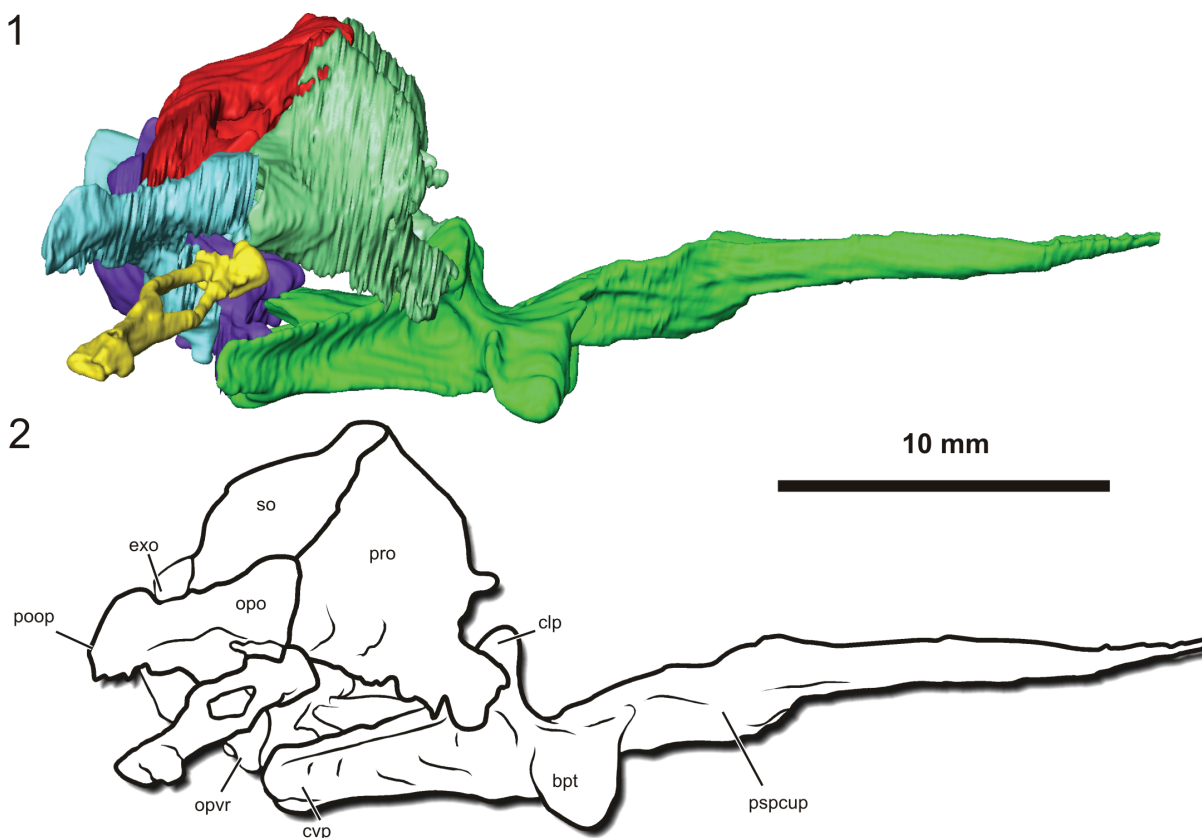


FIGURE 6. Right lateral view of the braincase. 1, Model; 2, Line Drawing. (Abbreviations and color codes in Appendix.)

recess that extended ventrally along the ventral ramus of the opisthotic. The rostral and lateral semicircular canals meet rostrally within the ampullary recess of the prootic. The caudal and lateral semicircular canals meet caudomedially within the recessus utriculi between the supraoccipital and the opisthotic. The rostral and caudal semicircular canals meet dorsal to the sacculus within the superior utriculus. The endolymphatic duct extends medially under the supraoccipital from the main body of the sacculus.

The lateral semicircular canal has the greatest path diameter compared to the other two canals (6.77 mm; rostral semicircular canal: 4.79 mm, caudal semicircular canal: 4.35 mm). However, it does not trend as far laterally as the anterior canal in that the ratio of the length of the path diameter of the canal versus the greatest path radii of the canal is 3.62 compared to 2.01 in the rostral semicircular canal and 2.33 in the caudal semicircular canal. The lateral semicircular canal has a wider diameter than the rostral semicircular canal (1.12 mm compared to 1.05 mm), and the widest preserved portion of the caudal semicircular canal is 1.12 mm.

The lateral and caudal canals are at right angles to each other, while the rostral and caudal canals are oriented at 84 degrees to each other, and the lateral and rostral canals are oriented at 66 degrees to each other.

Anatomy of the Columellar Apparatus

Our HRXCT data set allows examination of the complete stapes (or columella) in *Youngina* for the first time (Figure 7.4-6). In most modern reptiles, the stapes is ossified, while the extrastapes (or extracolumella) is cartilaginous. In *Youngina*, both appear ossified, as in *Sphenodon* and more primitive reptiles. In TM 3603, the left stapes is fragmented, and the right stapes preserves the footplate only (Evans 1987). In AMNH 5561, the right stapes is reasonably complete and appears to be attached to a lateral ossification, which we interpret as the ossified extrastapes. No suture was identified between these elements. The left stapes could not be identified. Evans (1987), Gow (1975) and Olsen (1936) interpreted the stapes in *Youngina* as being slender and rodlike, but Carroll (1981) correctly interpreted it as being a massive

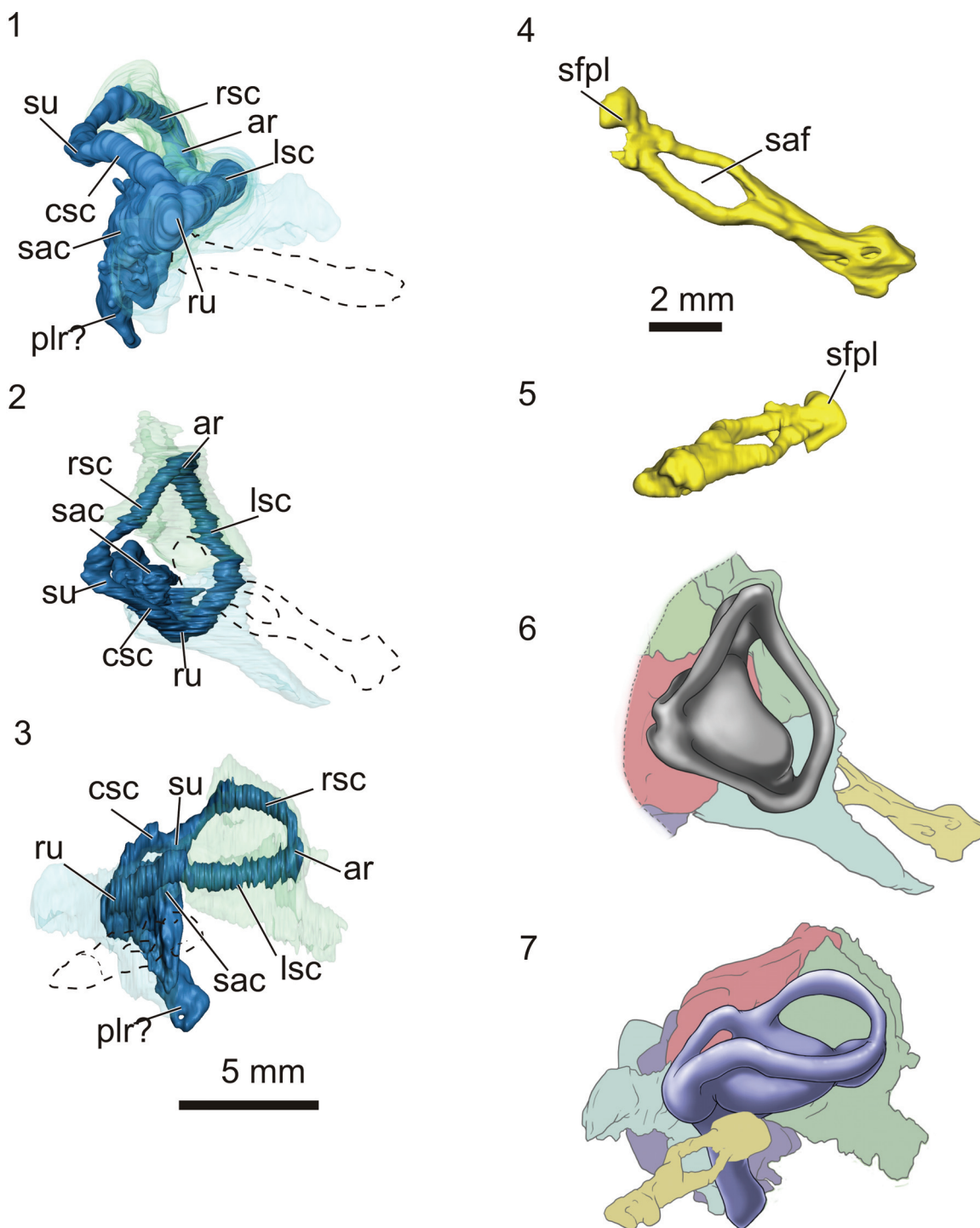


FIGURE 7. Vestibulocochlear organs in *Youngina*. 1, Caudal view; 2, Dorsal view; 3, Right lateral view. Stapes. 4, Dorsal view; 5, Right lateral view. Artist reconstruction of the vestibulocochlear organs. 6, Dorsal view; 7, Right lateral view. (Abbreviations and color codes in Appendix.)

rod, presumably retaining a support function for the dermal skull elements as the stapes contacts the suspensorium medially. There is no evidence of a dorsal process on the stapes, unlike the condition in captorhinids. There is a large stapedial foramen

through which the stapedial artery would have passed, unlike the condition in most modern reptiles in which the stapedial artery passes around the stapes. This is similar to the primitive condition found in captorhinids (Heaton 1979). Gow (1975)

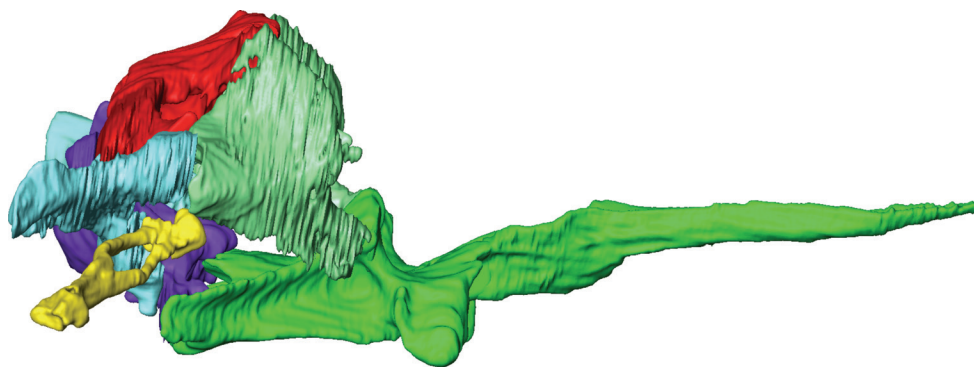


FIGURE 8. Braincase of *Youngina*, 3D model presented as a Quicktime movie (Roll) (see online version for animation). (Abbreviations and color codes in Appendix.)

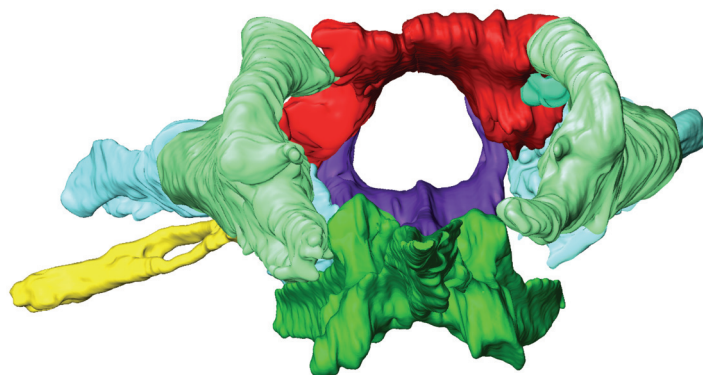


FIGURE 9. Braincase of *Youngina*, 3D model presented as a Quicktime movie (Yaw) (see online version for animation). (Abbreviations and color codes in Appendix.)

described this foramen as medially positioned in the stapes and “bounded by an extremely thin bridge which is bowed slightly outward.” Our data support Gow’s description of the stapedia foramen and the nature of its surrounding bone. It appears that the stapes and an ossified extrastapes were closely articulated without a definite joint, as in *Sphenodon* (Gans and Wever 1976). The extrastapedial portion appears to be pierced laterally by a foramen which could be homologous to Huxley’s foramen, as present in crown-group diapsids (Laurin and Gauthier 2000).

Three-Dimensional Movies

In order to aid visualization of the braincase elements and their manner of articulation, we also present three Quicktime movies that allow rotation of the entire structure in lateral roll (Figure 8) and rostral-caudal yaw (Figure 9). A Quicktime movie of the osseous labyrinth with its surrounding bones depicted transparently is presented in Figure 10.

DISCUSSION

Comparisons between the Braincase of *Youngina* and Other Reptiles

In many Permo-Triassic higher stem-diapsids, the neurocranial anatomy is not well-known or well-described; however, *Youngina* shows many plesiomorphic conditions. For example, it compares well with captorhinids in the presence of a large, open and poorly ossified fenestra ovalis. Further, the basioccipital tubers are weakly developed unlike the elongated tubera found in *Sphenodon* and the archosauromorphs, the occipital condyle is kidney-shaped unlike the hemispherical condyle in archosauriforms, the paroccipital processes are not dorsoventrally expanded in posterior view unlike in squamates and archosauriforms. The open vidian canal on the basisphenoid and lack of fusion between the opisthotic and exoccipitals also distinguish it from squamates. The stapes is intermediate between captorhinids and more derived reptiles in being relatively slender and lack-

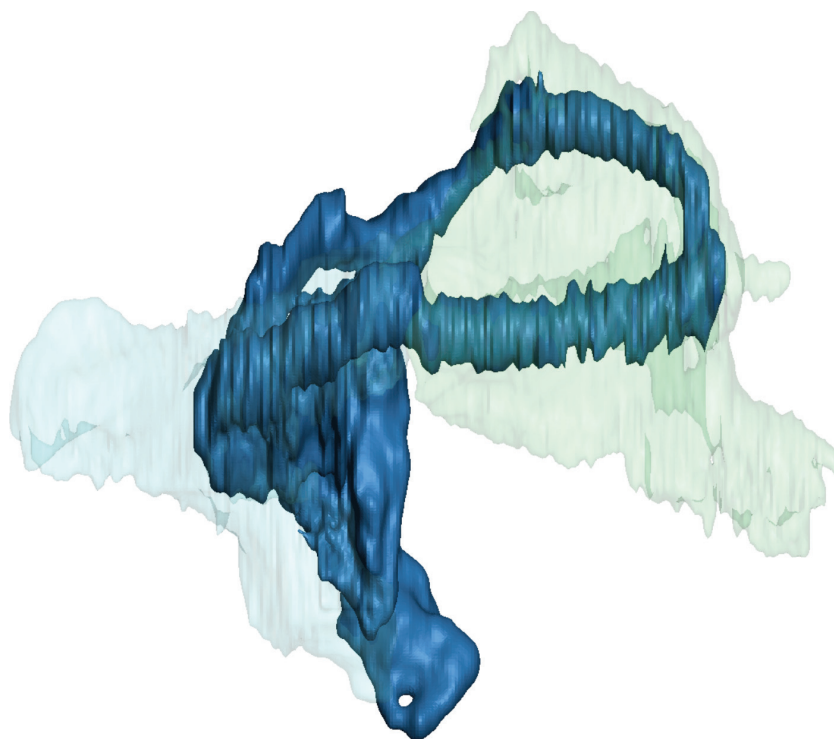


FIGURE 10. Balance organs of *Youngina*, 3D model presented as a Quicktime movie (Roll) (see online version for animation). (Abbreviations and color codes in Appendix.)

ing a dorsal process, yet still possessing a large stapedia foramen. On the other hand, *Youngina* shows a number of derived braincase characters. The paroccipital processes contact the quadrate, unlike in more primitive reptiles. The abducens nerve occupies a groove on the dorsum sellae rather than piercing through as in captorhinids (Price 1935); in this, *Youngina* resembles basal archosauromorphs like *Prolacerta* and *Tanystropheus* (Evans 1986). The basiptyergoid processes of the basisphenoid are fairly large as in crown-group diapsids, unlike the relatively smaller processes found in captorhinids (Price 1935), and they are not sutured to the palatal elements unlike in some derived groups (such as sauropterygians and turtles). New anatomical reinvestigations of previously described higher-stem diapsids for which the braincase is preserved would complement the anatomy we have described here for *Youngina* and permit more detailed comparisons as suggested by both Modesto and Sues (2002) and Bickelmann et al. (2009).

Hearing in Stem-diapsids

While Evans (1987) described many of the bony structures of the braincase, we present the first reconstruction of the vestibular system in

Youngina, and in fact in any Permian diapsid, and the first complete stapes known for *Youngina*. Our HRXCT data show that earlier reconstructions of the stapes as a slender, gracile element (Evans 1987; Gow 1975) are not correct, and that the stapes is a supporting element within the skull, as illustrated by Carroll (1981). This has important implications for hearing in *Youngina*.

The stapes in *Youngina* was not specialized as a middle ear ossicle and consequently did not function in hearing--instead it served as a mechanical part of the skull architecture, a brace between the braincase and the quadrate. This is the plesiomorphic function of the stapes in tetrapods (Carroll 1980). Turtles and crown-group diapsids have freed the stapes from the quadrate so that it can swing freely and conduct airborne sounds between the tympanic membrane and the fenestrae ovalis (Rieppel 1993). Given the lack of the deep caudal emargination found in crown-group diapsids, or the caudolateral emargination found in turtles, the quadrate probably did not support a tympanic membrane (Reisz 1981). Impedance-matching hearing is not known among any other Paleozoic diapsid, let alone any amniote, except some parareptiles (Müller and Tsuji 2007). Recognizing the absence of these structures in *Youngina* agrees

with its position as an early stem-diapsid, rather than an early lepidosauiromorph as once suggested (Benton 1985).

Despite the fact that the stapes is not transformed into a middle ear ossicle, and the lack of a tympanic membrane, *Youngina* was not necessarily insensitive to sound. The gross structure of its auditory apparatus is similar to *Sphenodon* in that the stapes is not columelliform and articulates with the quadrate posteromedially and there is no tympanic membrane. *Sphenodon* has a range of auditory sensitivity in the lower frequencies of 100-900 Hz (Gans and Wever 1976), and it has been suggested that m. depressor mandibulae may perform a secondary function in sound absorption (Lombard and Hetherington 1993). Additional research could be performed to test the approximate hearing capabilities in *Youngina* based on the dimensions of the cochlear duct and comparison with the large data set of reptiles and birds published by Walsh et al. (2009). Comparing this data from *Youngina* to that of modern sauropsids could provide insight into the hearing capabilities and vocal complexity of derived stem-diapsids and the evolution of hearing in modern reptiles, and possible new interpretations of a previously reported aggregation of juvenile stem-diapsid specimens as evidence of group sociality (Smith and Evans 1996).

SUMMARY AND CONCLUSIONS

We used high-resolution X-ray computed tomography scanning to prepare a digital reconstruction of the braincase of *Youngina*. We largely agree with the description presented by Evans (1987) of the braincase of *Youngina*, but we have provided new information on the shape of the stapes in *Youngina*, which differs from previous interpretations by Evans and other authors. We present the first 3D visualizations of the semicircular canals in *Youngina*, as well as offering possible implications for hearing in this important early stem-diapsid. Our reconstruction and anatomical description will prove useful in the development of new phylogenetic analyses of diapsid reptiles, and help resolve the relationships of *Youngina* and the other “younginiform” grade taxa within the Diapsida.

ACKNOWLEDGMENTS

We wish to thank L. Witmer and R. Ridgely (Ohio University) for sharing their experience and advice regarding Amira and large CT data sets. We also thank T. Ryan and A. Grader for HRXCT scanning services at Penn State University. We wish to thank H. Zhu (Marshall University) for contributing her artistic talents to Figure 7.6-7.

Research funding was provided by a fellowship from the SURE Program to N. M. Gardner funded through the West Virginia Research Challenge Fund, and administered by the West Virginia Higher Education Policy Commission, Division of Science and Research, Grant Number: 208125. Support for HRXCT scanning of the holotype was provided through NYCOM research funds to F. R. O’Keefe.

REFERENCES

- Benton, M.J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society*, 84 (2):97-164.
- Bever, G.S., Bell, C.J., and Maisano, J.A. 2005. The Ossified Braincase and Cephalic Osteoderms of *Shinisaurus crocodilurus* (Squamata, Shinisauridae). *Palaeontologia Electronica*, 8: 4A: 36p.
- Bhullar, B.S. and Bever, G.S. 2009. An archosaur-like laterosphenoid in early turtles (Reptilia: Pantestudines). *Breviora*, 518:1-11.
- Bickelmann, C., Müller, J., and Reisz, R. R. 2009. The enigmatic diapsid *Acerosodontosaurus piveteaui* (Reptilia: Neodiapsida) from the Upper Permian of Madagascar and the paraphyly of “younginiform” reptiles. *Canadian Journal of Earth Sciences*, 46:651-661.
- Broom, R. 1914. A new thecodont reptile. *Proc. Zool. Soc. London*, 1914:1072-1077.
- Broom, R. 1915. Catalogue of types and figured specimens of fossil vertebrates in the American Museum of Natural History. II.—Permian, Triassic and Jurassic reptiles of South Africa. *Bulletin of the American Museum of Natural History* 25(2):105-164.
- Carroll, R.L. 1976. *Galesphyrus capensis*, a younginid eosuchiain from the Cistephalus zone of South Africa. *Annals of the South African Museum*, 72: 59-68.
- Carroll, R.L. 1980. The hyomandibular as a supporting element in the skull of primitive tetrapods, p. 293-317. In Panchen, A. L. (ed.), *The Terrestrial Environment and the Origins of Land Vertebrates*. Systematics Association Special Volume No. 15. London/New York.

- Carroll, R.L. 1981. Plesiosaur ancestors from the Upper Permian of Madagascar. *Philosophical Transactions of the Royal Society of London, Series B*, 293:315-383.
- Carroll, R.L. 1988a. *Vertebrate Paleontology and Evolution*. W. H. Freeman and Company.
- Carroll, R.L. 1988b. Late Paleozoic and Early Mesozoic Lepidosauromorphs and Their Relation to Lizard Ancestry, p. 99-118. In Estes, R. and Pregill, G. (ed.), *The Phylogenetic Relationships of the Lizard Families*. Stanford University Press, Palo Alto.
- Clark, J.M., Welman, J., Gauthier, J.A., and Parrish, M.J. 1993. The laterosphenoid bone of early archosauriforms. *Journal of Vertebrate Paleontology*, 13(1): 48-57.
- Colbert, E.H. 1970. The Triassic gliding reptile *Icarosaurus*. *Bull. Amer. Mus. Nat. Hist.* 143: 85-142.
- Currie, P.J. 1980. A new younginid (Reptilia: Eosuchia) from the Upper Permian of Madagascar. *Canadian Journal of Earth Sciences*, 17:500-511.
- Currie, P. 1981. *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. *Palaeontologia Africana*, 24:99-168.
- Currie, P. 1982. The osteology and relationships of *Tangasaurus mennelli* Haughton (Reptilia, Eosuchia). *Annals of the South African Museum*, 86 (8):247-265.
- deBraga, M. and Rieppel, O. 1997. Reptile phylogeny and the affinities of turtles. *Zoological Journal of the Linnean Society* 120:281-354.
- Evans, S.E. 1986. The braincase of *Prolacerta broomi* (Reptilia, Triassic). *N. Jb. Geol. Paläont. Abh.*, 173 (2):181-200.
- Evans, S.E. 1987. The braincase of *Youngina capensis* (Reptilia: Diapsida; Permian). *N. Jb. Geol. Paläont. Mh.*, 1987 (4):293-203.
- Evans, S.E. 1988. The early history and relationships of the Diapsida. p. 221-260. In Benton, M. J. (ed.), *The phylogeny and classification of the tetrapods, vol. 1: Amphibians, reptiles, birds*. Systematics Association, Special Vol. 35A. Clarendon Press, Oxford, UK.
- Evans, S.E. 2009. An early kuehneosaurid reptile (Reptilia: Diapsida) from the Early Triassic of Poland. *Palaeontologica Polonica* 65:145-178.
- Gaffney, E.S. 1980. Phylogenetic relationships of the major groups of reptiles. pp. 593-610. In Panchen, A. L. (ed.), *The terrestrial environment and the origin of vertebrates*. Academic Press, London, UK.
- Gaffney, E.S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bull. Amer. Mus. Nat. Hist.* 194:1-263.
- Gaffney, E.S. and Jenkins, Jr., F.A. 2010. The cranial morphology of *Kayentachelys*, an Early Jurassic cryptodire, and the early history of turtles. *Acta Zoologica* (Stockholm), early view doi:10.1111/j.1463-6395.2009.00439.x.
- Gans, C. and Wever, E.G. 1976. Ear and hearing in *Sphenodon punctatus*. *PNAS*, 73: 4244-4246.
- Gow, C.E. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia Africana*, 18:89-131.
- Gregory, W.K. 1946. Pareiasaurs versus placodonts as near ancestors to the turtles. *Bull. Amer. Mus. Nat. Hist.* 86:276-323.
- Harris, J.M. and Carroll, R.L. 1977. *Kenyasaurus*, a new eosuchian reptile from the Early Triassic of Kenya. *Journal of Paleontology*, 51 (1):139-149.
- Heaton, M.J. 1979. Primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian of Oklahoma and Texas. *Oklahoma Geological Survey Bulletin* 127: 1-84.
- Hedges, S.B. and Poling, L.L. 1999. A molecular phylogeny of reptiles. *Science* 283:988-1001.
- Holliday, C.M. and Witmer, L.M. 2008. Cranial kinesis in dinosaurs: intracranial joints, protractor muscles, and their significance for cranial evolution and function in diapsids. *Journal of Vertebrate Paleontology*, 28 (4):1073-1088.
- Hopson, J.A. 1979. Paleoneurology, p. 39-146. In Gans, C., Northcutt, R. G. and Ulinski, P. S. (ed.), *Biology of the Reptilia, Neurology A*, volume 9, Academic Press, London.
- Hopson, J.A. and Radinsky, L.B. 1980. Vertebrate paleontology: new approaches and new insights. *Paleobiology*, 6 (3):250-270.
- Ivachnenko, M.F. 1987. [Permian parareptiles of the USSR]. *Trudy Pal. Inst. Acad. Nauk SSR* 223: 3-160. [In Russian]
- Kordikova, E.G. 2002. Comparative morphology of the palate dentition in *Proganochelys quenstedti* Baur 1887 from the Upper Triassic of Germany and Chelonian Ancestry. *N. Jb. Geol. Paläont., Abh.* 225 (2):195-249.
- Laurin, M. 1991. The osteology of a Lower eosuchian from Texas and a review of diapsid phylogeny. *Zoological Journal of the Linnean Society*, 101 (1):59-95.
- Laurin, M. and Gauthier, J. A. 2000. Diapsida. Lizards, *Sphenodon*, crocodylians, birds, and their extinct relatives. Version 22 June 2000. <http://tolweb.org/Diapsida/14866/2000.06.22> in The Tree of Life Web Project, <http://tolweb.org>
- Laurin, M. and Reisz, R.R. 1995. A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society* 101:59-95.
- Lee, M.S.Y. 1997. Pareiasaur phylogeny and the origin of turtles. *Zoological Journal of the Linnean Society* 120:197-280.
- Lee, M.S.Y. 2001. Molecules, morphology, and the monophyly of diapsid reptiles. *Contributions to Zoology* 70 (1): 1-22.
- Li, C., Wu, X.C., Rieppel, O., Wang, L.T., and Zhao, J. 2009. Ancestral turtle from the late Triassic of southwestern China. *Nature* 456: 497-501.

- Lombard, R.E. and Hetherington, T.E. 1993. Structural basis of hearing and sound transmission, p. 241-302. In Hanken, J. and Hall, B. K. (ed.), *The Skull: Functional and evolutionary mechanisms*, volume 3, University of Chicago Press, Illinois.
- Lyson, T.R., Bever, G.S., Bhullar, B.S., Joyce, W.G. and Gauthier, J.A. 2010. Transitional fossils and the origin of turtles. *Biology Letters*, early view doi:10.1098/rsbl.2010.0371
- Modesto, S. and Sues, H.D. 2002. An Enigmatic Diapsid Reptile from the Upper Permian of Eastern Europe. *Journal of Vertebrate Paleontology*, 22(4): 851-855.
- Müller, J. 2003. Early loss and multiple return of the lower temporal arcade in diapsid reptiles. *Naturwissenschaften*, 90:473-476.
- Müller, J. and Tsuji, L.A. 2007. Impedance-matching hearing in Paleozoic reptiles: evidence of advanced sensory perception at an early stage of amniote evolution. *PLoS ONE* 2(9): e889, doi:10.1371/journal.pone.0000888
- Olsen, E.C. 1936. Notes on the skull of *Youngina capensis* Broom. *Journal of Geology*, 44 (4): 523-533.
- Price, L.I. 1935. Notes on the Braincase of *Captorhinus*. *Proceedings of the Boston Society of Natural History* 40(7):377-386.
- Reisz, R. 1977. *Petrolacosaurus*, the Oldest Known Diapsid Reptile. *Science*, 196: 1091-1093.
- Reisz, R. 1981. A diapsid reptile from the Pennsylvanian of Kansas. *Special Publications of the Museum of Natural History, University of Kansas*, 7:1-74.
- Reisz, R., Laurin, M., and Marjanovic, D. 2010. *Apsisaurus witteri* from the Lower Permian of Texas: yet another small varanopid synapsid, not a diapsid. *Journal of Vertebrate Paleontology*, 30(5): 1628-1631.
- Rieppel, O. 1993. Patterns of Diversity in the Reptilian Skull. pp. 344-390. In Hanken, J. and Hall, B. K. (ed.), *The Skull: Functional and evolutionary mechanisms*, volume 2, University of Chicago Press, Illinois.
- Rieppel, O. 1995. The Genus *Placodus*: Systematics, Morphology, Paleobiogeography, and Paleobiology. *Fieldiana, Geology, New Series* 31:1-44.
- Rieppel, O. 2002. Turtles as diapsid reptiles. *Zoologica Scripta*, 29 (3):199-212.
- Rieppel, O. and deBraga, M. 1996. Turtles as diapsid reptiles. *Nature* 384:453-455.
- Rieppel, O. and Reisz, R.R. 1999. The origin and early evolution of turtles. *Ann. Rev. Ecol. Syst.* 20:1-22.
- Romer, A.S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Illinois.
- Smith, R.M.H. and Evans, S.E. 1996. New material of *Youngina*: evidence of juvenile aggregation in Permian diapsid reptiles. *Palaeontology*, 39 (2):289-303.
- Walsh, S.A., Barrett, P.M., Milner, A.C., Manley, G., and Witmer, L.M. 2009. Inner ear anatomy is a proxy for deducing auditory capability and behavior in reptiles and birds. *Proc. R. Soc. B*, 279:1355-1360.
- Werneburg, I. and Sánchez-Villagra, M.R. 2009. Timing of organogenesis support basal position of turtles in the amniote tree of life. *BMC Evolutionary Biology*, 9:82.
- Witmer, L.M. and Ridgely, R.C. 2008. Structure of the brain cavity and inner ear of the centrosaurine ceratopsid dinosaur *Pachyrhinosaurus* based on CT scanning and 3D visualization. pp. 117-144 in P. J. Currie, W. Langston, Jr. and D. H. Tanke (eds.), *A New Horned Dinosaur from an Upper Cretaceous Bone Bed in Alberta*. NRC Research Press, Ottawa.
- Witmer, L.M. and Ridgely, R.C. 2009. New insights into the brain, braincase, and ear region of tyrannosaurs (Dinosauria, Theropoda), with implications for sensory organization and behavior. *The Anatomical Record* 292:1266-1296.
- Witmer, L., Ridgely, R., Dufeu, D., and Semones, M. 2008. Using CT to peer into the past: 3D visualization of the brain and ear regions of birds, crocodiles, and nonavian dinosaurs. pp. 67-88 in H. Endo and R. Frey (eds.), *Anatomical Imaging: Towards a New Morphology*. Springer-Verlag, Tokyo.
- Zardoya, R. and Meyer, A. 1998. Complete mitochondrial genome indicates diapsid affinities of turtles. *Proc. Natl. Acad. Sci.* 95:14226-14231.

**APPENDIX
ABBREVIATIONS AND COLORS INDEX**

Figure abbreviations in alphabetical order.

ar: ampullary recess

bpt: basiptyergoid process of basisphenoid

bs: basisphenoid

bt: basal tubera of the basioccipital

clp: clinoid process of the basisphenoid

csc: caudal semicircular canal

cvp: crista ventrolateralis process of the parasphenoid

ds: dorsum sellae

exo: exoccipital

fm: foramen magnum

gec: groove for ethmoid cartilage

gcn6: groove for the abducens nerve

icf: internal carotid foramina

lsc: lateral semicircular canal

oc: occipital condyle

opo: opisthotic

opvr: opisthotic ventral ramus

plr?: postlagenar recess?

poop: paroccipital process of the opisthotic

pro: prootic

pspcup: parasphenoid cultriform process

rsc: rostral semicircular canal

ru: recessus utriculus

sac: identifiable portion of the saccular maculae

saf: stapedia artery foramen

sfpl: stapedia footplate

so: supraoccipital

st: sella turcica

sta: stapes

su: superior utriculus

Representative colors for the braincase model in alphabetical order.

Basioccipital: purple

Opisthotic: light blue

Parabasisphenoid: light green

Prootic: green

Supraoccipital: red

Stapes: yellow