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A VIRTUAL PHYTOSAUR ENDOCAST AND ITS IMPLICATIONS FOR SENSORY SYSTEM EVOLUTION IN ARCHOSAURS

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ABSTRACT—Many recent studies have detailed the morphology of archosaurian endocrania. However, the outgroup to Archosauria, Phytosauria, has yet to be studied with modern techniques that would allow reconstruction of their internal anatomy. *Pseudopalatus mccauleyi* is a derived phytosaur from the Upper Triassic Chinle Formation, Arizona. A skull of *P. mccauleyi*, USNM 15839, was imaged using computed tomography in order to create the first high-quality, digitally reconstructed phytosaur endocranium. *Pseudopalatus mccauleyi* exhibits overall endocranial morphology that is similar to that of an extant crocodylian. These clades, phytosaurs and extant crocodylians, exhibit convergent Baupläne and similar inferred ecologies. A notable difference between the endocrania of the two clades is a considerable dural expansion in *P. mccauleyi* that denotes a large pineal body. This expansion, and the overall morphology of the endocranium, is consistent with the historic endocranial reconstructions of the phytosaurs *Pseudopalatus buceros*, *Smilosuchus gregorii*, and *Parasuchus hislopi*. A comparison with phylogenetically diverse archosaurian endocrania reveals that endocranial morphologies are highly conserved within Pseudosuchia, regardless of Bauplan or ecology. This conservatism is in contrast to the diversity of endocranial morphology observed within Theropoda and Sauropodomorpha, or between members of those clades and Pseudosuchia. The most pronounced variability in pseudosuchian endocranial morphology is a trend in size reduction of the pineal region, from a large basal condition to a reduced derived condition wherein the pineal region is indistinguishable from the rest of the endocranium. A similar trend in pineal reduction is also seen in theropods and sauropods.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline/UJVP

INTRODUCTION

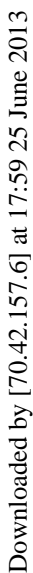
Phytosauria is considered to be the outgroup to Archosauria (Avenetatarsalia + Pseudosuchia) and the basal-most clade of the Crurotarsi (Fig. 1; Nesbitt, 2011). These extinct archosauromorphs were semiaquatic predators and the largest and most common crurotarsans in western North America during the Late Triassic (e.g., Hurlburt et al., 2003). The Upper Triassic Chinle Formation of Arizona has yielded a number of phytosaur specimens, including those of highly derived genera, such as *Pseudopalatus*, belonging to a group known as the Pseudopalatinae (e.g., Lucas, 1998; Heckert and Lucas, 2002; Parker, 2006; Stocker, 2010). Phytosaurs had a Bauplan and inferred ecology similar to extant crocodylians (e.g., Hunt, 1989). Several recent comparative studies have been conducted on phytosaurs, particularly focusing on the external morphology of the skull (Zeigler et al., 2002, 2003; Irmis, 2005; Parker and Irmis, 2006; Stocker, 2010). Phytosaur internal cranial anatomy, however, has not received significant attention in recent decades, but it has great potential for morphological insight, as has occurred in recent studies of avemetatarsalians (e.g., Witmer et al., 2003; Domínguez Alonso et al., 2004; Witmer and Ridgely, 2009).

The brains of most non-avian archosaurs fill a relatively small portion of the endocranial cavity, unlike the condition in birds and mammals (e.g., Jerison, 1973; Hopson, 1979; Witmer et al., 2008; Evans et al., 2009). In crocodylians, less than 50% of the volume of the endocranial cavity is filled by the brain, with the

remainder of the space consisting of the dura mater and venous sinuses within the dura (Hopson, 1979). This endocranial composition means that the morphology of deeper structures, like many of those of the brain, are overlain and obscured by these superficial structures. Thus, a cranial endocranium represents the contours of the external surface of the dura mater and other superficial structures where it was in contact with the internal surface of the braincase, rather than the actual morphology of the brain and brainstem (Witmer et al., 2008; Witmer and Ridgely, 2009). However, because of the close relationship between the deeper structures of the brain and the overlying dura mater, the positions, orientations, and relative sizes of many of the deeper features (cranial nerve trunks and various brain regions) are imparted upon the internal surface of the braincase via the dura mater (e.g., Kley et al., 2010). Furthermore, many features of the dura mater itself, such as many of the dural venous sinuses, constitute some of the most easily and accurately reconstructed elements of cranial endocrania (Kley et al., 2010). The relative size information obtained from an endocranium enables comparisons of various functional aspects of neuromorphology because the mass of neural tissue of a particular area of the brain is correlated with the amount of information processing involved in performing a corresponding function (Jerison, 1973). Such functional capacities include consideration of specific sensory-related features such as the optic lobe or olfactory bulb, as well as other features such as the cerebrum.

Convergence of endocranial morphology has been documented among some archosaurs, such as pterosaurs and *Archaeopteryx* (Witmer, 2004), both of which are interpreted as being aerial carnivores (e.g., Hecht et al., 1985; Hazlehurst and Rayner, 1992; Feduccia, 1996; Elzanowski, 2002; Paul, 2002; Claessens et al.,

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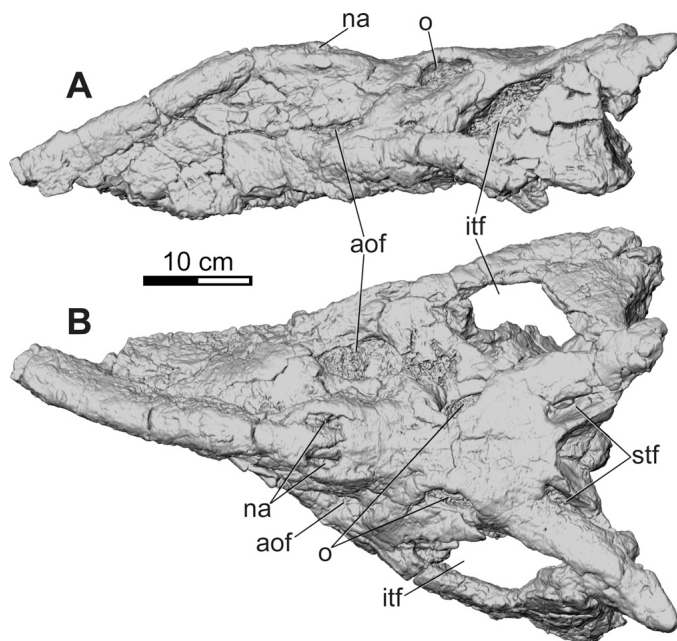


FIGURE 2. Computer-generated skull of *Pseudopalatus mccauleyi* (USNM 15839) in **A**, left lateral view, showing numerous examples of brittle deformation throughout the specimen; and **B**, dorsal view, illustrating torsion effects of plastic deformation on the rostrum and right-hand side of the specimen. **Abbreviations:** aof, antorbital fenestra; itf, infratemporal fenestra; na, nasus; o, orbit; stf, supratemporal fenestra.

a bone algorithm and exported from the scanner computer in DICOM format. DICOMs were then imported into Amira 4.0.1 (Mercury-TGS, Chelmsford, Massachusetts) for viewing, analysis, and visualization. The scan data were analyzed on a 32-bit personal computer workstation with 2 GB of RAM, an Intel Core 2 Duo E6850 (4 MB cache, 3.0 GHz) processor, and nVidia Quadro FX 3000 video card installed with Microsoft Windows XP Professional operating system. The data set was cropped to include only those anatomical features of interest to this study (i.e., cranial endocast and endosseous labyrinth) and resampled at an effective voxel size of $0.035 \times 0.035 \times 0.035$ mm. Voxels representing space once occupied by the anatomical features of interest were digitally highlighted and assigned to virtual materials using the Amira segmentation editor. Assigned voxels were then rendered as a three-dimensional (3D) virtual model and visualized for both qualitative and quantitative assessments (Online Supplemental Data, Fig. 1S).

DESCRIPTION

The digital endocast of *Pseudopalatus mccauleyi* (USNM 15839) provides a fair amount of detail, allowing for a general description of the larger structures of the brain, brainstem, endosseous labyrinth, cranial nerve trunks, and craniocerebral vascular elements once housed therein. There is evidence of torsion of the rostrum and numerous examples of breakage throughout the skull, some of which pass entirely through the skull along a given plane (Fig. 2). A notable example of breakage involves the foramina through which the cranial nerve roots once passed. Most of the cranial nerve spaces are either truncated or entirely obscured by a large fracture that traverses the dorsal aspect of both the basisphenoid and basioccipital and the ventral portion of the endocast along a horizontal plane that is largely the same

as that of most of the cranial nerve foramina. This break also affects the inner ears and precludes description and analysis of ventral inner ear structures such as the cochlea. Still, enough of the braincase remains undistorted that a feature absent from one side of the endocast is typically preserved on the opposite side (Fig. 3). The volume of the endocast, excluding the inner ear and cranial nerve trunks, is 18.68 cm^3 .

The olfactory apparatus is well defined and constrained by the internal surface of the frontal and the dorsal surface of the interorbital septum. The olfactory bulbs are exposed in the olfactory region of the nasal cavity along the anteroventral margin of their anterior-most terminus. The cerebral hemispheres are slightly broad, relative to the width of the rest of the endocast, and taper both anteriorly and posteriorly. Postcerebral portions of the endocast exhibit an indistinct neural morphology. A large, dorsal projection of dura mater at the junction of the fore- and midbrain is present and is one of the more clearly defined features observable in the scan data (Fig. 3). This dorsal projection is completely ensconced within the braincase and shows no sign of connections with additional features outside the braincase (Supplementary Data, Fig. S1). The prominence of this structure exceeds the typical size of the dorsal longitudinal dural venous sinus in archosaurs and is inconsistent with the typical morphology thereof. Although the dorsal longitudinal dural venous sinus undoubtedly contributes to its appearance, this dorsal prominence is more consistent in size and morphology to the pineal expansion of some archosaurs and is therefore referred to the pineal expansion. The flocculus is distinguishable just anterior to the anterior semicircular canal.

The hypophyseal fossa is not apparent in the scan data. Unlike the cranial nerve foramina, however, the hypophyseal fossa is not obscured by breakage. The reason that the hypophyseal fossa is not readily identifiable is unclear, although one possible explanation is that the region of the endocranial cavity corresponding to the hypophyseal fossa experienced a high degree of deformation and adjacent bones were displaced to occupy that fossa. However, the lack of a noticeable boundary, indicating a point of contact between displaced bones, in any of the cross-sectional views and the highly localized and specific nature of the concealment make this an unlikely cause. Instead, it seems likely that sedimentary matrix fills this fossa and is of a density similar to that of the surrounding fossil material, preventing differentiation of the matrix and bone (Supplementary Data, Fig. S1).

The most distinctive features of the cranial endocast of *Pseudopalatus mccauleyi* are found along its dorsal surface (Fig. 3). The dorsal contour of the endocast can be described in terms of three distinct linear surfaces. The anterior segment consists of the olfactory apparatus and is nearly linear along the horizontal plane. The middle segment is represented by the dorsal longitudinal dural venous sinus, cerebrum, and the large, distinctive pineal expansion. The posterior segment is curvilinear, dorsoventrally concave, and consists of the mid- and hindbrain.

The dural venous sinus system is illustrated in the reconstruction (Fig. 3). The dorsal longitudinal dural venous sinus overlies the olfactory apparatus, including the olfactory lobe, and the anterior-most process of the cerebrum. Proceeding posteriorly, the dorsal longitudinal dural venous sinus then becomes undifferentiated within the dorsal projections of the cerebrum and pineal expansion before becoming evident once again just posterior to the pineal expansion, where it presumably overlies tectal and cerebellar structures. The sphenoparietal dural venous sinus is transversely oriented, occupying the constriction between the cerebrum and tectum, and would have connected the dorsal longitudinal sinus with the cavernous sinus lateral to the hypophysis, as well as other ventrally positioned sinuses. The occipital dural venous sinus overlies, and therefore obscures details of, the tectum, cerebellum, and medulla. The ventral longitudinal dural venous sinus is identifiable at the posterior-most portion of the

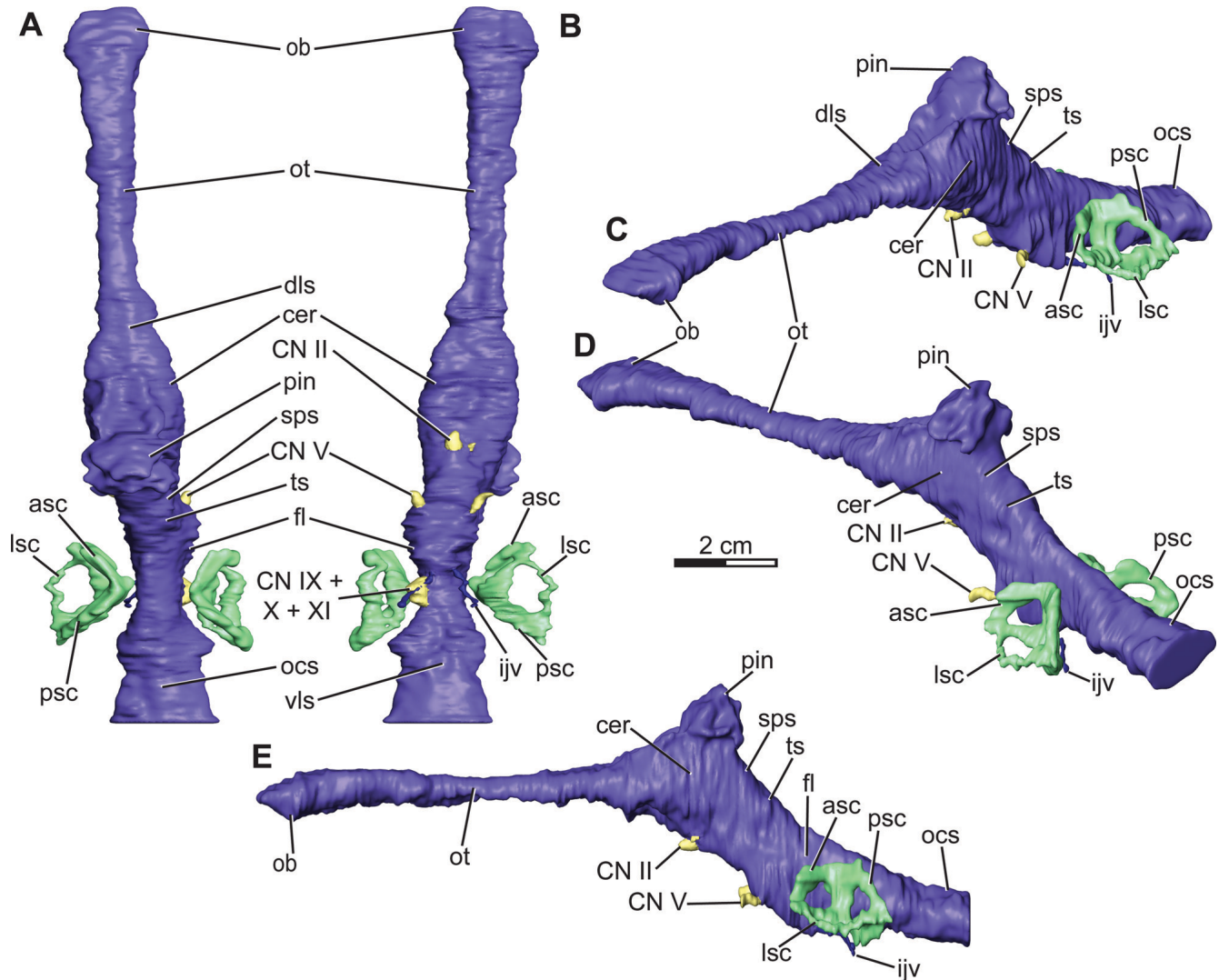


FIGURE 3. Reconstruction of the cranial cavity of *Pseudopalatus mccauleyi* (USNM 15839). Digital endocast in **A**, dorsal; **B**, ventral; **C**, left rostdorsolateral; **D**, left caudodorsolateral; and **E**, left lateral views generated from CT scans. Selected cranial nerve trunks, the endosseous labyrinth, and cranial vasculature are illustrated. **Abbreviations:** asc, anterior semicircular canal (or endocast thereof); cer, cerebrum (region of endocast); CN II, optic nerve; CN V, trigeminal nerve; CN IX + X + XI, glossopharyngeal, vagus, and accessory nerves; dls, dorsal longitudinal dural venous sinus; fl, flocculus (region of endocast); ijv, interior jugular vein; lsc, lateral semicircular canal (or endocast thereof); ob, olfactory bulb (region of endocast); ocs, occipital dural venous sinus; ot, olfactory tract (region of endocast); pin, pineal expansion of endocast; psc, posterior semicircular canal (or endocast thereof); sps, sphenoparietal dural venous sinus; ts, transverse dural venous sinus; vls, ventral longitudinal dural venous sinus.

ventral surface of the endocast where it overlies and obscures the medulla, ventrally.

It was possible to reconstruct part of the endosseous labyrinth, although reconstruction of the more ventral components of the vestibular apparatus was not possible (see above). The three semicircular canals are oriented, as they are in all tetrapods, at approximately right angles to one another in the three planes of space. The anterior semicircular canal is slightly longer (1.60 cm) and more arched than the posterior semicircular canal (1.57 cm), and the lateral semicircular canal is the shortest (1.55 cm) of the three.

DISCUSSION

Endosseous Labyrinth

The reconstructed inner ear features of *Pseudopalatus mccauleyi* exhibit similar morphologies to those of extant crocodylians

(Witmer et al., 2008) and a variety of other non-avian archosaurs (e.g., Witmer et al., 2008; Evans et al., 2009; Kley et al., 2010), but they are slightly larger, relative to the overall size of the endocast, than they are in extant crocodylians (Witmer et al., 2008). The morphology and large size of the endosseous labyrinth of *P. mccauleyi* is consistent with previous descriptions of phytosaurs (Case, 1928; Camp, 1930). The lateral semicircular canal has been used to infer the resting, alert head posture of various extinct archosaurs by orienting the head such that the lateral semicircular canal is parallel to Earth horizontal (e.g., Witmer et al., 2003; Sereno et al., 2007; Witmer and Ridgely, 2009). Reviews by Hullar (2006) and Taylor et al. (2009), however, noted that experiments on extant animals reveal the resting but alert head posture to be such that the lateral semicircular canals are inclined slightly anterodorsally, relative to Earth horizontal (e.g., Vidal et al., 1986; Erichsen et al., 1989; Graf et al., 1995). Such an orientation has also been used to support head posture estimates in

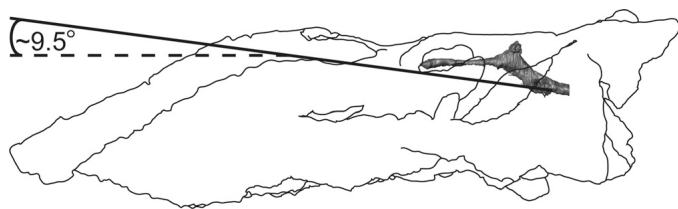


FIGURE 4. Line drawing of the skull and digital endocast of *Pseudopalatus mccauleyi* (USNM 15839). The skull, in left lateral view, is oriented according to the inferred resting, alert head posture, with the orientation of the lateral semicircular canal (solid line) relative to Earth horizontal (dashed line) indicated.

at least one fossil form (Kley et al., 2010). Using the typical head posture of *Crocodylus johnstoni* (Witmer et al., 2008) as a guide for semiaquatic predator head posture, the skull of *P. mccauleyi* was oriented in an inferred resting, alert posture such that both the cranial table and plane of the palate and basicranium are horizontally oriented (Fig. 4), as is typical for quadrupedal tetrapods (Kley et al., 2010). In this position, the lateral semicircular canals are anterodorsally inclined by $\sim 9.5^\circ$; consistent with the $5\text{--}15^\circ$ range seen in *Columba livia* in a resting, alert position (Erichsen et al., 1989) and used by Kley et al. (2010) to substantiate inferred head posture in *Simosuchus clarki*. This head posture also places the nares at a slightly higher horizontal plane than that of the orbits. Such an arrangement would be appropriate for a semi-aquatic ambush predator because it would allow both the nares and orbits to be held above the water surface while much of the rest of the head could be submerged.

Phytosaur Endocasts

The morphology of the *Pseudopalatus mccauleyi* endocast presented here is similar to those of earlier phytosaur endocast reconstructions (Fig. 5). The endocast of *P. mccauleyi* exhibits a longitudinal flexure that is similar to that of the endocast of *Smilosuchus gregorii* (Camp, 1930) but slightly different from those of the endocasts of *Parasuchus hislopi* (Chatterjee, 1978) and *Pseudopalatus buceros* (Cope, 1888). The locations, orientations, and relative sizes of cranial nerves II, V, and IX + X + XI and of the internal jugular vein of *P. mccauleyi* are similar to those features in both *P. hislopi* (Chatterjee, 1978) and *S. gregorii* (Camp, 1930). A large ventral expansion, described as the pons varioli in the endocasts of *P. hislopi* (Chatterjee, 1978) and *S. gregorii* (Camp, 1930), is not readily apparent in the endocast of *P. mccauleyi*. However, this feature may simply be obscured by the large break that intersects the ventral aspect of the endocast of the specimen (see above).

The endocasts of *Parasuchus hislopi*, *Pseudopalatus buceros*, and *Smilosuchus gregorii* (Fig. 5) all exhibit large dorsal expansions just posterodorsal to the cerebral hemispheres and almost directly dorsal to the hypophysis (Cope, 1888; Camp, 1930; Chatterjee, 1978). In each description, the expansion is attributed to the epiphysis or pineal body. The pineal expansion of the endocast of *P. mccauleyi* is similar to the pineal expansion of the endocast of other phytosaurs in terms of relative size—particularly to those of *P. buceros* and *S. gregorii*—and morphology—particularly to that of *S. gregorii* (Cope, 1888; Camp, 1930). The recent endocast of *P. pristinus* was described by Smith et al. (2010) as showing no indication of a large epiphysis, and the referred structure in *Smilosuchus gregorii* was instead attributed to the dorsal longitudinal sinus (Smith et al., 2010). The position and morphology of this expansion in *P. mccauleyi* is consistent, however, with a large pineal expansion (e.g., Cope, 1888; Case, 1921; Camp, 1930; Dempster, 1935; Chatterjee, 1978; Hopson, 1979; Witmer et al., 2008; Kemp, 2009; Witmer

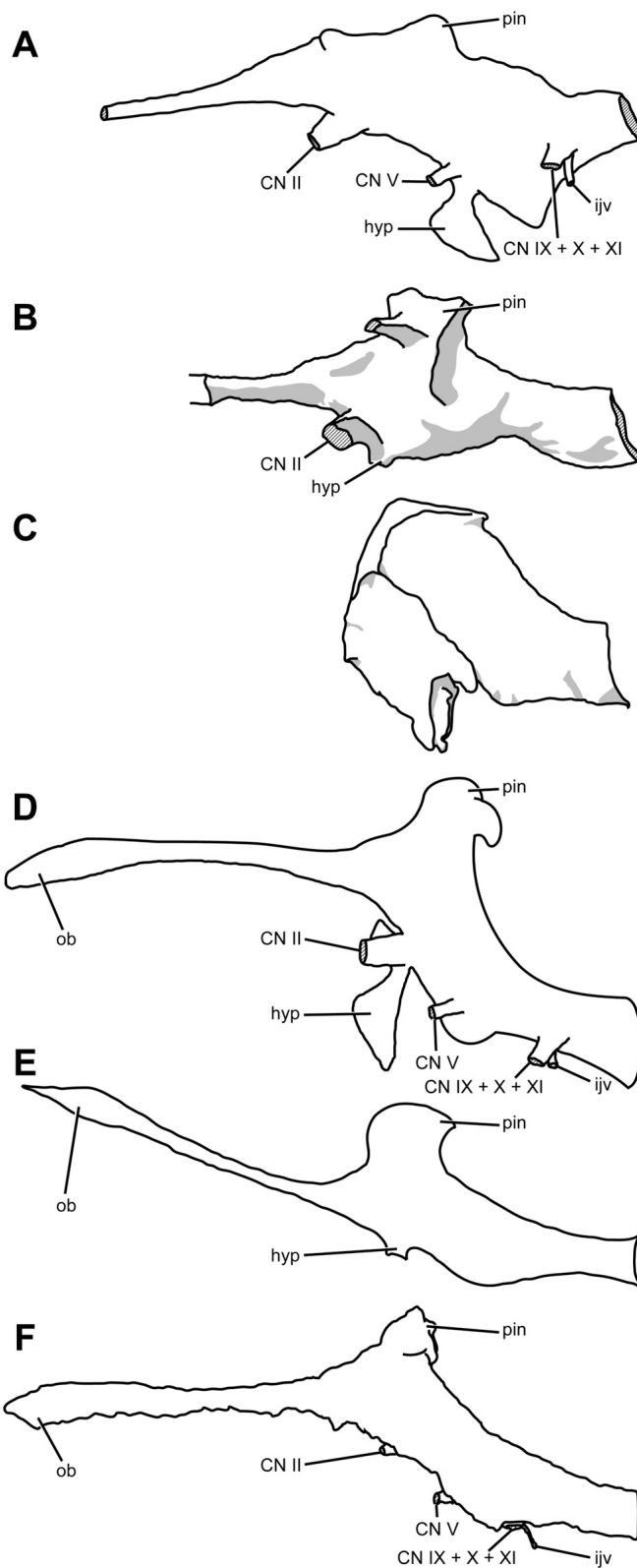


FIGURE 5. A comparison of the outlines of the endocasts of the phytosaurs. **A**, *Parasuchus hislopi*, redrawn from Chatterjee (1978); **B**, *Pseudopalatus buceros*, redrawn from Cope (1888); **C**, *Leptosuchus* sp., redrawn from Case (1928); **D**, *Smilosuchus gregorii*, redrawn from Camp (1930); **E**, the endocranial cavity of *Pseudopalatus pristinus*, redrawn from Mehl (1928); and **F**, *Pseudopalatus mccauleyi*. Drawings not to scale. **Abbreviations:** CN II, optic nerve; CN V, trigeminal nerve; CN IX + X + XI, glossopharyngeal, vagus, and accessory nerves; hyp, hypophyseal fossa (or endocast thereof); ijv, interior jugular vein; ob, olfactory bulb (region of endocast); pin, pineal expansion of endocast.

and Ridgely, 2009) and not the dorsal longitudinal sinus, which, in archosaurian endocasts lacking a large pineal expansion, is typically a far less pronounced expansion (e.g., Witmer et al., 2008; Kley et al., 2010). The endocast of *P. buceros* exhibits lateral processes of the epiphysis that were reported by Cope (1888) as connecting the pineal expansion of the endocast to the orbits through an orbitopineal canal, but neither this process nor canal have been described in other phytosaurs (Case, 1928; Cope, 1930; Chatterjee, 1978) and they do not appear in *Pseudopalatus mccauleyi*. A 'nervus orbitopinealis' was proposed by Cope (1888) that would connect the pineal body and orbits, presumably supplying the pineal gland with light stimulus in lieu of a parietal foramen. However, this 'canalis orbitopinealis' is likely the orbitocerebral vein canal noted in some other archosaurs (e.g., Witmer and Ridgely, 2008a; Witmer et al., 2008).

The endocranial morphology of the holotype of *Pseudopalatus pristinus* presented by Mehl (1928) exhibits limited similarity to the endocasts of other phytosaurs, including *P. mccauleyi*. Even the cranial nerves of *P. pristinus* are described as having a completely different organization from those of other phytosaurs (Mehl, 1928). However, the odd morphology of the reconstructed endocast of *P. pristinus* may partly result from breaks or other deformation, as the braincase of this specimen was described as being in several large fragments (Mehl, 1928). Additionally, the sagittal section of the braincase of *P. pristinus* (Fig. 5) shows an endocranial cavity similar to that of *P. mccauleyi* (Mehl, 1928). Although not labeled as such, the braincase of *P. pristinus* also exhibits a dorsal projection of the endocranial cavity that is consistent with the relative size and morphology of the pineal expansion of the endocast of *P. mccauleyi*.

Endocast Comparison

The digitally reconstructed endocast of *Pseudopalatus mccauleyi* offers an excellent opportunity for comparisons between the endocasts of the basal-most crurotarsans and more derived pseudosuchians. Furthermore, it allows for comparison of endocranial morphologies in taxa with similar ecologies as inferred from their convergent Baupläne and the discovery of their remains in similar depositional environments (e.g., Hunt, 1989). The endocast of *P. mccauleyi* is largely, though not entirely, similar to endocasts of extant crocodylians such as *Gavialis gangeticus* (Wharton, 2000), *Alligator mississippiensis* (Witmer and Ridgely, 2008b), and *Crocodylus johnstoni* (Witmer et al., 2008) in overall shape and organization.

The olfactory bulbs of *Pseudopalatus mccauleyi* are similar in relative size and shape to those of an extant crocodylian (Fig. 6). The olfactory tracts of *P. mccauleyi* and extant crocodylians are also similar in size and length, although the angle at which the tract projects from the rest of the endocast in *P. mccauleyi* is considerably more horizontal than the more anteroventrally oriented olfactory tracts of *Alligator mississippiensis* (Witmer and Ridgely, 2008b) and *Crocodylus johnstoni* (Witmer et al., 2008). This difference in orientation is likely the result of differences in the planar organization of major skull elements, rather than functional changes of the olfactory tract (Kley et al., 2010). The close proximity and dorsal location of the external nares of a phytosaur, relative to the location of the endocast, are another possible explanation for this difference in orientation.

In *Pseudopalatus mccauleyi*, dural venous sinuses obscure the organization and morphology of many of the elements associated with the tectum, cerebellum, and medulla, as in extant crocodylians (Sedlmayr, 2002; Witmer et al., 2008). It is reasonable to project a similar organization of the endocranial elements overlain by, and closely associated with, these sinuses because each of these dural venous sinuses exhibits an organization similar to that exhibited in extant crocodylians (Witmer et al., 2008). This inference is supported by the identification of elements de-

marked by their lateral surfaces, such as the cerebrum and flocculus, the locations of which are consistent with those observed in extant crocodylians (Witmer et al., 2008).

A few differences can be discerned between the endocrania of *Pseudopalatus mccauleyi* and extant crocodylians (Fig. 6). The cerebrum of *P. mccauleyi*, for example, exhibits a similar morphology to that of an extant crocodylian, yet cerebrum size, relative to the size of the overall endocast, and the extent of lateral expansion of the cerebrum are both smaller in *P. mccauleyi* (Fig. 3). This observation is consistent with that on the cerebrum of the phytosaur *Pseudopalatus pristinus* (Smith et al., 2010). The flocculus of *P. mccauleyi* appears to be relatively small, although deformation in this region of the specimen makes a more definitive relative size comparison difficult. One feature that is of greater relative size in *P. mccauleyi* than in extant crocodylians is the dorsally located dural expansion that denotes the position of the pineal body (e.g., Rogers, 1999; Larsson, 2001; Sampson and Witmer, 2007). A small cerebrum and flocculus and a large pineal body are all consistent with descriptions of primitive conditions in more basal reptiles (e.g., Hopson, 1979).

Archosaur Endocasts

Kley et al. (2010) provided an endocranial description of the notosuchian *Simosuchus clarki*. *Simosuchus clarki* exhibits both an inferred ecology—as a fully terrestrial herbivore—and morphology—being small (length of ~0.75 m) and short-tailed (Georgi and Krause, 2010), with osteoderm-covered limbs (Hill, 2010), a pug nose, and clover-shaped teeth (Kley et al., 2010)—that are distinct from other pseudosuchians. Interestingly, the overall morphology of the cranial endocast of *S. clarki* is similar to the endocasts of extant crocodylians (Fig. 6), as noted by Kley et al. (2010). This similarity is surprising given the large number of differences between the Baupläne and inferred ecologies of these two taxa, and it suggests that the similarities exhibited between the endocasts of *Pseudopalatus mccauleyi* and extant crocodylians are not necessarily linked to Bauplan or ecological convergence but are instead a function of phylogenetic conservatism. Additional taxa were compared in order to gauge the likelihood of a similarity in endocast morphology appearing as a result of phylogenetic bias.

The endocast of the aetosaur *Desmotosuchus spurensis* (Case, 1921) is similar to that of an extant crocodylian (Fig. 6). One notable difference in the aetosaur is in the hypophyseal region and the ventral part of the olfactory tract, where there is a large ventral expansion. It seems plausible that deformation is responsible for this feature, however, because of the odd, laterally compressed morphology of the anteroventral region of the *Desmotosuchus* endocast and the truncation of its olfactory tract. As in *Simosuchus clarki*, the overall similarity to extant crocodylians is surprising given the distinctiveness of the aetosaur Bauplan and their inferred ecology—being a heavily armored, fully terrestrial herbivore (e.g., Carroll, 1988). A reconstruction of the cranial endocast of the poposaurid *Shuvosaurus inexpectatus* was illustrated by Lehane (2005). As is the case with both *Simosuchus clarki* and *Desmotosuchus spurensis*, *Shuvosaurus inexpectatus* exhibits an overall morphology and inferred ecology that is distinctive among pseudosuchians—it was a fully terrestrial, bipedal herbivore with a toothless beak (Chatterjee, 1993; Nesbitt, 2007)—yet its overall endocast morphology is similar to that of an extant crocodylian. These similarities strongly suggest that pseudosuchian endocranial morphologies are highly conserved, exhibiting only relatively minor changes that might be attributable to variations in the planar organization of major elements of the skull or to the expansion or reduction of features associated with evolutionary trends from the basal-most to more derived conditions.

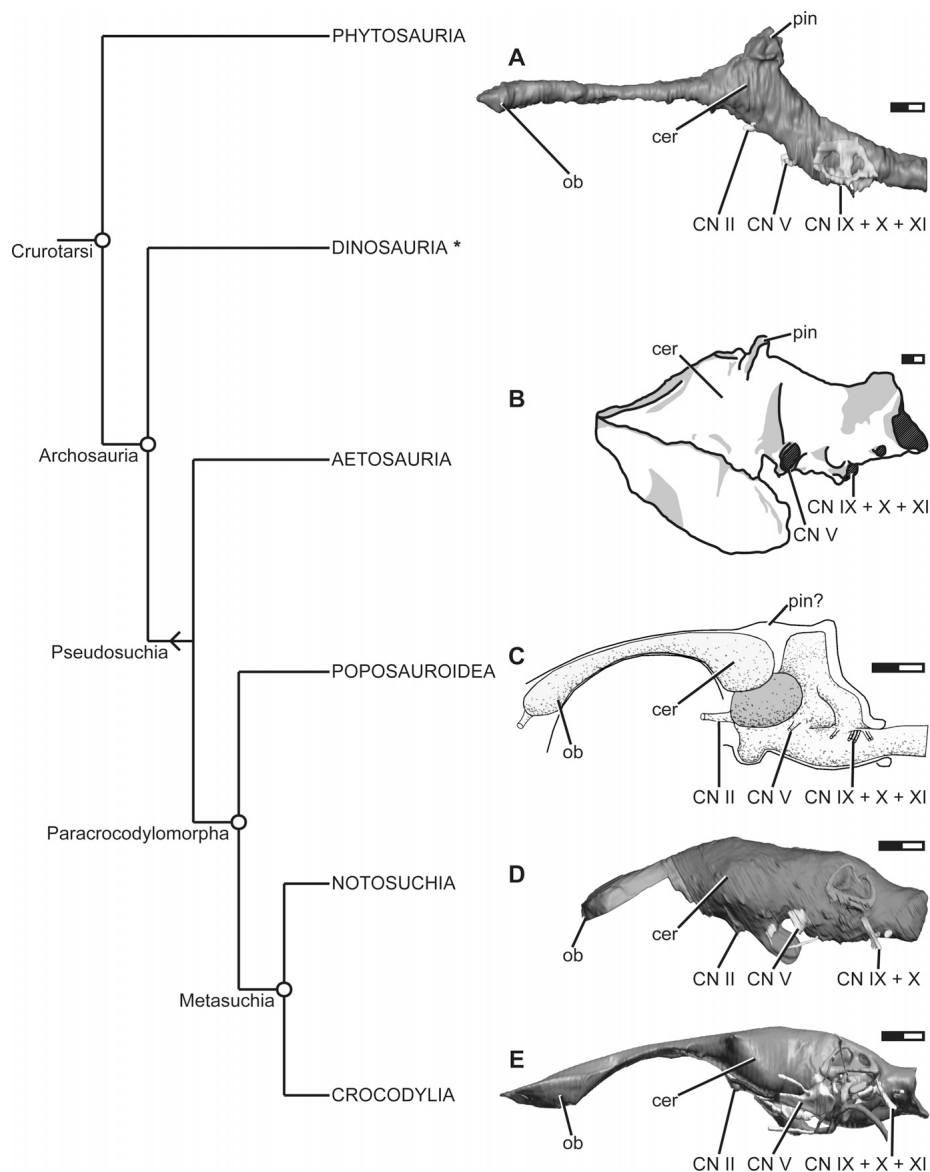


FIGURE 6. A series of endocrasts of Crurotarsi and the phylogenetic relationships of the taxa they represent. A comparison of the endocrasts of **A**, the phytosaur *Pseudopalatus mccauleyi*; **B**, the poposauroid *Shuvosaurus inexpectatus*, modified from Lehane (2005); **C**, the aetosaur *Desmotosuchus spurensis*, redrawn from Case (1921); **D**, the notosuchian *Simosuchus clarki*, modified from Kley et al. (2010); and **E**, the crocodylian *Crocodylus johnstoni*, modified from Witmer et al. (2008). Cladogram modified from Figure 1. For dinosaurs examined in this study, see Witmer and Ridgely (2009:fig. 4) and Sereno et al. (2007:fig. 1). **Abbreviations:** cer, cerebrum (region of endocrast); CN II, optic nerve; CN V, trigeminal nerve; CN IX + X + XI, glossopharyngeal, vagus, and accessory nerves; ob, olfactory bulb (region of endocrast); pin, pineal expansion of endocrast. Scale bars equal 1 cm.

The most notable and readily apparent difference between the endocrania of *Pseudopalatus mccauleyi* and members of Pseudosuchia is the presence, in the former, of a large, dorsally positioned dural expansion that indicates the position of the pineal body (the pineal expansion). In contrast, a pineal expansion is entirely absent in the reconstructions of both extant crocodylians and *Simosuchus clarki* (Fig. 6). The endocranial reconstruction of *Shuvosaurus inexpectatus* includes a feature that is consistent with the position of the pineal expansion, but it is much smaller than that in *P. mccauleyi*. The endocrast of the aetosaur *Desmotosuchus spurensis* exhibits a dorsal expansion, described by Case (1921) as the epiphysis, which is much more pronounced than the potential pineal expansion seen in *S. inexpectatus* and far smaller

than the pineal expansion of *P. mccauleyi*. A figure of the braincase of the aetosaur *Stagonolepis olenkae* in Sulej (2010) shows a projection of the endocranial cavity consistent with a pineal expansion of the endocrast, although this feature was not specifically noted or identified in the description and a reconstructed endocrast was not included. The relative size of the potential pineal expansion in *Stagonolepis olenkae* is slightly larger than that seen in *Shuvosaurus inexpectatus* and considerably smaller than that of *P. mccauleyi*, as in *D. spurensis*. Moreover, the figure of the interior of the braincase of this aetosaur, *S. olenkae*, indicates an overall endocranial morphology that appears to be consistent with those of other pseudosuchians. This pattern suggests that the pineal expansion of the endocrast, which is at its greatest relative size in

P. mccauleyi, seems to be gradually but quickly reduced among basal pseudosuchian taxa so that it no longer appears in the cranial endocasts of derived pseudosuchians.

In order to determine whether the conservatism seen in the endocranial morphologies of pseudosuchians is unique or more widespread, the endocasts of other archosaur clades were considered. Theropod and sauropodomorph dinosaur endocasts were described by Witmer and Ridgely (2009) and Sereno et al. (2007), respectively, and were examined for comparison (Fig. 6). The endocasts of theropods and sauropods are generally discernable from one another (e.g., Witmer et al., 2008), despite the two clades being phylogenetically closer to each other than phytosaurs are to extant crocodylians. Both dinosaur groups are also discernable from pseudosuchians. Furthermore, although general trends seen in the endocranial morphologies of Theropoda and Sauropodomorpha make the clades discernable from one another, the variability in overall endocast morphology within each of these clades is greater than the variability seen among pseudosuchians. The representative sauropodomorph endocast, *Massospondylus carinatus*, is overall similar to the phytosaur endocast, but the stereotypical sauropod endocast is relatively dorsoventrally tall and rostrocaudally short, whereas the most derived sauropod endocast condition includes a posteriorly located dural peak, lack of a notable pineal expansion, and increase in the relative sizes of the cerebrum and flocculus (see Sereno et al., 2007:fig. 1). Theropod endocasts exhibit a great deal of morphological variability, with the basal-most representative, an endocast of the ceratosaur *Majungasaurus crenatissimus*, being the most overall similar to the phytosaur endocast. These variations include increases and decreases in the relative sizes of the olfactory bulbs and the appearance and loss of a posterior dural peak. The derived, avian condition lacks a notable pineal expansion and exhibits an increase in the relative sizes of the cerebrum, flocculus, and optic lobe. Overall theropod endocast morphologies range from rostrorodorsally elongate to dorsoventrally tall and rostrocaudally short (see Witmer and Ridgely, 2009:fig. 4). Of the endocasts published for both theropods and sauropodomorphs (e.g., Sereno et al., 2007; Witmer and Ridgely, 2009), the basal-most members of each clade (see above) are the most morphologically similar to each other and to *Pseudopalatus mccauleyi*. This similarity suggests that the phytosaur-style cranial endocast is the most similar to the primitive condition for Archosauria.

Whereas various dinosaur clades evolved derived endocast morphologies, interpreted to be related to derived and differentiated ecologies (e.g., Witmer et al., 2008; Witmer and Ridgely, 2009), pseudosuchians maintained a highly conservative, and largely plesiomorphic, endocast morphology throughout their evolution of differentiated ecologies and Baupläne. A trend of relative size reduction of the pineal expansion—from the large primitive condition to the greatly reduced derived condition—is apparent through both theropod and sauropodomorph dinosaur lineages, though not discussed in the respective studies (see Sereno et al., 2007:fig. 1; Witmer and Ridgely, 2009:fig. 4). This trend is similar to the pineal reduction trend seen in Pseudosuchia.

Pineal Reduction

Because the pineal gland has important physiological functions, it is important to consider the implications of its size decrease in archosaur evolution. The pineal gland produces melatonin, which has sleep-inducing and temperature-lowering effects, in at least some animals (Macchi and Bruce, 2004; Arendt and Skene, 2005), related to its function of regulating circadian rhythm and seasonal cycles (Hopson, 1979). A link has also been suggested between melatonin and several seasonal processes in birds, including egg production (Siopes and Underwood, 1987), cellular and humoral immune responses (Moore and Siopes,

2000; Singh and Haldar, 2007), cold resistance and thermogenesis (Saarela and Heldmaier, 1987), and endocrine activity of the adrenal glands (Ramachandran et al., 1996). In rats, exposure to constant light decreases pineal weight, and both a pinealectomy and exposure to constant light have the same effect of increasing and accelerating gonad growth (Aleandri et al., 1996). In at least some birds (Ramachandran et al., 1996) and mammals (Aleandri et al., 1996), the pineal gland affects gonad production activity associated with seasonal breeding. The pineal gland has also been linked to migration patterns in newts, and metabolic and hibernation functions in at least some other animals (Hopson, 1979).

The functional benefits of pineal reduction are not readily apparent and are not agreed upon (Hopson, 1979). The exact function(s) of a large pineal gland in phytosaurs may be difficult to determine, but it seems unlikely that functions such as migration or hibernation were important for a semiaquatic predator. Exposed at the skull surface in the form of a photoreceptive patch, the pineal gland ('parietal eye') of lizards serves as a receptor of light/dark sensory information (Hopson, 1979). Most archosauromorphs basal to phytosaurs exhibit a pineal foramen (e.g., Romer, 1956). The rhynchosaur *Hyperodapedon gordonii*, however, has no pineal foramen but does show a pit on the ventral aspect of the parietals that has been attributed to a large pineal expansion (Benton, 1983). The presence of a pineal foramen in immature phytosaurs was reported by Camp (1930), and a deep pit excavating the dorsal aspect of the parietals, consistent with the location of a pineal foramen but which does not extend into the cranial cavity, was described in the basal phytosaur *Paleorhinus scurriensis* (Langston, 1949). Based on these observations, it appears that the relative size of the pineal body was reduced following loss or reduction of the parietal foramen. Presumably, pineal function changed and was adequate at a reduced size, and the pineal body no longer needed to be large enough to reach the skull exterior, potentially saving the metabolic expense of developing and maintaining the gland at large size. The large pineal expansion of *Pseudopalatus mccauleyi* appears to represent a transitional state from the basal condition of a 'parietal eye' to the reduced pineal expansion of derived archosaurs. The occurrence of a large pineal expansion in a eucynodont that does not exhibit a pineal foramen (Kemp, 2009) suggests that a similar transitional pineal reduction may have occurred in other clades as well. The trends of further reductions in pineal size in pseudosuchians, theropods, and sauropods are interesting because these clades apparently derived the reduced state independently. The functional implications for the reduction are difficult to ascertain, however, and it is not possible to determine if it occurred for either the same or different reasons in each of these clades.

CONCLUSIONS

A comparison of the phytosaur *Pseudopalatus mccauleyi* to extant crocodylians demonstrates that the two share similar overall endocast morphologies. These similarities do not appear to be due to their similar Baupläne or ecologies, but rather result from phylogenetic conservatism.

In avemetatarsalians, similar overall endocast morphologies, such as in *Archaeopteryx* and pterosaurs, have been ascribed to neurological convergence linked to the inferred shared ecologies of these taxa (Witmer et al., 2003; Domínguez Alonso et al., 2004). The neurological adaptive strategy of various dinosaur clades contrasts with the phylogenetic conservatism seen in pseudosuchians. Whereas dinosaurs exhibit a variety of endocast morphologies, sometimes showing a great deal of variation between closely related taxa, pseudosuchians seem to diverge into a wide range of Baupläne and ecologies without requiring a similar amount of derivation from the primitive endocast morphology. Although differences in endocast morphology exist between pseudosuchians, theropods, and sauropods, trends of pineal

expansion reduction are found in each clade, independent of the others.

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LITERATURE CITED

- Aleandri, V., V. Spina, and A. Moroni. 1996. The pineal gland and reproduction. *Human Reproduction* 2:225–235.
- Arendt, J., and D. J. Skene. 2005. Melatonin as a chronobiotic. *Sleep Medicine Reviews* 9:25–39.
- Ballew, K. L. 1989. A phylogenetic analysis of Phytosauria from the Late Triassic of the western United States; pp. 309–339 in S. G. Lucas and A. P. Hunt (eds.), *Dawn of the Age of Dinosaurs in the American Southwest*. New Mexico Museum of Natural History, Albuquerque, New Mexico.
- Benton, M. J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London, Series B* 302:605–718.
- Camp, C. L. 1930. A study of the phytosaurs with description of new material from western North America. *Memoirs of the University of California* 10:1–174.
- Carroll, R. L. 1988. *Vertebrate Paleontology and Evolution*. W. H. Freeman and Company, New York, 698 pp.
- Case, E. C. 1921. On an endocranial cast from a reptile, *Desmatosuchus spurensis*, from the Upper Triassic of western Texas. *Journal of Comparative Neurology* 33:133–147.
- Case, E. C. 1928. An endocranial cast of a phytosaur from the Upper Triassic beds of western Texas. *Journal of Comparative Neurology* 45:161–168.
- Chatterjee, S. 1978. A primitive parasuchid (Phytosaur) reptile from the Upper Triassic Maleri Formation of India. *Palaeontology* 21:83–127.
- Chatterjee, S. 1993. *Shuvosaurus*, a new theropod: an unusual theropod dinosaur from the Triassic of Texas. *National Geographic Research and Exploration* 9:274–285.
- Claessens, L. P. A. M., P. M. O'Connor, and D. M. Unwin. 2009. Respiratory evolution facilitated the origin of pterosaur flight and aerial gigantism. *PLoS ONE* 4:e4497.
- Cope, E. D. 1888. The pineal eye in extinct vertebrates. *The American Naturalist* 22:914–917.
- Dempster, W. T. 1935. The brain case and endocranial cast of *Eryops megacephalus* (Cope). *Journal of Comparative Neurology* 62:171–196.
- Domínguez Alonso, P., A. C. Milner, R. A. Ketcham, M. J. Cookson, and T. B. Rowe. 2004. The avian nature of the brain and inner ear of *Archaeopteryx*. *Nature* 430:660–669.
- Elzanowski, A. 2002. *Archaeopterygidae*; pp. 129–159 in L. M. Chiappe and L. M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*. University of California Press, Berkeley, California.
- Erichsen, J. T., W. Hodos, C. Evinger, B. B. Bessette, and S. J. Phillips. 1989. Head orientation in pigeons; postural, locomotor, and visual determinants. *Brain, Behavior, and Evolution* 33:268–278.
- Evans, D., L. M. Witmer, and R. C. Ridgely. 2009. Endocranial anatomy of lambeosaurine dinosaurs: a sensorineural perspective on cranial crest function. *The Anatomical Record* 292:1315–1337.
- Feduccia, A. 1996. *The Origin and Evolution of Birds*. Yale University Press, New Haven, Connecticut, 420 pp.
- Georgi, J. A., and D. W. Krause. 2010. Postcranial axial skeleton of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Memoir of the Society of Vertebrate Paleontology* 10:99–121.
- Graf, W., C. de Waele, and P. P. Vidal. 1995. Functional anatomy of the head-neck movement system of quadrupedal and bipedal mammals. *Journal of Anatomy* 186:55–74.
- Hazlehurst, G. A., and J. M. Rayner. 1992. Flight characteristics of Triassic and Jurassic Pterosauria: an appraisal based on wing shape. *Paleobiology* 4:447–463.
- Hecht, M. K., J. H. Ostrom, G. Viohl, and P. Wellnhofer. 1985. The Beginnings of Birds: Proceedings of the International *Archaeopteryx* Conference, Eichstätt, 11–15 September 1984. Freunde des Jura Museums, Eichstätt, Germany, 382 pp.
- Heckert, A. B., and S. G. Lucas. 2002. Revised Upper Triassic stratigraphy of the Petrified Forest National Park. *New Mexico Museum of Natural History and Science, Bulletin* 21:1–36.
- Hill, R. V. 2010. Osteoderms of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Memoir of the Society of Vertebrate Paleontology* 10:154–176.
- Hopson, J. A. 1979. Paleoneurology; pp. 39–146 in C. Gans, R. G. Northcutt, and P. S. Ulinik (eds.), *Biology of the Reptilia*. Neurology A, Volume 9. Academic Press, New York.
- Hullar, T. E. 2006. Semicircular canal geometry, afferent sensitivity, and animal behavior. *The Anatomical Record* 288:466–472.
- Hunt, A. P. 1989. Cranial morphology and ecology among phytosaurs; pp. 349–354 in S. G. Lucas and A. P. Hunt (eds.), *Dawn of the Age of Dinosaurs in the American Southwest*. New Mexico Museum of Natural History, Albuquerque, New Mexico.
- Hurlburt, G. R., A. B. Heckert, and J. O. Farlow. 2003. Body mass estimates of phytosaurs (Archosauria: Parasuchidae) from the Petrified Forest Formation (Chinle Group: Revueltian) based on skull and limb bone measurements; pp. 105–114 in K. E. Zeigler, A. B. Heckert, and S. G. Lucas (eds.), *Paleontology and Geology of the Snyder Quarry*. New Mexico Museum of Natural History, Albuquerque, New Mexico.
- Irmis, R. B. 2005. The vertebrate fauna of the Upper Triassic Chinle Formation in northern Arizona; pp. 63–88 in S. J. Nesbitt, W. G. Parker, and R. B. Irmis (eds.), *Guidebook to the Triassic Formations of the Colorado Plateau in Northern Arizona: Geology, Paleontology, and History*. Mesa Southwest Museum Bulletin 9.
- Jerison, H. J. 1973. *Evolution of the Brain and Intelligence*. Academic Press, New York, 482 pp.
- Kemp, T. S. 2009. The endocranial cavity of a nonmammalian eucynodont, *Chiniquodon theotenicus*, and its implications for the origin of the mammalian brain. *Journal of Vertebrate Paleontology* 29:1188–1198.
- Kley, N. J., J. J. W. Sertich, A. H. Turner, D. W. Krause, P. M. O'Connor, and J. A. Georgi. 2010. Craniofacial morphology of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Memoir of the Society of Vertebrate Paleontology* 10:13–98.
- Langston, W. L., Jr. 1949. A new species of *Paleorhinus* from the Triassic of Texas. *American Journal of Science* 247:324–341.
- Larsson, H. C. E. 2001. Endocranial anatomy of *Carcharodontosaurus saharicus* (Theropoda: Allosauroidea) and its implications for theropod brain evolution; pp. 19–33 in D. H. Tanke, K. Carpenter, and M. W. Skrepnick (eds.), *Mesozoic Vertebrate Life*. Indiana University Press, Bloomington, Indiana.
- Larsson, H. C. E., and H.-D. Sues. 2007. Cranial osteology and phylogenetic relationships of *Hamadasuchus rebouli* (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Morocco. *Zoological Journal of the Linnean Society* 149:533–567.
- Lehane, J. 2005. *Anatomy and relationships of Shuvosaurus*, a basal theropod from the Triassic of Texas. M.S. thesis, Texas Tech University, Lubbock, Texas, 92 pp.
- Lucas, S. G. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 143:347–384.
- Macchi, M. M., and J. N. Bruce. 2004. Human pineal physiology and functional significance of melatonin. *Frontiers in Neuroendocrinology* 25:177–95.
- Martin, J. E., and M. J. Benton. 2008. Crown clades in vertebrate nomenclature: correcting the definition of Crocodylia. *Systematic Biology* 57:173–181.
- Mehl, M. G. 1928. *Pseudopalatus pristinus*, a new genus and species of phytosaurs from Arizona. *University of Missouri Studies* 3: 1–22.
- Moore, C. B., and T. D. Siopes. 2000. Effects of lighting conditions and melatonin supplementation on the cellular and humoral immune responses in Japanese quail *Coturnix coturnix japonica*. *General and Comparative Endocrinology* 81:1898–1903.

- Nesbitt, S. J. 2007. The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod-like convergence, and the distribution of related taxa. *Bulletin of the American Museum of Natural History* 302:1–84.
- Nesbitt, S. J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History* 352:1–292.
- Parker, W. G. 2006. The stratigraphic distribution of major fossil localities in Petrified Forest National Park, Arizona. *Museum of Northern Arizona Bulletin* 62:46–62.
- Parker, W. G., and R. B. Irmis. 2006. A new species of the Late Triassic phytosaur *Pseudopalatus* (Archosauria: Pseudosuchia) from the Petrified Forest National Park, Arizona. *Bulletin of the Museum of Northern Arizona* 62:126–143.
- Paul, G. S. 2002. *Dinosaurs of the Air: The Evolution and Loss of Flight in Dinosaurs and Birds*. Johns Hopkins University Press, Baltimore, Maryland, 472 pp.
- Ramachandran, A., M. Patel, and C. Patel. 1996. Effects of pineal indoles and parachlorophenylalanine on seasonal reproduction in the pigeon. *Journal of Experimental Biology* 199:793–800.
- Rogers, S. W. 1999. *Allosaurus*, crocodiles, and birds: evolutionary clues from spiral computed tomography of an endocast. *The Anatomical Record* 257:162–173.
- Romer, A. S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Chicago, Illinois, 772 pp.
- Saarela, S., and G. Heldmaier. 1987. Effect of photoperiod and melatonin on cold resistance, thermoregulation and shivering/nonshivering thermogenesis in Japanese quail. *Journal of Comparative Physiology B* 157:625–633.
- Sampson, S. D., and L. M. Witmer. 2007. Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Memoir of the Society of Vertebrate Paleontology* 8:32–102.
- Sedlmayr, J. C. 2002. Anatomy, evolution, and functional significance of cephalic vasculature in Archosauria. Ph.D. dissertation, Ohio University, Athens, Ohio, 398 pp.
- Sereno, P. C., H. C. E. Larsson, C. A. Sidor, and B. Gado. 2003. A new notosuchian from the Early Cretaceous of Niger. *Journal of Vertebrate Paleontology* 23:477–482.
- Sereno, P. C., J. A. Wilson, L. M. Witmer, J. A. Whitlock, A. Maga, O. Ide, and T. A. Rowe. 2007. Structural extremes in a Cretaceous dinosaur. *PLoS ONE* 2:e1230.
- Singh, S. S., and C. Haldar. 2007. Peripheral melatonin modulates seasonal immunity and reproduction of Indian tropical male bird *Perdica asiatica*. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 146:446–450.
- Siopes, T. D., and H. Underwood. 1987. Pineal gland and ocular influences on turkey breeder hens. 1. Reproductive performance. *Poultry Science* 66:521–527.
- Smith, D., R. Sanders, W. Parker, and J. Cavanaugh. 2010. The endocranium, inner ear, and pneumatic structure of the Upper Triassic phytosaur *Pseudopalatus pristinus*. *Journal of Vertebrate Paleontology, Program and Abstracts* 2010:167A.
- Stocker, M. R. 2010. A new taxon of phytosaur (Archosauria: Pseudosuchia) from the Late Triassic (Norian) Sonsela Member (Chinle Formation) in Arizona, and a critical reevaluation of *Leptosuchus*, Case, 1922. *Palaeontology* 53:997–1022.
- Sulej, T. 2010. The skull of a Late Triassic aetosaur and the evolution of the stagonolepidid archosaurian reptiles. *Zoological Journal of the Linnean Society* 158:860–881.
- Taylor, M. P., M. J. Wedel, and D. Naish. 2009. Head and neck posture in sauropod dinosaurs inferred from extant animals. *Acta Palaeontologica Polonica* 54:213–220.
- Vidal, P. P., W. Graf, and A. Berthoz. 1986. The orientation of the cervical vertebral column in unrestrained awake animals. I. Resting position. *Experimental Brain Research* 61:549–559.
- Wharton, D. S. 2000. An enlarged endocranial venous system in *Steneosaurus pictaviensis* (Crocodylia: Thalattosuchia) from the Upper Jurassic of Les Lourdines, France. *Comptes Rendus de l'Académie des Sciences, Paris, Série IIA* 331:221–226.
- Witmer, L. M. 2004. Inside the oldest bird brain. *Nature* 430:619–620.
- Witmer, L. M., and R. C. Ridgely. 2008a. Structure of the brain cavity and inner ear of the centrosaurine ceratopsid *Pachyrhinosaurus* based on CT scanning and 3D visualization; pp. 117–144 in P. J. Currie (ed.), *A New Horned Dinosaur from an Upper Cretaceous Bone Bed in Alberta*. National Research Council Press, Ottawa, Ontario, Canada.
- Witmer, L. M., and R. C. Ridgely. 2008b. The paranasal air sinuses of predatory and armored dinosaurs (Archosauria: Theropoda and Ankylosauria) and their contribution to cephalic structure. *The Anatomical Record* 291:1362–1388.
- Witmer, L. M., and R. C. Ridgely. 2009. New insights into the brain, braincase, and ear region of tyrannosaurs, with implications for sensory organization and behavior. *The Anatomical Record* 292:1266–1296.
- Witmer, L. M., S. Chatterjee, J. Franzosa, and T. Rowe. 2003. Neuroanatomy of flying reptiles and implications for flight, posture and behaviour. *Nature* 425:950–953.
- Witmer, L. M., R. C. Ridgely, D. L. Dufeu, and M. C. Semones. 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.
- Zeigler, K. E., S. G. Lucas, and A. B. Heckert. 2002. The Late Triassic Canjilon quarry (Upper Chinle Group, New Mexico) phytosaur skulls: evidence of sexual dimorphism in phytosaurs. *New Mexico Museum of Natural History and Science, Bulletin* 21:179–188.
- Zeigler, K. E., S. G. Lucas, and A. B. Heckert. 2003. Variation in the Late Triassic Canjilon quarry (Upper Chinle Group, New Mexico) phytosaur skulls: evidence of sexual dimorphism. *Paläontologische Zeitschrift* 77:341–351.

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