A virtual phytosaur endocast and its implications for sensory system evolution in archosaurs

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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 Archosaurus, 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 endocast endocast. *Pseudopalatus mccauleyi* exhibits overall endocast morphology that is similar to that of an extant crocodylian. These clades, phytosaurs and extant crocodylians, exhibit convergent Bauplan and similar inferred ecologies. A notable difference between the endocasts 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 endocast, is consistent with the historic endocranial reconstructions of the phytosaurs *Pseudopalatus buceros*, *Smilosuchus gregorii*, and *Parasuchus hislopi*. A comparison with phylogenetically diverse archosaurian endocasts reveals that endocast morphologies are highly conserved within Pseudosuchia, regardless of Bauplan or ecology. This conservatism is in contrast to the diversity of endocast morphology observed within Theropoda and Sauropodomorpha, or between members of those clades and Pseudosuchia. The most pronounced variability in pseudosuchian endocast 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 endocast. 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/UVJP

INTRODUCTION

Phytosauria is considered to be the outgroup to Archosaurus (Avemetatarsalia + 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 intracranial 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 endocast 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 endocasts (Kley et al., 2010). The relative size information obtained from an endocast 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 endocast 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.,
Areas of the endocast and inner ear of *Archaeopteryx* that are neurologically important for flight exhibit an expansion and reorganization that would have been sufficient for a lifestyle involving full flight ability (Domínguez Alonso et al., 2004). The endocasts and inner ears of pterosaurs exhibit a similar expansion and reorganization (Witmer et al., 2003). This convergence suggests that certain key anatomical regions and systems, such as the brain and inner ear, may require, or at least benefit from, a specialized morphology in order for an organism to perform certain behaviors, just as a particular Bauplan may be beneficial, if not required, for a certain ecology.

The purpose of this study is to describe the endocranial morphology of phytosaurs and further explore the relationship between endocranial morphology and behavior in archosaurs. We hypothesize that because of the high degree of similarity in Bauplan and ecological convergence between phytosaurs and extant crocodylians, the cranial endocasts of these two groups will exhibit a great deal of overall similarity. In order to reject this hypothesis, substantial differences would need to be identified between them. The examination of such a hypothesis has the potential to add not only to our understanding of archosaur evolution but also to illuminate the mechanisms of behavioral and ecological convergence within Archosauria. The phylogenetic position of Phytosauria as the sister taxon to Archosauria (Fig. 1) makes phytosaurs an appropriate clade to examine as the first step in a larger study to determine what, if any, overall morphological similarities or differences exist among the endocasts of pseudosuchian taxa or between members of Pseudosuchia and Avemetatarsalia. Because it is a member of the derived phytosaur group Pseudopalatinae, the use of *Pseudopalatus mccauleyi* reduces the likelihood that similarities between its endocast and those of extant crocodylians would result solely from retention of a symplesiomorphic condition.


**MATERIALS AND METHODS**

**Specimen Identification and Provenance**

USNM 15839 is a nearly complete skull (skull length 64 cm) of a moderately sized, robust-snouted, and high-crested phytosaur (Fig. 2). The skull is almost complete, with the notable exceptions of the lower jaw, anterior portion of the rostrum, and the teeth, which are not preserved. The specimen exhibits both plastic and brittle deformation, evidenced in the preserved external morphology of the skull, yet the large amount of matrix infilling and lack of apparent bonding agents suggests that little, if any, reconstructive work was performed on the specimen. USNM 15839 was identified by Ballew (1989) as a reference specimen of *Pseudopalatus mccauleyi*. George F. Sternberg collected this specimen in 1937 from the Upper Triassic Chinle Formation, Arizona.

**CT Scanning and 3D Visualization**

The specimen was computed tomographically (CT) scanned at Cabell Huntington Hospital, Huntington, West Virginia, using a General Electric (GE) Healthcare LightSpeed CT scanner. The specimen was scanned helically at a slice thickness of 0.625 mm, 120 kV, and 200 mA. Raw scan data were reconstructed using...
of the endocast along a horizontal plane that is largely the same obscured by a large fracture that traverses the dorsal aspect of the foramina through which the cranial nerve roots once passed. A notable example of breakage involves the skull, some of which pass entirely through the skull along of the rostrum and numerous examples of breakage throughout the dural venous sinus is identifiable at the posterior-most portion of the tectum, cerebellum, and medulla. The ventral longitudinal dural venous sinus, 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.

**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 cranio-cerebral 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 cm³.

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 anteroven tral 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 posteri orly. 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 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.
FIGURE 3. Reconstruction of the cranial cavity of *Pseudopalatus mccauleyi* (USNM 15839). Digital endocast in A, dorsal; B, ventral; C, leftrostrodorsalateral; D, left caudodorsalateral; 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); pvs, 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
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 basioccipital 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 \(-9.5^\circ\); consistent with the 5–15° 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 semiaquatic 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 variolii 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 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

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**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.

**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 Mehli (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, internal 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 mccaeleyi*. A ‘nervis orbitopinalea’ 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 orbitopinalea’ 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. mccaeleyi*. 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. mccaeleyi* (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. mccaeleyi*.

**Endocast Comparison**

The digitally reconstructed endocast of *Pseudopalatus mccaeleyi* 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. mccaeleyi* 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 mccaeleyi* are similar in relative size and shape to those of an extant crocodilian (Fig. 6). The olfactory tracts of *P. mccaeleyi* 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. mccaeleyi* is considerably more horizontal than the more anterodorsally 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 mccaeleyi*, 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 mccaeleyi* and extant crocodylians (Fig. 6). The cerebrum of *P. mccaeleyi*, for example, exhibits a similar morphological relationship 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. mccaeleyi* (Fig. 3). This observation is consistent with that on the cerebrum of the phytosaur *Pseudopalatus pristinus* (Smith et al., 2010). The flocculus of *P. mccaeleyi* 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. mccaeleyi* 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 mccaeleyi* 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 *Desmatosuchus spurensis* (Case, 1921) is similar to that of an extant crocodylian (Fig. 6). One notable difference in the aetosaur is in the hypophysial 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 anterodorsal region of the *Desmatosuchus* 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 *Desmatosuchus 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.
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 endocast of the aetosaur Desmatosuchus 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 Sułej (2010) shows a projection of the endocranial cavity consistent with a pineal expansion of the endocast, although this feature was not specifically noted or identified in the description and a reconstructed endocast 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 endocast, 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 saurapods are generally discernible from one another (e.g., Witmer et al., 2008), despite the two clades being phylogenetically closer to each other than phytosaurs are to extant crocodilians. Both dinosaur groups are also discernible 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 floculus (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, floculus, and optic lobe. Overall theropod endocast morphologies range from rostrodorsally 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 Archosauromorpha.

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 evident 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 (Saarel 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., Witmer, 1996). The rhyolosuchus 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; Dominguez 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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