

Neurosensory anatomy and function in *Seymouria*

Kayla D. Bazzana-Adams^{1,2}  | David C. Evans^{1,2} | Joseph J. Bevitt³ | Robert R. Reisz^{4,5}

¹Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Canada

²Department of Natural History, Royal Ontario Museum, Toronto, Canada

³Australian Centre for Neutron Scattering, Australian Nuclear Science and Technology Organisation, Lucas Heights, New South Wales, Australia

⁴Department of Biology, University of Toronto Mississauga, Mississauga, Canada

⁵International Center of Future Science, Dinosaur Evolution Research Center, Jilin University, Changchun, Jilin Province, China

Correspondence

Kayla D. Bazzana-Adams
Email: kayla.bazzana@mail.utoronto.ca

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Abstract

Seymouria is among the best-known stem amniotes and holds an important phylogenetic position for discussions of amniote evolution. Previous work has focused primarily on the osteology of *Seymouria*, with recent interest turning to the application of computed tomography (CT) to study the internal features. We utilized neutron CT to reconstruct the first virtual cranial endocast and the first complete otic endocasts of *Seymouria*, revealing previously unrecognized details of its palaeoneuroanatomy. The brain and inner ear of *Seymouria* are largely plesiomorphic relative to later-diverging crown amniotes, showing no indication of increased encephalization or braincase ossification. Our results also clarify the plesiomorphic condition for carotid artery morphology in amniotes, with *Seymouria* showing a similar condition to basal members of both the synapsid and sauropsid lineages. The reconstructed neuroanatomy also indicates that *Seymouria* did not possess any particular neuroanatomical specializations, despite the probable presence of an impedance matching hearing system.

KEYWORDS

endocast, Paleozoic tetrapod, Permian, stem amniote

1 | INTRODUCTION

The seymouriamorphs, of which *Seymouria* is among the best known, are a group of stem amniotes known primarily from the Lower Permian of North America, Europe, and Russia (Amalitzky, 1921; Berman & Martens, 1993; Berman et al., 1987; Broili, 1904; Bulanov, 2014; Sullivan & Reisz, 1999; Vaughn, 1966; White, 1939). Seymouriamorphs are consistently recovered as monophyletic and as stem amniotes in phylogenetic analyses (Pardo et al., 2017; Ruta et al., 2003); along with diadectomorphs, seymouriamorphs are the most common outgroups used to establish character polarity near the base of crown Amniota (Pardo et al., 2017; Ruta et al., 2003). There is growing emphasis on incorporating neurocranial information, both hard- and soft-tissue,

into phylogenetic analyses (Klembara et al., 2020; Pardo et al., 2017); given their important role in analyses of both Palaeozoic tetrapods and early amniotes, clarifying the neuroanatomy of seymouriamorphs is critical for informing discussions of early amniote evolution.

Seymouria holds a particularly important position for understanding sensory evolution in early amniotes, especially as pertains to hearing. Aquatic and terrestrial environments require dramatically different auditory specializations, with aerial hearing requiring the evolution of an impedance matching mechanism to compensate for the transmission of sound waves from the surrounding air into the liquid-filled inner ear (see Ekdale, 2016). Taxa with biphasic lifestyles that spend a substantial portion of their life in water, as hypothesized for *Seymouria*

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(Berman et al., 2000; Berman & Martens, 1993), will likely experience trade-offs in their hearing sensitivity, as their auditory systems must function, to varying degrees of efficacy, in both aquatic and aerial environments. As taxa transition to fully terrestrial lifestyles and no longer require the ability to hear in aquatic environments, hearing systems can fully adapt to aerial transmission, a shift which should be reflected in their sensory anatomy and function. Phylogenetic analyses frequently recover *Seymouria* close to the origin of amniotes and the adults are hypothesized to have been fully terrestrial (Bazzana et al., 2020; Pardo et al., 2017; Ruta et al., 2003; Sullivan & Reisz, 1999); as such, *Seymouria* represents an important data point for understanding the transition to full terrestriality and any associated palaeoneurological changes (Klembara et al., 2020).

Historically, little has been known of the neurocranial anatomy and palaeoneurology of seymouriamorphs; however, with the widespread application of computed tomography (CT) to paleontological specimens, increasing attention is being paid to these previously under-studied aspects of seymouriamorph anatomy. Bazzana et al. (2019) described the hard-tissue neurocranial anatomy of *Seymouria* and Klembara et al. (2020) described the inner ear of both seymouriamorphs and the more crown-ward diadectomorphs. The specimen of *Seymouria* described by Klembara et al. (2020) preserved much of the ventral portion of the inner ear, including the otic tube, cochlear recess, vestibule, and the majority of the lateral semicircular canal (LSC), but preserved very little of the vertical semicircular canals. One of the specimens described by Bazzana et al. (2019) includes a complete, articulated, undistorted braincase, and otic capsule, allowing us to describe these missing elements and to clarify the morphology of the inner ear of *Seymouria*.

While all early tetrapod specimens pose a similar challenge of relatively low ossification of the internal surface of the braincase and, consequently, poor surface detail on any resulting endocast (Clack, 1997; Pardo & Anderson, 2016; Szostakiwskyj et al., 2015), the latter specimen comes from the Dolese Brothers Quarry in Richards Spur, Oklahoma, a locality known for its exceptional preservation (Bazzana et al., 2019; Gee, Bevitt, Garbe, et al., 2019; Gee, Bevitt, & Reisz, 2019). Neutron CT imaging has been successfully applied to fossil specimens from Richards Spur, producing three-dimensional renderings of remarkable quality (Bazzana et al., 2019; Gee, Bevitt, Garbe, et al., 2019; Gee, Bevitt, & Reisz, 2019). Here, we apply neutron CT to the specimen described by Bazzana et al. (2019) to present a more complete endocast of the inner ear of *Seymouria* and the first virtual cranial endocast of any definitive stem amniote (see Klembara et al. [2020] for debate regarding the position of diadectomorphs), providing important details on previously poorly known aspects of seymouriamorph anatomy that augment the growing body of CT work on Palaeozoic tetrapods and on early tetrapod palaeoneurology.

2 | METHODS

2.1 | Specimen

OMNH 79343, partial skull with roof posterior to nasals, occiput, braincase, and palate.

2.2 | Scanning

The external morphology of OMNH 79343 was described by Bazzana et al. (2019) using neutron tomography data taken in Berlin, Germany; details of this scan are given in Bazzana et al. (2019). To improve scan resolution for this study, neutron tomography measurements of OMNH 79343 were carried out at the DINGO thermal-neutron radiography/tomography/imaging stations located at the 20 MW Open-Pool Australian Lightwater reactor (OPAL) at the Australian Nuclear Science and Technology Organisation. For this study, a collimation ratio (L/D) of 1000 (Garbe et al., 2015) was used to ensure the highest available spatial resolution, where L is the neutron aperture-to-sample length and D is the neutron aperture diameter. The final voxel size is $25.0 \times 25.0 \times 25.0 \mu\text{m}$. The individual radiographs were summed in post-acquisition processing using the "Grouped ZProjector" plugin in ImageJ v.1.51h (National Institutes of Health); this plugin was developed by Holly (2004). Tomographic reconstruction of the 16-bit raw data was performed using commercially available Octopus Reconstruction v.8.8 software package and the filtered back-projection algorithm to yield virtual slices perpendicular to the rotation axis. When these slices are stacked in a sequence, they form a three-dimensional volume image of the sample. The cranial and otic endocasts were produced by manual segmentation in Avizo Lite 9.7.0.

2.3 | Institutional abbreviations

OMNH, Sam Noble Museum of Natural History, Norman, OK, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA.

3 | RESULTS

Endocast studies of early tetrapods all face a similar challenge: early tetrapods, including stem and many early amniotes, simply do not display the same degree of braincase ossification or encephalization as that seen in more derived members of either the sauropsid or synapsid lineages. While advances in CT methods allow for much greater resolution of detail than ever before, there is no amount of technological innovation that can eliminate the effects of genuine anatomical differences. While segmentation

software often allows users to artificially smooth the surfaces of segmentations to produce endocasts more visually similar in texture to those of crown taxa, such practices obscure the true nature of the data and should always be avoided (see Balanoff et al., 2016 for discussion of best practices for endocasts). Therefore, due to the low degree of ossification within the braincase and low encephalization resulting in a poor fit between the brain and the surrounding hard tissues in many early tetrapods, including *Seymouria*, the endocast presented here is, by necessity, rough.

3.1 | Brain

The brain endocast of *Seymouria* exhibits a flexure between the hind- and midbrain of approximately 43 degrees (Figure 1; see Macrini et al., 2007 for measurement protocol). The dorsal surface of the hindbrain, bounded laterally by the otic capsule and dorsally by the synotic tectum ossification, is obscured by what appear to be large dorsolaterally expanded sinuses (Figure 2a); these may reflect venous sinuses, or endolymphatic sacs such as have been described in some Palaeozoic temnospondyls (Romer & Edinger, 1942).

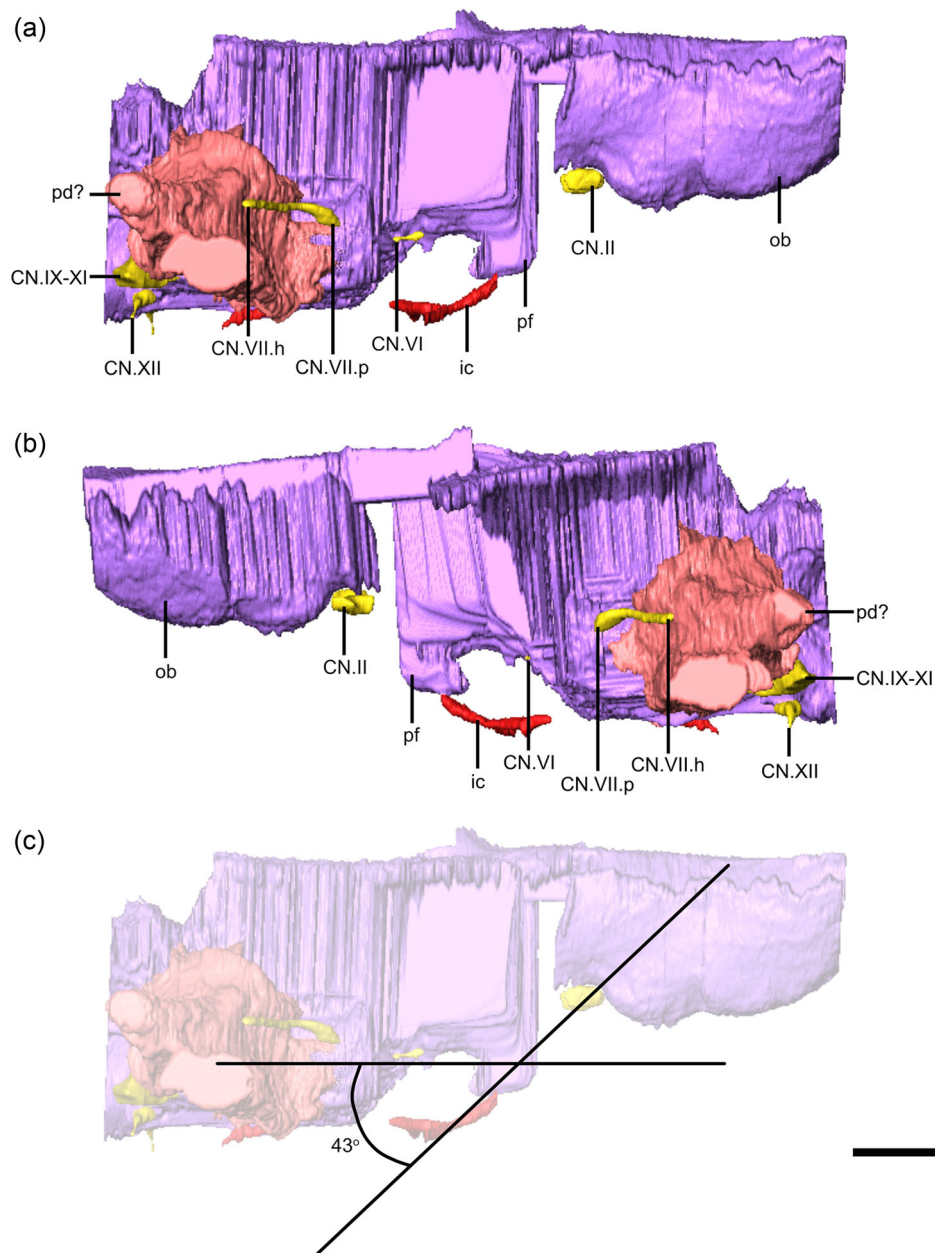


FIGURE 1 Virtual endocast of OMNH 79343 showing the brain, inner ear, and cranial innervations in (a) right and (b) left lateral views, with (c) flexure measurement protocol. Scale bar equals 5 mm. cer, cerebrum; CN. II, optic nerve; CN. VI, abducens nerve; CN. VII.h, hyomandibular branch of the facial nerve; CN. VII.p, palatal branch of the facial nerve; CN. IX-XI, metotic foramen; ic, internal carotid; ob, olfactory bulb; ot, olfactory tract; pd?, putative perilymphatic duct; pf, pituitary fossa.

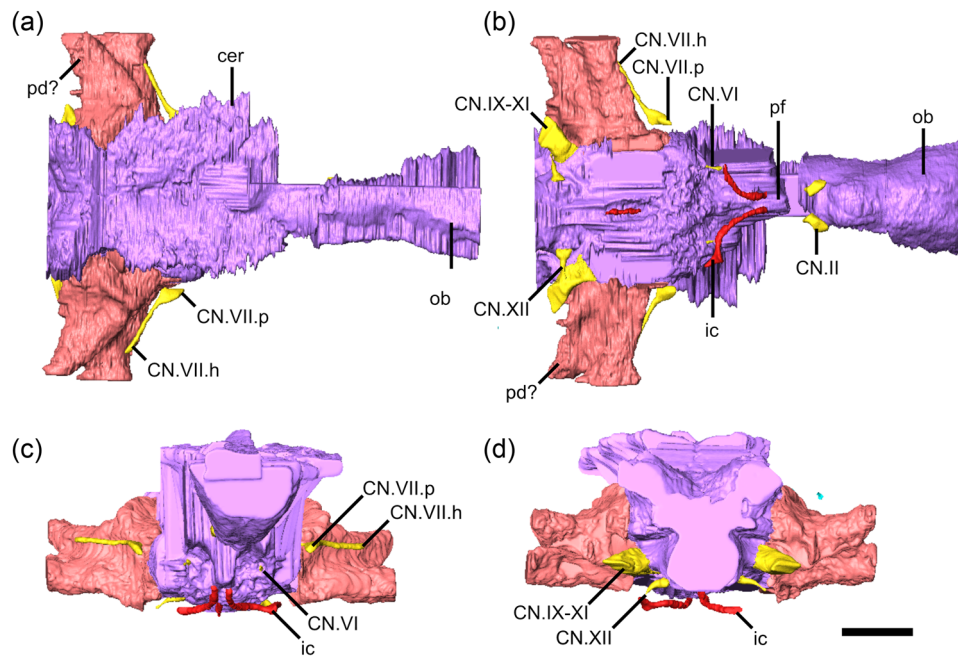


FIGURE 2 Virtual endocast of OMNH 79343 showing the brain, inner ear, and cranial innervations. (a–d) Endocast in (a) dorsal, (b) ventral, (c) anterior, and (d) posterior views. Scale bar equals 5 mm. cer, cerebrum; CN. II, optic nerve; CN. VI, abducens nerve; CN. VII.h, hyomandibular branch of the facial nerve; CN. VII.p, palatal branch of the facial nerve; CN. IX–XI, metotic foramen; ic, internal carotid; ob, olfactory bulb; ot, olfactory tract pd?, putative perilymphatic duct; pf, pituitary fossa.

The region between the posterior margin of the orbitosphenoid and the dorsum sellae and the anterior margin of the otic capsule is unossified, such that only the impression of the cerebrum on the overlying parietals is evident; from this impression the cerebrum does not appear to be expanded; the pituitary fossa is contiguous with the ventral surface of the brain, but its shape cannot be confidently determined (Figure 1). Due to the lack of ossification between the anterior region of the otic capsule and the posterior region of the orbitosphenoid in OMNH 79343, the endocast in this region is amorphous. With the exception of the olfactory bulbs and the pituitary fossa, the ventral surface of the brain is obscured (Figure 2b). The olfactory tracts, which are housed in the U-shaped orbitosphenoid, are short, such that the olfactory bulbs are situated only slightly anterior to the exit of the optic nerve (CN. II; Figure 2b).

3.2 | Innervations and vascularization

The paths of several cranial nerves are preserved in OMNH 79343. The optic nerve (CN. II) passes through the posteroventral-most corner of the orbitosphenoid (Bazzana et al., 2019; Figures 1 and 2b). The abducens nerve (CN. VI) passes anteroposteriorly through the dorsum sellae (Figures 1 and 2b). The facial nerve (CN. VII) enters the prootic anterior to the vestibule, at approximately the dorsoventral midpoint of the inner ear; the palatal branch immediately exits the prootic at the anteriormost edge of the element, while the hyomandibular branch extends posterolaterally at its approximate anteroposterior midpoint (Figures 1 and 2). The metotic foramen,

which typically carries the vagus nerve (CN. X) and associated structures (e.g., CN. IX and CN. XI), is large (Figure 2b,d). A small foramen on the left opisthotic of OMNH 79343 (Bazzana et al., 2019:fig. 5D–E) could represent the exit of cranial nerve IX, but the opening is unpaired and as such its identity remains uncertain. A single hypoglossal nerve (CN. XII) originates ventromedial to the metotic foramen and extends posterolaterally to exit through the exoccipital (Bazzana et al., 2019; Figures 1 and 2d). The internal carotids enter the braincase immediately posterior to the basipterygoid processes and pass anterodorsally to exit the braincase in the pituitary fossa (Figures 1 and 2b–d).

3.3 | Inner ear

Due to the poor ossification of the interior otic capsule in OMNH 79343, the otic endocast reveals rough impressions of all three canals, but their relative lengths cannot be determined, and the ampullae are not discernable (Figures 3 and 4). The anterior semicircular canal (ASC) and the anteriormost portion of the LSC are bounded by the prootic; if present, the anterior and lateral ampullae would also be housed in the prootic based on the highly conserved placement of the ampullae across tetrapods (e.g., Bazzana et al., 2021, 2022; Pardo & Anderson, 2016; Sobral et al., 2016). The opisthotic bounds the posterior semicircular canal (PSC) and the posterior portion of the LSC. The lateral portion of the LSC is heavily obscured in the endocast by what may be a perilymphatic duct or cistern (Figure 2), as have been identified in other anamniotes

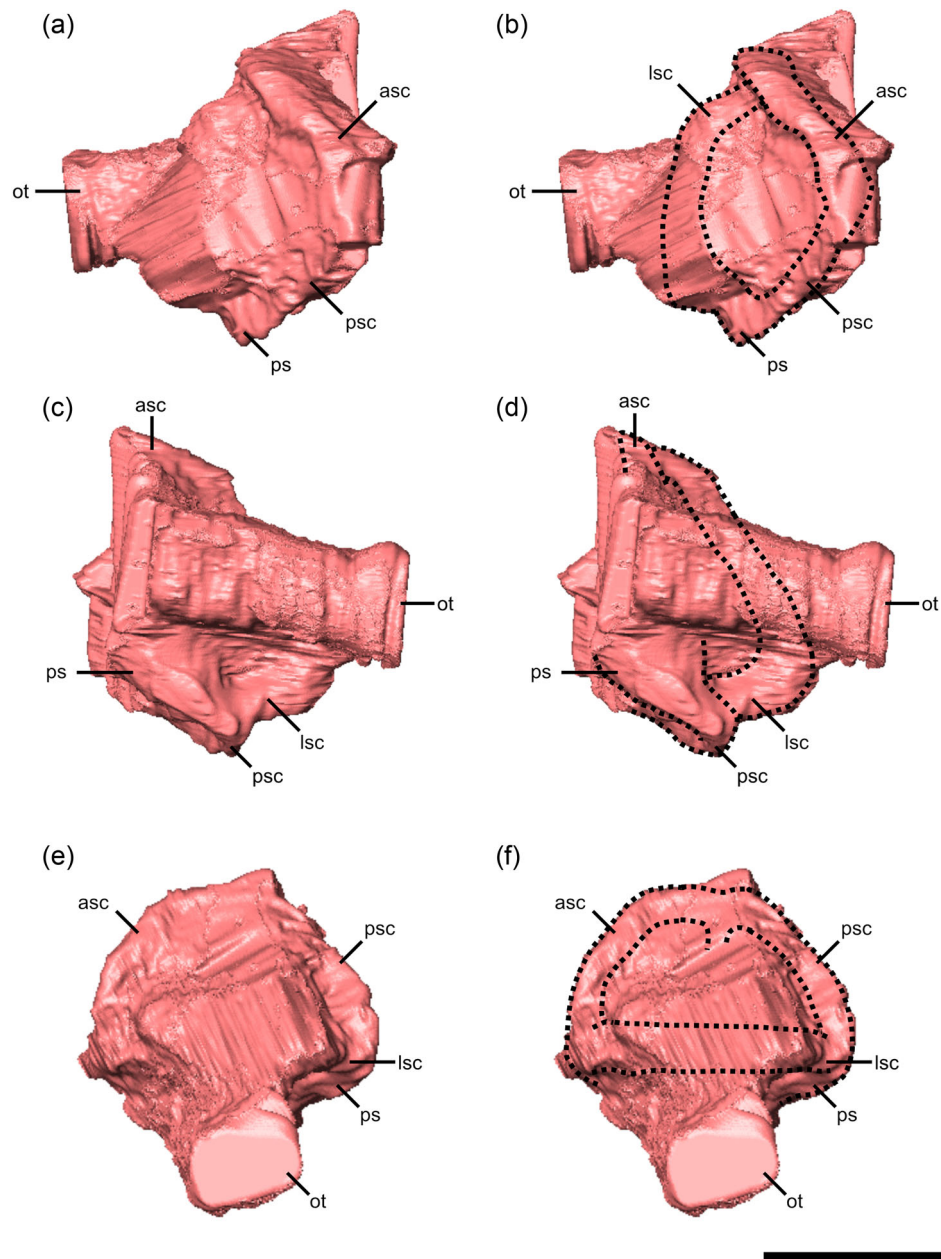


FIGURE 3 Virtual endocast of the left inner ear of OMNH 79343 in (a, b) dorsal, (c, d) ventral, and (e, f) left lateral views. Lines in views (b, d, and f) illustrate the paths of the semicircular canals as visible on the endocast, with dashed lines indicating inferred regions. Scale bar equals 5 mm. asc, anterior semicircular canal; lsc, lateral semicircular canal; ot, otic tube; ps, posterior sinus; psc, posterior semicircular canal; v, vestibule.

(Sigurdson, 2008). An isolated endocast of the inner ear of OMNH 79343, from which the presumed duct is excluded, reveals the impressions of much of the ASC, PSC, and the anterior and posterior portions of the LSC (Figures 3 and 4). The PSC and LSC both enter the posterior sinus before entering the vestibule itself, with the PSC appearing to pass laterally and ventrally to the LSC (Figure 4c,d). While the junction of the ASC and PSC within the common crus is not visible, the relative angles of the two canals in lateral view indicates that the ASC is more dorsally elevated than the PSC, suggesting that it is likely longer as well (Figure 3e,f). The semicircular canals are

suborthogonal (Table 1), with the angle between the PSC and LSC being the most orthogonal and that between the ASC and LSC being the least orthogonal. The radius of curvature and degree of eccentricity of the canals cannot be determined.

The morphology of the vestibule is obscured by the otic tube, which connects the vestibule to the fenestra vestibuli (Figures 3 and 4) and is framed jointly by the prootic, opisthotic, and parasphenoid (Bazzana et al., 2019). Despite the apparent presence of a cochlear recess on the anterior surface of the opisthotic (Bazzana et al., 2019) and the description of a cochlear recess in another

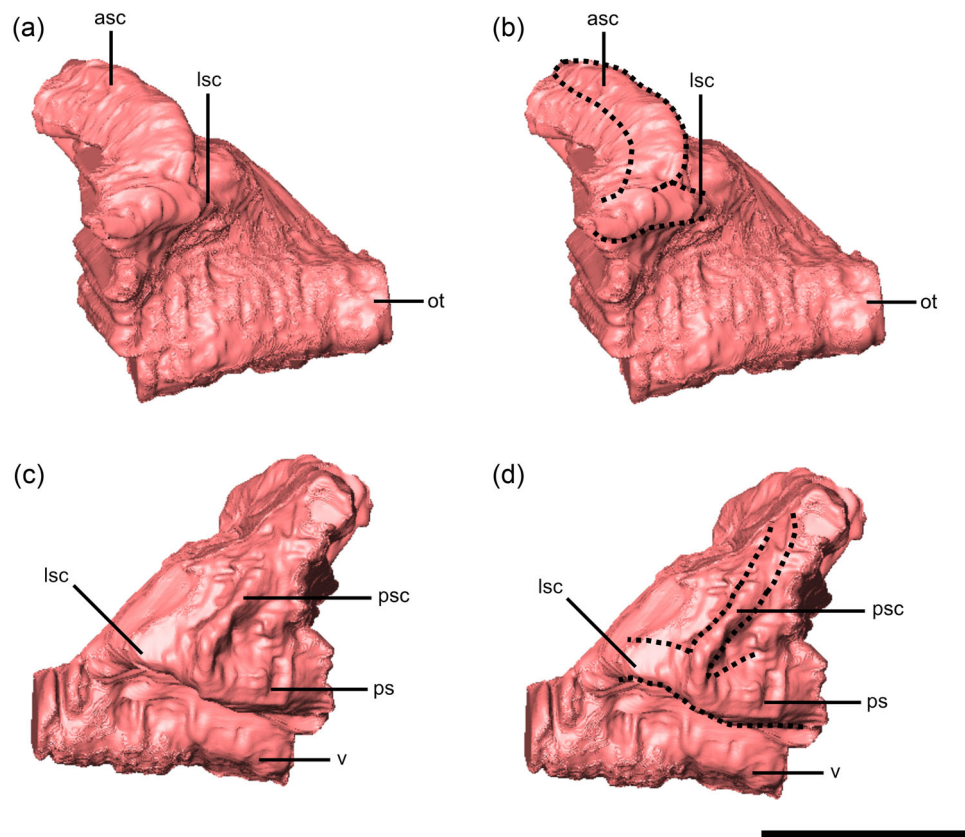


FIGURE 4 Virtual endocast of the left inner ear of OMNH 79343 in (a, b) anterior, and (c, d) posterior views. Lines in views (b and d) illustrate the inferred paths of the semicircular canals. Scale bar equals 5 mm. asc, anterior semicircular canal; lsc, lateral semicircular canal; ot, otic tube; ps, posterior sinus; psc, posterior semicircular canal; v, vestibule.

TABLE 1 Orthogonality measurements for the semicircular canals of *Seymouria*.

	Left	Right	Average
\angle ASC-PSC ($^{\circ}$)	83	79	81
\angle PSC-LSC ($^{\circ}$)	94	86	90
\angle ASC-LSC ($^{\circ}$)	75	76	75.5

Abbreviations: ASC, anterior semicircular canal; LSC, lateral semicircular canal; PSC, posterior semicircular canal.

specimen of *Seymouria* (Klembara et al., 2020), we are unable to identify a distinct recess on the endocast of OMNH 79343.

4 | DISCUSSION

4.1 | Comparative anatomy

Here, we provide a brief comparative discussion of our findings with those of previous workers regarding other Palaeozoic tetrapods, focusing on taxa on either side of the transition to crown amniotes. Comparisons with taxa outside of crown Amniota are limited due to

the paucity of endocast studies on anamniotes. Table 2 provides a brief summary of some key differences in selected traits across taxa.

The brain of *Seymouria* is similar to those of other Palaeozoic taxa, in particular in the generally amorphous nature of the cranial endocast (Bazzana et al., 2021; Romer & Edinger, 1942). The flexion is similar to that seen in captorhinids (Bazzana et al., 2022), contrasting with the more tubular brains of the temnospondyl *Edops* or the varanopid synapsids (Bazzana et al., 2021; Romer & Edinger, 1942); however, the flexion in *Seymouria* is markedly less than that seen in more derived therapsids (Benoit, Fernandez, et al., 2017). The lysorophian *Brachydectes* also shows a slight degree of flexion, but with the hindbrain angled posterodorsal to the midbrain, rather than posteroventral (Pardo & Anderson, 2016: fig. 13). The positioning of the olfactory bulbs directly next to each other in *Seymouria* differs from the condition seen in *Edops* wherein the bulbs are laterally separated (Romer & Edinger, 1942).

As with the brain, the inner ear of *Seymouria* appears largely plesiomorphic in most aspects relative to crown amniotes. The lack of an ossified medial wall is a trait shared across many Palaeozoic taxa including temnospondyls (Romer & Edinger, 1942), captorhinids (Heaton, 1979), microsaur (Maddin et al., 2011), and several early synapsids (Bazzana et al., 2021; Clack, 1997). Similarly, the lack of a distinct cochlear recess is common in early tetrapods, including

TABLE 2 Comparison of various palaeoneurological traits in selected Palaeozoic taxa.

	Temnospondyli*	Seymouria*	Varanopidae ⁺	Dimetrodon ⁺	Microsauria [^] ^Δ	Captorhinus [^] ^Δ
Encephalization	Low	Low	Low	Low	Low	Low
Brain flexure	15°	43°	17°	45°	38°	42°
Medial wall of otic capsule	Unossified	Unossified	Partially ossified	Partially ossified	Unossified	Unossified
Cochlear recess	Absent	Absent	Absent	Absent	Absent	Small
Stapes attachment	Immobile	Mobile	Immobile	Immobile	Immobile	Immobile
Stapes morphology	Large, robust	Small, gracile	Large, robust	Large, robust	Large, robust	Large, robust

Note: Character states for temnospondyls from Romer and Edinger (1942) and Schoch (2019), varanopids from Bazzana et al. (2021), Captorhinus from Bazzana et al. (2022), and microsauria from Pardo and Anderson (2016) and Maddin et al. (2011). Character states for Dimetrodon from personal observations of endocasts by KBA. Phylogenetic position of microsauria taken from Pardo et al. (2017). Labels: *anamniote taxa, ^amniote taxa, +synapsids, Δsauropsids.

varanopids (Bazzana et al., 2021) and microsauria (Maddin et al., 2011). Bazzana et al. (2019) described a lagenar (cochlear) recess on the anterior surface of the opisthotic of OMNH 79343; however, given the absence of an identifiable recess on the endocast, the identified recess on the opisthotic likely simply represents the posterior surface of the vestibule.

Cochlear recesses have been identified previously in *Seymouria* and in several diadectomorphs (Klembara et al., 2020, 2021); the lack of an identifiable recess in OMNH 79343 suggests two possibilities. First, there may simply be preservational differences between the specimen described here and that described in Klembara et al. (2020; MCZ 1086), such that the ventral portion of the opisthotic is more fully ossified in the latter specimen and thus preserves the cochlear recess where OMNH 79343 does not. However, given the greater surface detail overall in the otic endocast of OMNH 79343 relative to MCZ 1086 (Figures 3 and 4; Klembara et al., 2020:fig. 8C-D), this seems unlikely. Alternatively, both OMNH 79343 and MCZ 1086 may be preserving the same structures but with preservational differences creating difficulties in their interpretation. In OMNH 79343, the only visible protrusion on the posterior surface of the inner ear is the posterior sinus wherein the posterior and lateral canals enter the vestibule. In MCZ 1086, the lack of much of the dorsal portion of the inner ear precludes identification of the path of the posterior canal or its entrance into the vestibule, with the identified cochlear recess being strongly similar in shape to the posterior sinus of OMNH 79343 (Klembara et al., 2020:figs. 3E-F, 8C-D).

The cochlear recesses identified in the diadectomorphs are situated at the junction of the lateral and posterior semicircular canals (Klembara et al., 2020:figs. 3-4; Klembara et al., 2021:fig. 13). We were unable to locate any examples of a cochlear recess situated at the junction of the lateral and posterior canals in any taxa other than those described by Klembara et al. (2020, 2021); while it is possible that diadectomorphs independently evolved a recess that both housed the cochlea and allowed for the passage of the posterior and lateral canals into the vestibule, no such structure is currently known in any other taxon, and how such a structure would function is

unclear. Not only would the recess need to house two different sensory organs that require different sensory input, but the basilar papilla (the sensory organ contained within the cochlea that is responsible for the perception of sound) would not be immediately accessible by any pressure waves produced by activation of the fenestra vestibuli. In light of the lack of any other examples of this particular morphology or of a clear functional explanation, comparison of the identified recesses in the diadectomorphs with the endocast of OMNH 79343, and with those of other Palaeozoic tetrapods, suggests that the protrusions identified as cochlear recesses may instead represent the posterior sinus.

The inner ear of *Seymouria* differs from that of the diadectomorphs in being housed primarily within the prootic and opisthotic, with no apparent contribution by the synotic tectum ossification, a structure similar but not necessarily homologous to the supraoccipital of diadectomorphs and crown amniotes (see discussion in Bazzana et al., 2019); in the diadectomorphs *Diadectes* and *Orobates*, the supraoccipital houses the dorsalmost portion of the inner ear (Klembara et al., 2020). The curved outline of the semicircular canals of OMNH 79343 in lateral view indicate that the canals of *Seymouria* are more circular than those of the diadectomorphs *Limnoscelis* and *Diadectes* (Klembara et al., 2020, 2021), being more similar in curvature to those seen in the early-diverging synapsid clade Varanopidae (Bazzana et al., 2021) and in captorhinids (Bazzana et al., 2022; Klembara et al., 2020). The lack of obvious ampullae of the semicircular canals is a trait shared between *Seymouria* and *Limnoscelis* (Klembara et al., 2021), differing from the more prominent ampullae of some temnospondyls (Robinson et al., 2005), varanopids (Bazzana et al., 2021), and captorhinids (Bazzana et al., 2022; Klembara et al., 2020). A canal for the endolymphatic duct has been identified in both *Diadectes* and *Limnoscelis* (Klembara et al., 2020, 2021), but no canal could be seen in OMNH 79343.

The path of the internal carotids in *Seymouria* is similar to that seen in nonmammalian synapsids and early eureptiles (Müller et al., 2011). Due to the identification of a single path for the carotid arteries within the parabasisphenoid of *Seymouria*, it is most likely that the internal carotid identified here specifically represents the

cerebral branch of the carotid artery (Müller et al., 2011). A comprehensive overview of amniote carotid circulation by Müller et al. (2011) identified varying patterns of bifurcation of the cerebral and palatal branches of the carotid artery, with varying degrees of closure of the Vidian sulcus. An important conclusion proposed by Müller et al. (2011) was that the condition seen in many synapsids and early eureptiles, in which the carotid branches bifurcate before entering the (para)basisphenoid, such that the palatal branch continues anteriorly ventral to the braincase while the cerebral branch enters the braincase posterior to the basiptyergoid processes and exits into the pituitary fossa, is plesiomorphic for amniotes. While the foramina for the internal carotids in *Seymouria* were identified by White (1939), our reconstruction of the path of the arteries through the parabasisphenoid confirm the identification of these arteries as the cerebral branches and lend further support to the hypothesis of Müller et al. (2011) regarding the plesiomorphic state for crown Amniota.

4.2 | Functional implications

As a whole, the endocasts described here do not reveal any obvious neuroanatomical specializations in *Seymouria* (e.g., no expansion of any brain regions). While the low encephalization and the generally amorphous nature of the endocasts may well be obscuring evidence of specialization that was indeed present, the potential position of *Seymouria* as transitional along the development of an impedance-matching hearing system bears further consideration.

The osteology of *Seymouria* indicates that the taxon likely had an impedance-matching hearing system, although the mechanism by which this impedance matching occurred is unclear (Bazzana et al., 2019). The stapes of *Seymouria* is small, gracile, and positioned next to the fenestra vestibuli with the distal end directed toward the tympanum, and a possible pressure-relief window has been identified (Bazzana et al., 2019). However, there is no stapedia footplate and the stapes does not contact any of the surrounding elements, unlike that of many other Palaeozoic tetrapods (Heaton, 1979; Modesto et al., 2009; Schoch, 2019). While the lack of an ossified contact between the stapes and any other element results in a degree of uncertainty regarding its life position, the similarity in positioning of the stapes of OMNH 79343 and that of an additional skull of *Seymouria*, described by Bazzana et al. (2019), supports the inference that the stapes spanned the space between the fenestra vestibuli and the presumed tympanum (Bazzana et al., 2019:figs. 3D,4D).

Figure 5 illustrates the position of the stapes as preserved in OMNH 79343 and its relation to the otic notch, fenestra vestibuli, and otic tube. However, the morphology of the stapes as preserved does not clearly indicate how the stapes would have contacted either the tympanic membrane or the fenestra vestibuli. If *Seymouria* did in fact possess an impedance-matching hearing system, it is possible that both the footplate and the contact with the tympanum were cartilaginous; alternatively, OMNH 79343 may not represent a completely skeletally mature individual, as the stapedia footplate is

known to be the last portion of the stapes to ossify (Ollonen et al., 2018), and thus the lack of a footplate in described specimens of *Seymouria* may reflect immaturity. If the contact with the tympanum was cartilaginous, the dorsal process could represent the attachment for a cartilaginous process similar to that seen on the extrastapes of some modern sauropsids (Allin & Hopson, 1992). However, the inferred orientation of the stapes in life suggests that the dorsal process extended toward the skull roof (Bazzana et al., 2019), not laterally toward the presumed tympanum, rendering the possibility of a tympanum-stiffening function unlikely. This further muddles any determination of the precise functioning of the ear of *Seymouria* because, if the dorsal process did contact the skull, this would hinder the ability of the stapes to vibrate freely and therefore to activate the fenestra vestibuli, thus reducing the sensitivity of the ear.

Similarly, it is unclear how efficiently any pressure waves could be transmitted from the fenestra vestibuli to the basilar papilla in the inner ear. The vestibule, and any sensory structure therein, are separated from the fenestra vestibuli by the long otic tube, presenting two potential functional difficulties. First, any waves within the inner ear endolymph created by activation of the fenestra vestibuli would need to travel most, if not the entire length of the tube before reaching the basilar papilla. While fluids are excellent conductors of pressure waves, there are few examples of the basilar papilla being so widely separated from the fenestra vestibuli (see Benoit, Manger, et al., 2017), and as such the impact of such a large distance on the sensitivity of the basilar papilla is unknown. Second, the nature of the entry from the otic tube into the inner ear proper is as-yet unknown. An open meatus allowing for continuous fluid flow between the fenestra vestibuli and the basilar papilla would allow for much greater sensitivity than would a membranous window; such an additional window is not known in any taxon, extant or extinct, but neither is the presence of a large lateral extension of the vestibule such as would be required if the otic tube were in fact part of a continuous flow of endolymph. In either situation, depending on the characteristics of the fluid filling the otic tube and on the unknown nature of the transition from the otic tube to the vestibule, the power of those waves could be markedly reduced. This would in turn reduce the sensitivity of the hair cells on the basilar papilla to any sound waves, as the bending energy applied to them would be lessened.

Seymouria exhibits a mix of features, some of which support the presence of impedance-matching hearing (e.g., small gracile stapes, possible presence of a large tympanum, probable pressure relief window [see Bazzana et al., 2019]) and some which do not (e.g., apparent absence of stapedia footplate or contact with the tympanum, long otic tube). Impedance-matching hearing is known to have evolved independently multiple times within tetrapods (Clack, 2002; Laurin, 1998; Robinson et al., 2005). While the acquisition of impedance matching is always associated with certain similar adaptations (e.g., the development of small mobile middle ear ossicles and a pressure-release system), the various independent origins of impedance-matching are associated with variations in overall otic capsule structure, such that the impedance-matching ears

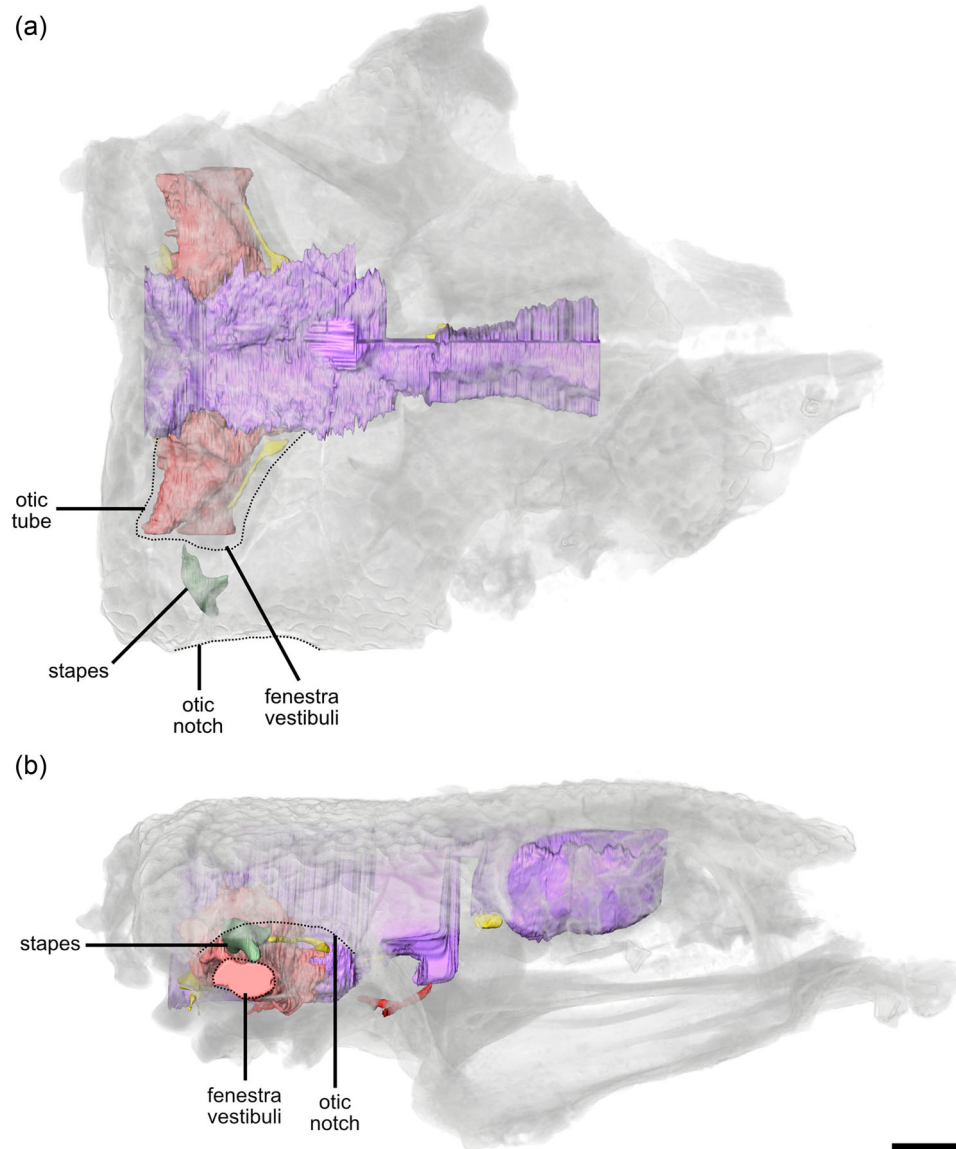


FIGURE 5 Semitransparent volume renderings showing position of endocranium within skull and relative positions of stapes, fenestra vestibuli, and otic notch in (a) dorsal and (b) right lateral views. Scale bar = 1 cm.

of sauropsids, synapsids, and amphibians can all be clearly shown to have arisen independently (Clack, 2002; Laurin, 1998; Robinson et al., 2005). The ear morphology of *Seymouria* is markedly different from that of any Palaeozoic amniote or temnospondyl, raising two possibilities: (i) that *Seymouria* did in fact possess an impedance-matching hearing system and thus represents yet another independent acquisition of impedance-matching among tetrapods, or (ii) that *Seymouria* represents a transitional stage in the development of impedance-matching, such that the apparent morphological contradictions reflect the on-going assembly of an auditory system specialized for aerial sound reception. Many of the functional systems observed in crown tetrapods are known to have developed in a piecemeal or mosaic fashion (e.g., Azuma et al., 2016; Luo, 2007; Rowe et al., 2011), and the ambiguity in *Seymouria* may be capturing this process.

While endocranium data for early amniotes is scarce, significant efforts are being made to describe the neuroanatomy of both stem amniotes and early crown amniotes (Bazzana et al., 2021, 2022; Klembara et al., 2020, 2021), and some tentative conclusions may begin to be drawn. The overall similarity between the brain and inner ear of *Seymouria* and those of basal representatives of both the sauropsid and synapsid lineages, in particular the low ossification, low encephalization, and the lack of expansion of any regions that would suggest particular sensory specializations, suggests that the palaeoneuroanatomy of early amniotes as a whole may have been largely conserved for much of the earliest phases of amniote evolution. The increase in encephalization and braincase ossification, and thus the strong relationship between endocranial cavities and the morphology of neurological structures, have long been suggested to arise independently in derived members of both the sauropsid and

synapsid lineages of amniotes (Jerison, 1973; Streidter, 2005; Tsuboi et al., 2018). Similarly, the otic capsules have long been hypothesized to have increased in ossification independently in either lineage (Clack, 1997). However, endocast-based evidence for the absence of these traits in stem amniotes has been lacking, with previous descriptions relying solely on osteological correlates for neuro-anatomical features. The cranial and otic endocasts described here add to the body of work begun by Klembara et al. (2020, 2021) to provide the first three-dimensional evidence that these traits were not yet present along the amniote stem and lend support to the hypothesis that increased encephalization and ossification only arose among crown Amniotes.

5 | CONCLUSION

This study represents the first tomographic study of the brain of any stem amniote, and the novel data described here reveal aspects of seymouriamorph neuroanatomy that have previously gone unrecognized or undescribed. The reconstructed neurosensory anatomy provides substantial evidence in support of multiple long-standing hypotheses regarding neuroevolution in early amniotes, including the path of the carotid artery and the pattern of ossification and encephalization. Differentiating between traits that are plesiomorphic to crown tetrapods, those generalized for crown amniotes, and those apomorphic for more exclusive clades will become clearer with increased sampling along the amniote stem, strengthening the foundation for neuroevolutionary interpretations in crown amniotes. The seemingly conflicting evidence for impedance-matching in *Seymouria* raises the possibility that seymouriamorphs may represent transitional morphologies in the sensory adaptations that frequently accompany full terrestrialization.

AUTHOR CONTRIBUTIONS

Kayla D. Bazzana-Adams: Conceptualization; investigation; writing—original draft; writing—review and editing; methodology; visualization. **David C. Evans:** Writing—review and editing; project administration; supervision; resources. **Joseph J. Bevitt:** Data curation; methodology. **Robert R. Reisz:** Conceptualization; funding acquisition; writing—review and editing; resources; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in MorphoSource at <https://www.morphosource.org/concern/media/000448879?locale=en>.

ORCID

Kayla D. Bazzana-Adams  <http://orcid.org/0000-0002-9982-6210>

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