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# Ontogenetic Changes in the Endocast and Endosseous Labyrinth of the Siamese Freshwater Crocodile (*Crocodylus siamensis* Schneider, 1801) from Thailand

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Ontogenetic changes in the brain and sensory systems play an essential role in shaping behavioral performance and ecological specialization in vertebrates; however, these developmental pathways are inadequately recorded in endangered crocodylians. Here, we present the first quantitative analysis of endocast and endosseous labyrinth development across ontogeny in the Siamese freshwater crocodile (*Crocodylus siamensis*), a critically endangered species from Southeast Asia. Using high-resolution computed tomography (CT) and three-dimensional reconstruction, we examined six skulls representing juvenile, subadult, and adult growth stages. Our findings reveal a consistent pattern of allometric scaling, correlated with marked morphological changes in sensory-related neuroanatomical structures. Juveniles display strongly curved forebrains and proportionally prominent olfactory regions, which is in line with their early reliance on chemosensory cues. As skull size increases, the encephalic endocast becomes longer and straighter, while regions corresponding to the midbrain and hindbrain show proportional morphological changes associated with visual processing and motor coordination, suggesting ontogenetic changes in regions associated with visual processing and motor coordination. Parallel ontogenetic transformations are also observed in the endosseous labyrinth, including increased lagena dimensions and more pronounced semicircular canal curvature in adults. These changes are consistent with ontogenetic variation in structures associated with auditory and vestibular functions. Strong correlations between dorsal cranial length and both endocast and labyrinthine parameters suggest that sensory-related neuroanatomical morphology in *C. siamensis* follows a consistent

ontogenetic scaling pattern. These findings establish an important neuroanatomical baseline for understanding sensory ecology in this endangered crocodilian and provide a comparative framework for interpreting fossil crocodylian neuroanatomy, with implications for conservation biology, functional morphology, and paleoneurology.

**Keywords:** Crocodylians, *Crocodylus*, Ontogenetic development, Endocast, Endosseous labyrinth

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## BACKGROUND

Ontogenetic changes of the vertebrate brain reflect a complex interplay among growth, sensory demands, and ecological transitions across life stages. As animals increase in size, the relative proportions and organization of endocast regions are reshaped in ways that reflect changing behavioral strategies, locomotor performance, and habitat use (Dodson 1975; Witmer 1995; Shingleton 2010; Gignac and Erickson 2015; Blanco et al. 2018; Schwab et al. 2022). These developmental trajectories provide valuable insights into neuroanatomical variation and offer an important framework for interpreting evolutionary patterns preserved in both living and fossil reptiles, including crocodylians, lizards, snakes, and turtles (Witmer et al. 2008; Vergne et al. 2009; Carabajal et al. 2013; Allemand et al. 2023).

Crocodylians represent an informative lineage for examining ontogenetic brain development among extant reptiles because they combine prolonged growth, marked increases in body size, and clear ecological shifts from juvenile to adult stages with a broadly conserved brain organization (Radloff et al. 2012; Hu et al. 2021; Lessner and Holliday 2022; Schwab et al. 2021 2022). The crocodylian brain is classically divided into the forebrain, midbrain, and hindbrain, each of which follows distinct developmental and functional pathways (Pritz 2015; Watanabe et al. 2019; Whitlock and Palominos 2022). Although encephalic endocast size increases throughout ontogeny, it scales more slowly than overall body growth, a common vertebrate pattern interpreted as reflecting evolutionary trade-offs in sensory processing and motor control (Chentanez et al. 1983; Ngwenya 2013; Schwab et al. 2022). Importantly, endocasts should not be interpreted as direct replicas of the brain. Jirak and Janacek (2017) emphasized that endocasts represent the dural envelope and associated interstitial space

rather than the brain itself, while Hu et al (2021) further clarified that endocasts capture the contents of the cranial cavity, including meninges and vasculature. These considerations underscore the need for caution when inferring brain morphology from digital endocasts.

Alongside the encephalic endocast, the endosseous labyrinth undergoes substantial ontogenetic and evolutionary modification. Variation in the geometry of the semicircular canals and lagena is closely associated with balance, spatial orientation, and hearing sensitivity, particularly in semi-aquatic taxa that occupy both aquatic and terrestrial environments (Ifediba et al. 2007; Georgi 2008; Ekdale 2016; Manley 2017; Lauprasert et al. 2019; Schwab et al. 2020 2021; Pochat-Cottilloux et al. 2024). Consequently, endocranial and labyrinthine morphologies together provide useful morphological proxies for generating hypotheses about sensory function, locomotor behavior, and ecological variation across growth stages (Barrios et al. 2022; Schwab et al. 2022). Beyond their morphological significance, crocodylian neuroanatomical structures have become increasingly important in evolutionary and phylogenetic studies, providing new insights into character evolution, developmental trajectories, and broader crocodylomorph relationships (Barrios et al. 2022; Dumoncel et al. 2021; Ristevski 2022; Pochat-Cottilloux et al. 2024; Burke et al. 2025; Burke and Mannion, 2026). Comparative studies of extant crocodylians have further demonstrated that braincase and endocranial morphology preserve important signals of developmental and evolutionary change (Kuzmin et al. 2021). However, despite these advances, neuroanatomical data for *Crocodylus siamensis* remain extremely limited, with previous work restricted primarily to adult specimens (Perrichon et al. 2023), emphasizing the importance of the present ontogenetic study. Recent advances in non-destructive imaging, particularly computed tomography (CT) and magnetic resonance imaging (MRI), have greatly improved the resolution and accuracy of such investigations (Witmer et al. 2008; Jirak and Janacek 2017).

Studies focusing on crocodylian neuroanatomy have increased in recent years, including reconstructions of extant species of *Alligator* (Dufeau and Witmer 2015; Witmer and Ridgely 2008; Barrios et al. 2022; Lessner and Holliday 2022; Perrichon et al. 2023), *Crocodylus* (Witmer et al. 2008; Kawabe et al. 2010; Perrichon et al. 2023), *Gavialis* (Gold et al. 2014; Pierce et al. 2017; Burke and Mannion 2023; Perrichon et al. 2023; Burke et al. 2025; Castillo and Gold 2025), and *Tomistoma* (Barrios et al. 2022; Burke and Mannion 2023; Perrichon et al. 2023; Burke et al. 2025). Several fossil crocodylians have also been reconstructed (Bona et al. 2013 2015; Ristevski et al. 2020 2021; Schwab et al. 2021; Dumont et al. 2022; Ristevski 2022; Barrios et al. 2022; Burke and Mannion 2023; Perrichon et al. 2024; Burke et al. 2025; Pligersdorffer et al. 2025; Donzé et al. 2026). Nevertheless, developmental or ontogenetic studies remain limited, with most research focusing either on specific

anatomical systems, such as the intertympanic sinus (Perrichon et al. 2023), or on single taxa, including recent work on gavialids (Castillo and Gold 2025). As of yet, detailed ontogenetic studies integrating both the encephalic endocast and endosseous labyrinth remain unavailable for Crocodyloidea and the genus *Crocodylus*. Furthermore, neuroanatomical development of *Crocodylus siamensis* has not previously been investigated, as existing studies have focused only on adult specimens (Perrichon et al. 2023). This gap is particularly important given the conservation status of the Siamese freshwater crocodile *(Crocodylus siamensis* Schneider, 1801), a large freshwater species formerly widespread across mainland Southeast Asia (Sam et al. 2015). The species is listed as Critically Endangered by the IUCN and has suffered dramatic population declines due to habitat loss, illegal hunting, and human–crocodile conflict (Bezuijen et al. 2012 2013; Chitchamnong et al. 2016; IUCN 2025). In Thailand, only small, fragmented wild populations persist, in stark contrast to the rapidly expanding captive-bred population, now estimated at 250,000–300,000 individuals (Yangprapakorn, 2009; Sudrajat and Saleh 2019; Ratanakorn et al. 2021).

Understanding ontogenetic changes in the endocast and sensory systems of *C. siamensis* can contribute to conservation planning because different life stages are likely to respond differently to environmental conditions and habitat disturbance. Juveniles typically inhabit structurally complex freshwater environments and rely heavily on cryptic behavior and early sensory detection, whereas larger individuals increasingly exhibit ecological and behavioral patterns associated with visually guided predation, more active locomotion, and broader habitat use (Hutton 1987; Dufeau and Witmer 2015; Sam et al. 2015; Schwab et al. 2022). Identifying how sensory structures change through ontogeny may therefore help explain age-specific ecological requirements and behavioral adaptations relevant to habitat management, captive breeding, and reintroduction programs in Thailand, where wild populations remain highly fragmented. To investigate these patterns, we examined ontogenetic variation in the endocast and endosseous labyrinth of *C. siamensis* using high-resolution computed tomography and three-dimensional digital reconstruction. Three-dimensional imaging provides a non-destructive approach for visualizing internal cranial anatomy with high anatomical accuracy, allowing quantitative assessment of endocast and endosseous labyrinth morphology that cannot be reliably observed through external examination alone (Witmer et al. 2008; Jirak and Janacek 2017). By quantifying changes in encephalic endocast morphology relative to skull growth, this study establishes the first integrated developmental framework for *C. siamensis* and provides new insights into ontogenetic neuroanatomical variation in crocodylians, with implications for conservation biology, functional morphology, and paleoneurology.

## MATERIALS AND METHODS

### Specimen collection and Ontogenetic stage groupings

Between June 2024 and March 2025, six cleaned skeletal skulls of the Siamese crocodile (*Crocodylus siamensis*) were examined to represent different ontogenetic stages within an exploratory developmental framework. The limited sample size reflects the rarity and Critically Endangered status of the species, as access to complete cranial material suitable for high-resolution analysis is inherently constrained. Specimens were selected based on completeness and size variation to capture broad ontogenetic trends rather than population-level variation. Based on the dorsal cranial length (DCL)-based ontogenetic classification, the sample comprised one juvenile specimen, three subadult specimens, and two adult specimens (total $n = 6$; Table 1). Four skulls (SMF01–SMF04) were obtained from the Sinsup Mulmat Crocodile Farm, Maha Sarakham Province, Thailand, and two specimens (SHM–R14 and SHM–R15) were examined from the collections of the Paleontological Research and Education Centre, Mahasarakham University, where all materials are permanently housed. The original provenance of SHM–R14 and SHM–R15 was not documented prior to donation; however, given the rarity of wild *C. siamensis* in Thailand and legal restrictions on wild specimens, these individuals are most likely to have originated from captive sources. All specimens were studied with institutional approval and in accordance with relevant regulations.

Dorsal cranial length (DCL) was measured from the tip of the premaxilla to the posterior margin of the parietal (Fig. 1), following established protocols (Chentanez et al. 1983; Platt et al. 2009). Measurements were taken using a measuring tape and 3D Slicer software, with a precision of ±0.01 mm. Each measurement was repeated three times for each specimen, and the mean value was used for subsequent analyses. Because cranial growth trajectories differ among crocodylian genera, the DCL-based ontogenetic categories used here are intended specifically for *Crocodylus*. Ontogenetic stages were assigned primarily based on DCL ranges following previous ontogenetic assessments (Perrichon et al. 2023), with juvenile, subadult, and adult stages interpreted as approximate developmental categories rather than strict size thresholds (Table 1).

**Tables 1.** Skull samples of freshwater crocodile (*Crocodylus siamensis*) skull length and Ontogenetic stage used in the study

| Specimens | Dorsal cranial length; DCL (cm) | Ontogenetic stage |
|---|---|---|
| SMF01 | 15.44 | juvenile |
| SMF02 | 25.03 | sub-adult |
| SMF03 | 22.11 | sub-adult |
| SMF04 | 24.37 | sub-adult |
| SHM-R14 | 44.38 | adult |
| SHM-R15 | 33.48 | adult |

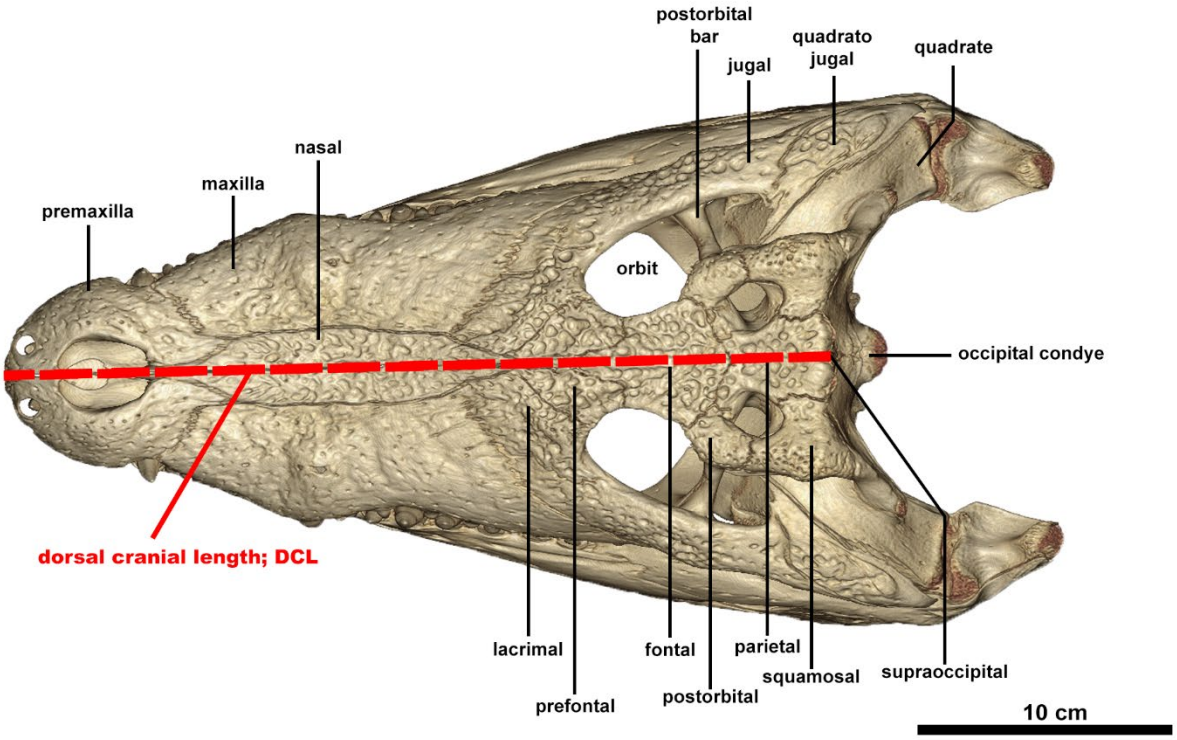


**Fig 1.** Measurement of the length from the tip of the premaxilla to the parietal bone (*Crocodylus siamensis*; SHM-R15).

## Computed Tomography (CT) Scanning

All six skulls were scanned at the Faculty of Medicine, Mahasarakham University, using a Canon Aquilion Prime SP CT scanner. Scans were acquired at 120 kV and 250 mA, with a slice thickness of 0.5 mm. Data were stored in DICOM format and subsequently imported into 3D Slicer (version 5.6.2) for digital processing. Manual segmentation and volume rendering were conducted in 3D Slicer using the brush tool to delineate the endocranial cavity and endosseous labyrinth through

consecutive CT slices, generating three-dimensional models for linear and volumetric analyses. The number of slices varied among specimens depending on skull size; however, all specimens were scanned using the same general acquisition settings described above. Delineation of the lagena from adjacent middle-ear and paratympanic regions was based primarily on osteological boundaries visible in the CT data, particularly within the prootic region, and was cross-checked in axial, sagittal, and coronal planes through consecutive slices to ensure consistent anatomical interpretation.

## Terminology

To ensure consistency and reproducibility, anatomical terminology used throughout this study follows standardized nomenclature established in previous comparative neuroanatomical and paleoneurological studies of crocodylians and other vertebrates (Witmer et al. 2008; Pierce et al. 2017; Barrios et al. 2022; Burke and Mannion 2023). Terminology for the endocranial cavity follows conventional vertebrate neuroanatomical definitions, whereas terminology for the inner ear follows established descriptions of the endosseous labyrinth in extant and extinct archosaurs (Ekdale 2016; Schwab et al. 2020 2022). The encephalic endocast, hereafter referred to as the endocast, is defined here as the three-dimensional digital reconstruction of the endocranial cavity derived from computed tomography (CT) data. It represents the internal space occupied by the brain and associated soft tissues, including the meninges, vascular structures, and cerebrospinal fluid spaces, rather than the brain alone (Jirak and Janacek 2017; Hu et al. 2021). For descriptive purposes, the endocast was divided into three major anatomical regions: the prosencephalon (forebrain), including the olfactory bulbs (OB**)**, olfactory tracts (OT**)**, cerebrum, and pituitary region; the mesencephalon (midbrain), represented primarily by the optic tectum; and the rhombencephalon (hindbrain), including the cerebellum, pons, and medulla oblongata.

The endosseous labyrinth refers to the osseous cavity of the inner ear that encloses the membranous labyrinth and comprises the anterior semicircular canal (asc), posterior semicircular canal (psc), lateral semicircular canal (lsc), associated ampullae (ana, poa, and laa), the common crus, vestibule, and lagena. These structures were identified and described following standard anatomical terminology used in previous crocodylian and vertebrate inner ear studies (Ifediba et al. 2007; Ekdale 2016; Schwab et al. 2020; Pochat-Cottilloux et al. 2024).

For all morphometric analyses, length was defined as the maximum anteroposterior dimension, width was defined as the maximum transverse (mediolateral) distance measured between the outermost left and right lateral boundaries of each reconstructed structure, and volume was calculated as the total

segmented three-dimensional space directly derived from CT-based digital reconstructions in 3D Slicer. Angular measurements of the encephalic endocast were defined as the forebrain–midbrain angle (FMA) and midbrain–hindbrain angle (MHA), which represent the relative curvature of the neuroaxis across ontogeny (Barrios et al. 2022).

**Endocast and Endosseous labyrinth Measurements**

All measurements were performed in 3D Slicer using the original CT voxel scale without rescaling. Prior to measurement, each three-dimensional reconstruction was manually aligned in a standardized anatomical orientation, using the rostrocaudal axis of the skull and the midsagittal plane as anatomical references, and positioned centrally to minimize rotational and positional bias. Linear and volumetric measurements were therefore taken directly from the CT-derived models at their original scale. To account for size differences among ontogenetic stages, dorsal cranial length (DCL) was used as the primary size-standardization metric for interspecific and ontogenetic comparisons.

For the encephalic endocast, six parameters were recorded (Fig. 2A, B): (1) endocast length (EL), (2) endocast width (EW), (3) olfactory bulb length (OBL), (4) endocast volume (VE), calculated using segmentation-based volumetric analysis in 3D Slicer, where the endocranial cavity was digitally segmented and total volume was computed using the software's built-in volume calculation tools, (5) forebrain–midbrain angle (FMA), and (6) midbrain–hindbrain angle (MHA) (Pierce et al. 2017; Erb and Turner 2021; Serrano-Martinez et al. 2021; Barrios et al. 2022; Burke and Mannion 2023). To visualize relative proportional changes across ontogeny, three additional indices were calculated from the measured parameters: the endocast length-to-width ratio (EL/EW), olfactory bulb length relative to total endocast length (OBL/EL × 100), and endocast length relative to dorsal cranial length (EL/DCL).

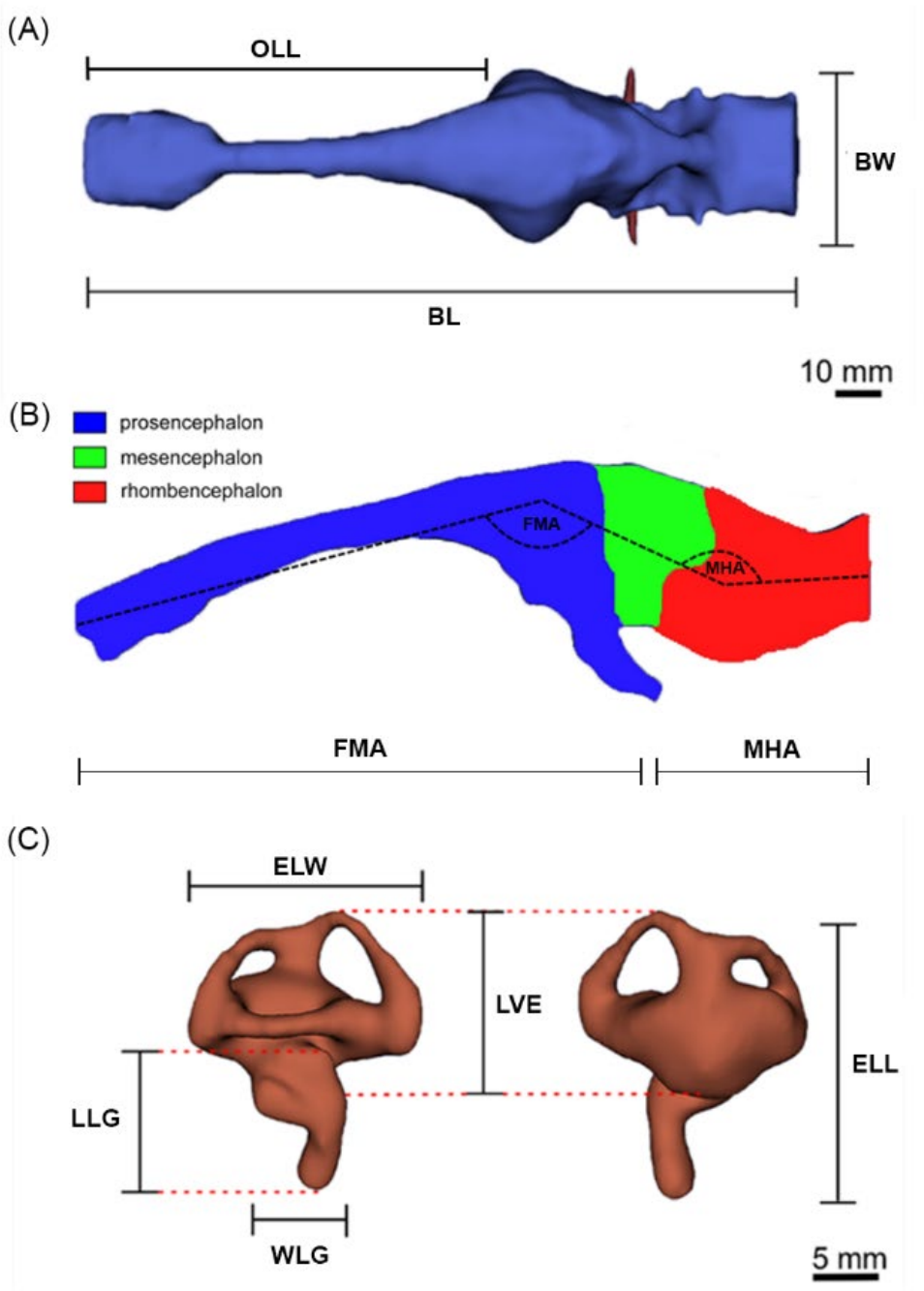


**Fig. 2.** Three-dimensional rendering of the encephalic endocast and endosseous labyrinth of (*Crocodylus siamensis*; SHM-R14) showing. A. measurements of encephalic endocast structures (endocast length; EL, endocast width; EW, olfactory bulb length; OBL). B. Measurements of the forebrain–midbrain angle (FMA; cephalic flexure angle) and midbrain–hindbrain angle (MHA; pontine flexure angle). C. measurements of the endosseous labyrinth (endosseous labyrinth length; ELL, endosseous labyrinth width; ELW, vestibular length; LVE, lagena length; LLG, lagena width; WLG).

For the endosseous labyrinth, six parameters were measured (Fig. 2C): (1) endosseous labyrinth length (ELL), (2) labyrinth width (ELW), (3) vestibular length (LVE), (4) lagena length (LLG), (5)

lagena width (WLG), and (6) labyrinth volume (VOL) (Pierce et al. 2017; Burke and Mannion 2023). The boundary between the cochlear duct (lagena) and the middle ear region of the paratympanic sinus was identified primarily using osteological boundaries, particularly the prootic region separating these structures, in combination with comparative anatomical interpretations from previous crocodylian neuroanatomical studies. During segmentation, these regions were assessed in multiple orthogonal planes (axial, sagittal, and coronal) and cross-checked across successive slices to ensure consistent anatomical interpretation. Each parameter was measured three times, and mean values were used for statistical analysis. No universally accepted absolute size threshold currently defines a "developed" vestibular system in crocodylians. Thus, our interpretation was based on comparative DCL-standardized measurements and ontogenetic trends. In this study, "developed" refers to relative enlargement and morphological differentiation of the endosseous labyrinth, not a fixed anatomical threshold.

### Statistical analyses

Statistical analyses were conducted to examine relationships between cranial size and measurements of the endocranial cavity and endosseous labyrinth. Because the sample size was small, Shapiro–Wilk tests confirmed normality ($p > 0.05$). Linear regression analyses were used to visualize ontogenetic scaling patterns and evaluate the direction and consistency of morphological changes across growth stages. Given the exploratory nature of this study and the conservation status of *C. siamensis*, these analyses were intended to identify biologically meaningful developmental trends rather than to support population-level inference or predictive modeling. Emphasis was therefore placed on relative scaling relationships and concordance among anatomical variables rather than on statistical significance.

Morphological data were further examined for ontogenetic trends by correlating endocast and labyrinth measurements with dorsal cranial length (DCL). All statistical analyses and graphical visualizations were performed in R (version 4.5.1) using the base lm() function, and graphical visualizations were generated using the package *ggplot2* to assess relationships among cranial size, endocast morphology, and endosseous labyrinth development (Script S1).

## RESULTS

**Ontogenetic changes in the endocranial morphology of *C. siamensis***

The endocast morphology of *Crocodylus siamensis* exhibits the typical reptilian tripartite organization, consisting of the prosencephalon, mesencephalon, and rhombencephalon. The prosencephalon comprises the olfactory bulbs, olfactory tract, cerebrum, and pituitary gland. The mesencephalon includes the optic tectum, while the rhombencephalon consists of the pons, medulla oblongata, and cerebellum (Fig. 3).

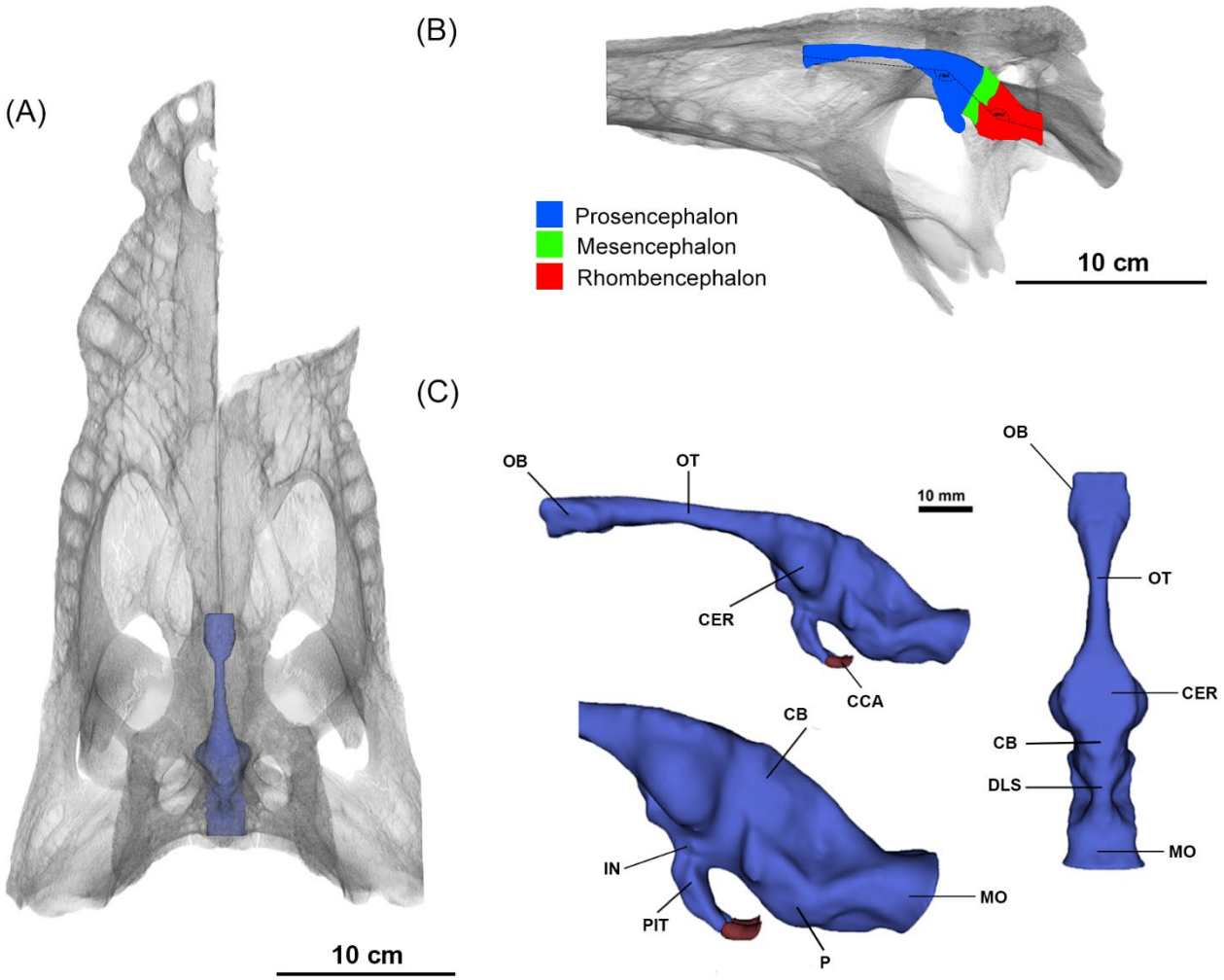


**Fig. 3.** Three-dimensional rendering of the skull and encephalic endocast of *Crocodylus siamensis* (SHM-R14), the largest specimen in the sample and the clearest for endocranial visualization, despite incomplete anterior snout preservation. A. Dorsal view showing position of encephalic endocast. B. Lateral view of the encephalic endocast showing the prosencephalon (blue), mesencephalon (green), and rhombencephalon (red), with the forebrain–midbrain angle (FMA; cephalic flexure angle) and midbrain–hindbrain angle (MHA; pontine flexure angle) indicated. C. Labeled anatomical regions (cerebrum; CER, cerebral carotid artery; CCA, cerebellum; CB dorsal longitudinal sinus; DLS,

infundibulum; IN, olfactory bulb; OB, olfactory tract; OT, pituitary gland; PIT, medulla oblongata; MO).

Both absolute encephalic endocast size and proportional development of major regions vary across ontogeny (Fig. 4). The juvenile specimen (skull length = 15.44 cm) exhibits an encephalic endocast length of 67.09 mm and a total volume of 6,922.79 $mm^3$. The ratio of endocast length to dorsal cranial length (EL/DCL) was 0.43 in the juvenile specimen. The olfactory bulb length is proportionally prominent, representing 42.93% of total endocast length. The juvenile specimen showed a forebrain–midbrain angle (FMA; cephalic flexure angle) of 143.4° and a midbrain–hindbrain angle (MHA; pontine flexure angle) of 158.0° (Fig. 4A; Table 2).

Subadult specimens (22.11–25.03 cm skull length; Fig. 4B–D) displayed marked increases in both encephalic endocast length (78.13–89.48 mm) and total endocast volume (9,715.86–13,523.80 $mm^3$). However, the EL/DCL ratio decreased to 0.35–0.36, indicating that endocast growth was proportionally slower than skull growth. The olfactory bulb also increased in absolute length (37.29–40.05 mm) and remained proportionally prominent, representing 43.71–47.73% of total endocast length. In contrast, the olfactory tract became more elongated in subadult specimens, indicating an increase in the length of the anterior neuroaxis. Subadult specimens exhibited a slightly straighter neuroaxis than the juvenile specimen, reflected by changes in both the forebrain–midbrain angle (FMA) of 148.0-150.8° and midbrain–hindbrain angle (MHA), with the MHA increasing from 158.0° in the juvenile to 160.2–164.5° in subadults, indicating progressive reduction in neuroaxial curvature during ontogeny (Table 2).

**Table 2.** Encephalic endocast measurements and proportional indices of *Crocodylus siamensis* across ontogenetic stages. Measurements include endocast length (EL), endocast width (EW), olfactory bulb length (OBL), endocast volume (VE), forebrain–midbrain angle (FMA), and midbrain–hindbrain angle (MHA). Proportional indices include the olfactory bulb length relative to total endocast length (OBL/EL × 100), endocast length-to-width ratio (EL/EW) and endocast length relative to dorsal cranial length (EL/DCL).

| Specimens | EL (mm) | EW (mm) | OBL (mm) | VE ($mm^3$) | FMA (degree) | MHA (degree) | OBL/EL (%) | EL/EW | EL/DCL |
|---|---|---|---|---|---|---|---|---|---|
| SMF01 | 67.09 | 21.90 | 28.80 | 6922.79 | 143.40 | 158.00 | 42.93 | 3.06 | 0.43 |
| SMF02 | 89.48 | 27.29 | 39.11 | 13523.80 | 150.80 | 164.50 | 43.71 | 3.28 | 0.35 |
| SMF03 | 78.13 | 23.66 | 37.29 | 9715.86 | 148.00 | 160.20 | 47.73 | 3.30 | 0.35 |
| SMF04 | 88.60 | 24.72 | 40.05 | 11913.10 | 148.10 | 162.00 | 45.20 | 3.58 | 0.36 |
| SHM-R14 | 136.90 | 33.46 | 71.67 | 32174.10 | 152.80 | 171.10 | 52.35 | 4.09 | 0.30 |
| SHM-R15 | 109.60 | 27.84 | 54.20 | 18556.00 | 151.60 | 163.50 | 49.45 | 3.94 | 0.32 |

In adults (33.48–44.38 cm skull length), the encephalic endocast became proportionally more elongated, with endocast length (109.60–136.90 mm) showing a greater absolute increase than width. This pattern is supported by the EL/EW ratio, which increased from 3.06 in the juvenile specimen to 3.28–3.58 in subadults and 3.94–4.09 in adults, indicating progressive proportional elongation of the encephalic endocast during ontogeny (Table 2; Fig. S1). In contrast, the ratio of endocast length to dorsal cranial length (EL/DCL) decreased to 0.30–0.32, consistent with negative allometric scaling relative to skull growth. Adults also exhibited the straightest neuroaxis, reflected by changes in both the forebrain–midbrain angle (FMA = 151.6–152.8°) and midbrain–hindbrain angle (MHA = 163.5–171.1°), indicating reduced cephalic and pontine flexure compared with juvenile and subadult stages. The olfactory bulb continued to increase in absolute length (54.20–71.67 mm) and remained proportionally prominent, representing 49.45–52.35% of total endocast length (Table 2; Fig. S1). Therefore, the observed ontogenetic pattern is better interpreted as coordinated endocast elongation and neuroaxis reorganization, rather than a simple reduction in olfactory dominance.

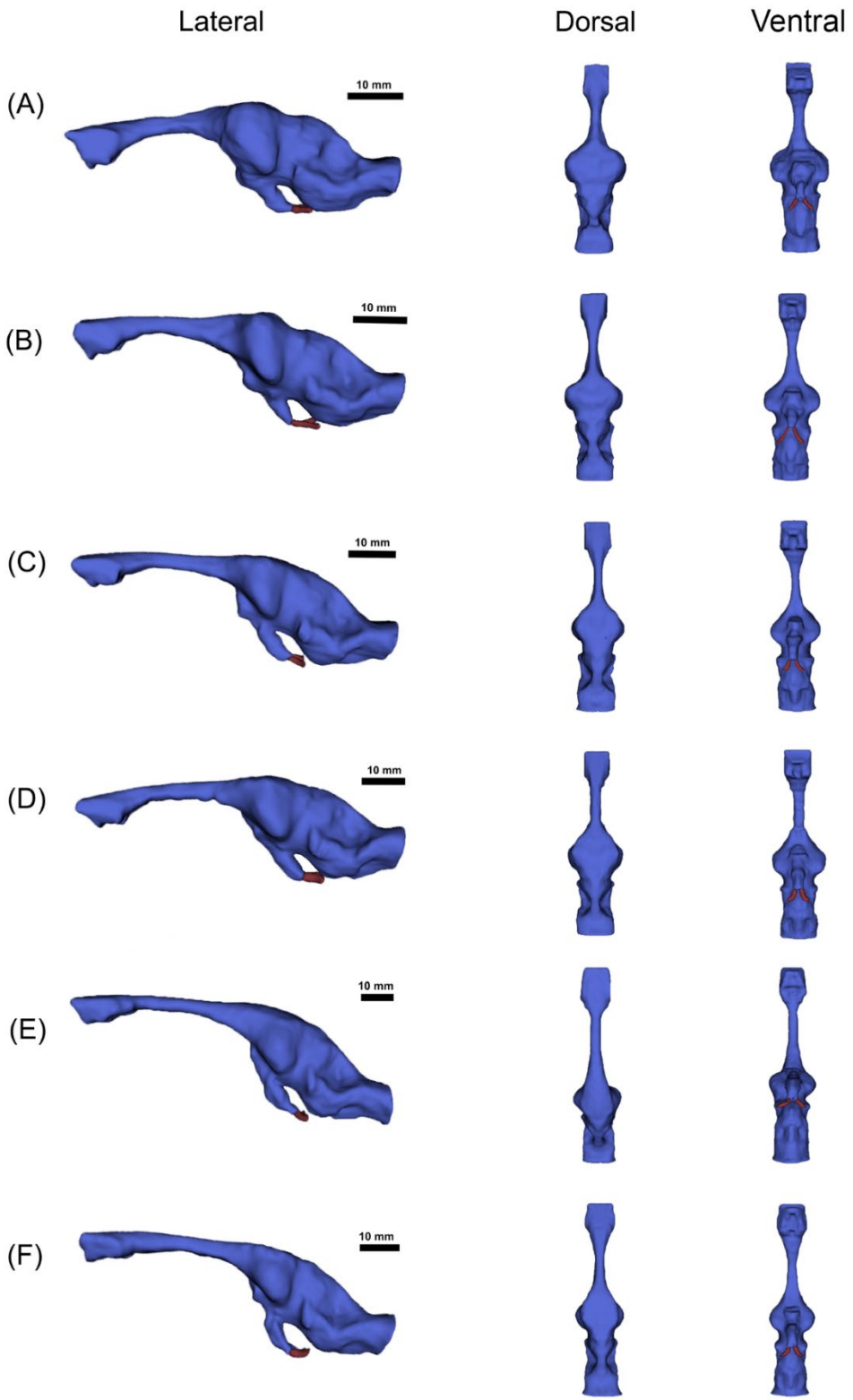


**Fig. 4.** Ontogenetic changes in encephalic endocast morphology of *Crocodylus siamensis*. Three-dimensional reconstructions of the endocast showing developmental differences across life stages. A. juvenile (SMF01). B–D. subadults (SMF02, SMF03, SMF04). E–F. adults (SHM-R14, SHM-R15), showing changes in forebrain curvature, olfactory bulb size, and endocast proportions across ontogeny.

In addition to changes in olfactory-associated structures and overall endocast elongation, the cerebrum-bearing region of the encephalic endocast shows a broadly conserved transverse morphology across ontogeny. In all examined specimens, the greatest transverse width of the cerebrum-bearing region occurs near the midpoint of the cerebral region rather than at its posterior margin (Fig. 4). This condition is visible in juvenile, subadult, and adult specimens, suggesting that the general cerebral outline remains relatively consistent throughout growth. Although the encephalic endocast becomes proportionally more elongated during ontogeny, no obvious posterior expansion of the cerebrum-bearing region is observed in the available specimens.

**Ontogenetic changes in the endosseous labyrinth structure of *C. siamensis***

The endosseous labyrinth of *C. siamensis* consists of the anterior (asc), posterior (psc), and lateral (lsc) semicircular canals, their associated ampullae (ana, poa, laa), the common crus, and the lagena (Fig. 5). In the juvenile specimens, the endosseous labyrinth is 12.46 mm in length and 12.83 mm in width, with a vestibular length of 10.63 mm and a total volume of 176 mm³. The endosseous labyrinth exhibited comparatively less pronounced semicircular canal curvature relative to subadult and adult specimens. This represents the smallest and least differentiated endosseous labyrinth in the sample, with reduced semicircular canal curvature and the shortest lagena relative to subadult and adult specimens (Fig. 6A; Table 3).

Subadult specimens showed endosseous labyrinth dimensions of 15.63–16.32 mm in length and 13.42–15.74 mm in width, with total volumes increasing to 229–338 mm³, representing a marked increase relative to the juvenile specimen. The lagena appears more elongated than in the juvenile specimen, and the anterior semicircular canal shows greater curvature (Fig. 6B–D; Table 3).

Adult specimens possessed the largest endosseous labyrinths in the sample, with lengths of 21.05–24.62 mm, widths of 16.18–19.35 mm, and volumes of 428.47–971.58 mm³. Adults also exhibited the longest anteroposterior lagena lengths and the most pronounced anterior semicircular canal curvature among the examined ontogenetic stages (Fig. 6E–F; Table 3).

**Tables 3.** Endosseous labyrinth dimensions of *Crocodylus siamensis* across ontogenetic stages. Measurements include endosseous labyrinth length, width, vestibular length, lagena length and width, and total labyrinth volume for each specimen

| Specimens | ELL (mm) | ELW (mm) | LVE (mm) | LLG (mm) | WLG (mm) | VOL ($mm^3$) |
|---|---|---|---|---|---|---|

| | | | | | | |
|---|---|---|---|---|---|---|
| SMF01 | 12.46 | 12.83 | 9.34 | 4.97 | 4.58 | 175.89 |
| SMF02 | 16.32 | 15.74 | 12.3 | 7.14 | 5.18 | 337.97 |
| SMF03 | 15.63 | 13.42 | 11.44 | 7.42 | 5.28 | 228.68 |
| SMF04 | 16.3 | 14.46 | 10.63 | 9.1 | 5.83 | 295.49 |
| SHM-R14 | 24.62 | 19.35 | 16.31 | 14.25 | 7.78 | 971.57 |
| SHM-R15 | 21.05 | 16.18 | 13.27 | 11.6 | 6.81 | 428.46 |

Note: ELL, endosseous labyrinth length; ELW, endosseous labyrinth width; LVE, vestibular length; LLG, lagena length; WLG, lagena width; VOL, volume of endosseous labyrinth.

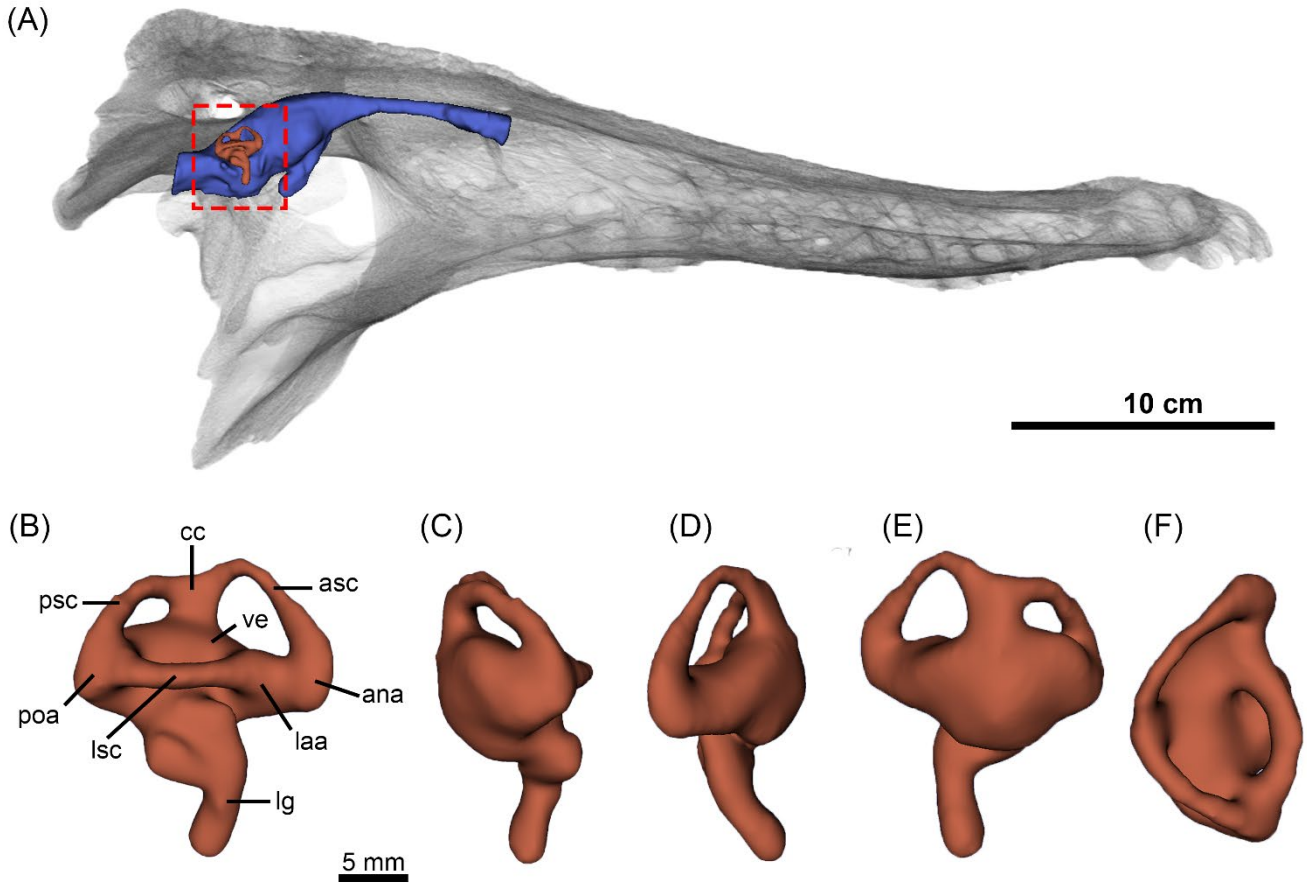


**Fig. 5.** Endosseous labyrinth of *Crocodylus siamensis* (SHM-R14*)* reconstructed from CT data. A. Lateral view of skull showing labyrinth position (red frame). B–F. Three-dimensional rendering of the right labyrinth in lateral, posterior, anterior, medial, and dorsal views. Major structures include the anterior semicircular canals; asc, posterior semicircular canals; psc, lateral semicircular canals; lsc, anterior ampullae; ana, posterior ampullae; poa, vestibule; ve, common crus; cc, and lagena; lg.

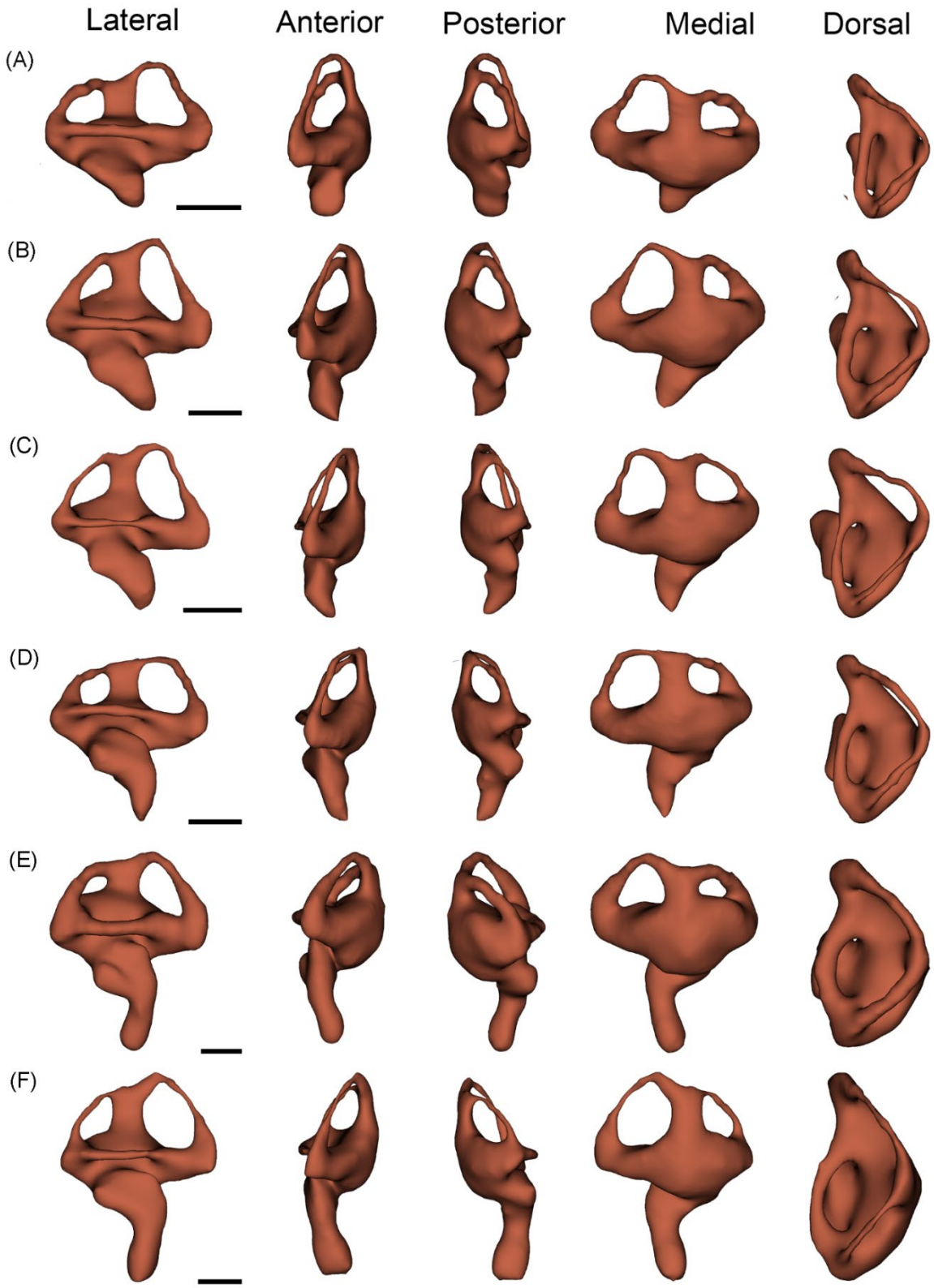


**Fig. 6.** Ontogenetic changes in the endosseous labyrinth of *Crocodylus siamensis*. 3D reconstructions of the right inner ear showing developmental variation in labyrinth size, canal curvature, and lagena elongation in A. juvenile (SMF01). B–D. subadults (SMF02, SMF03, SMF04) and E–F. adults (SHM-R14, SHM-R15). Scale bar = 5 mm.

**Correlation Between Neuroanatomical Development and Skull Growth**

Statistical analyses revealed strong positive relationships between dorsal cranial length (DCL) and both endocast and endosseous labyrinth parameters (Figs. 7, 8). Encephalic endocast measurements, including encephalic endocast length (EL), olfactory bulb length (OBL), endocast volume (VE), and endocast width (EW), showed high coefficients of determination ($R^2$ = 0.9391–0.9941), indicating consistent scaling with skull size. Similarly, even angular traits exhibited clear ontogenetic trends, with forebrain–midbrain angle (FMA) and midbrain–hindbrain angle (MHA) strongly correlated with skull growth ($R^2$ = 0.7756 and 0.8861, respectively), endosseous labyrinth parameters exhibited strong correlations with DCL, particularly labyrinth length (ELL; $R^2$ = 0.9907), lagena width (WLG; $R^2$ = 0.9522), and lagena length (LLG; $R^2$ = 0.9496). Vestibular length (LVE), labyrinth width (ELW), and total volume (VEL) also demonstrated robust scaling relationships ($R^2$ = 0.900–0.9472). These results indicate that both encephalic endocast and endosseous labyrinth structures follow coordinated and predictable ontogenetic scaling patterns in *Crocodylus siamensis*, suggesting a strong covariation between cranial growth and sensory-related neuroanatomical morphology.

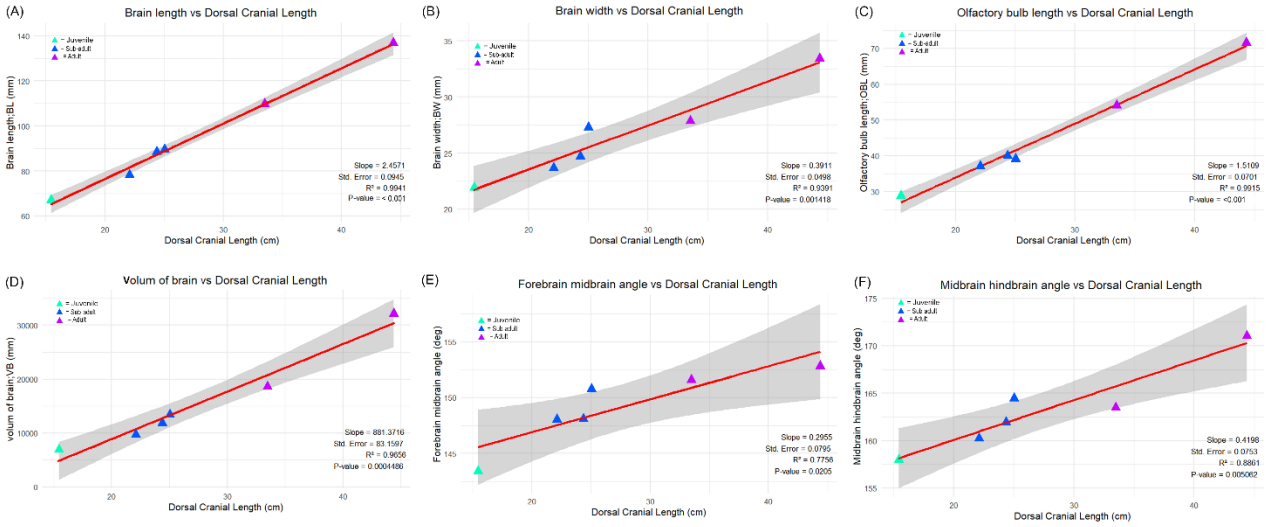


**Fig. 7.** Linear regression analysis showing the relationship between Dorsal Cranial Length (cm) and endocast measurements (mm) in *C. siamensis*. The plots, with 95% confidence intervals, illustrate consistent scaling patterns across ontogenetic stages. Blue triangle = juvenile; dark blue = sub-adult; purple = adult.

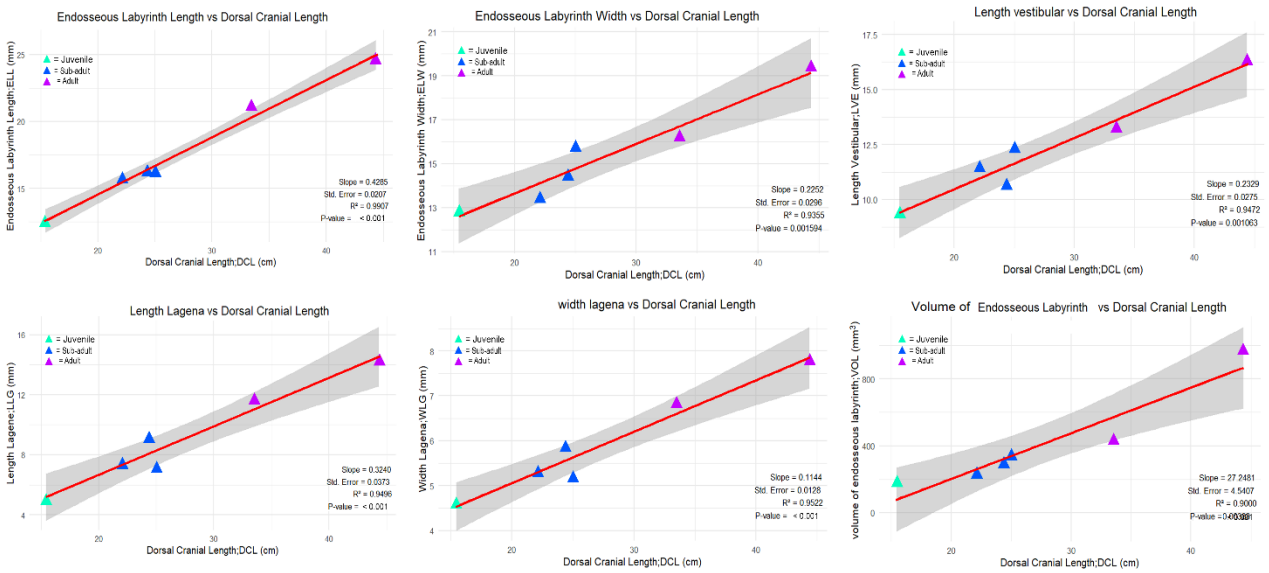


**Fig. 8.** Linear regression analyses of relationships between dorsal cranial length and endosseous labyrinth parameters in *Crocodylus siamensis*. Regression plots. A–F. with 95% confidence intervals illustrate strong correlations between skull length and key labyrinthine measurements (ELL, ELW, LVE, LLG, WLG, and VOL), illustrating consistent scaling of labyrinthine morphology across growth stages.

## DISCUSSION

### Ontogenetic Scaling and Shifts in Relative Sensory Emphasis

Our results demonstrate that encephalic endocast development in *Crocodylus siamensis* follows an allometric trajectory across ontogeny, consistent with the prosencephalon, mesencephalon, and rhombencephalon organization of the reptilian brain. Changes in endocast and regional proportions reflect coordinated developmental responses to shifting behavioral and ecological demands with increasing body size, rather than abrupt structural transformations (Morris et al. 2019; Gignac and Erickson 2016; King et al. 2024; Schwab et al. 2022). Strong correlations between skull length and multiple endocast metrics indicate that neuroanatomical growth is tightly constrained by cranial development, a pattern widely observed in crocodilians and other reptiles (Jirak and Janacek 2017).

The proportional indices further indicate that encephalic endocast growth is negatively allometric relative to skull length. Although endocast length increases absolutely during ontogeny, the EL/DCL ratio decreases from 0.43 in the juvenile specimen to 0.35–0.36 in subadults and 0.30–0.32 in adults, indicating that the encephalic endocast occupies a progressively smaller proportion of dorsal

cranial length during growth. Neuroaxial angular measurements show a related ontogenetic pattern. The forebrain–midbrain angle (FMA; cephalic flexure angle) increases from 143.4° in the juvenile to 148.0–150.8° in subadults and 151.6–152.8° in adults, whereas the midbrain–hindbrain angle (MHA; pontine flexure angle) increases from 158.0° in the juvenile to 160.2–164.5° in subadults and 163.5–171.1° in adults. These increasing angular values indicate a progressive reduction in cephalic and pontine flexure, consistent with a straighter neuroaxis in later ontogenetic stages.

Juvenile specimens of *Crocodylus siamensis* exhibit more pronounced forebrain curvature and relatively enlarged olfactory bulbs, relative to subadult and adult stages, suggesting a possible greater role of olfactory-associated structures during early ontogeny. This configuration is consistent with observations in *Crocodylus niloticus* and other reptiles including squamates such as lizards, where juveniles depend heavily on chemical cues for predator detection, prey localization, and social interactions within sheltered microhabitats (Ngwenya et al. 2013; Chabrolles et al. 2017; Cooper 1994; Hansen 2007; Sneddon 2018). Such early prominence of olfactory-associated regions in the encephalic endocast may reflect a broader ontogenetic trend among crocodylians, potentially linked to juvenile ecological requirements and chemosensory dependence. Comparable developmental patterns have also been noted in gavialids (Castillo and Gold 2025). Rather than indicating a simple reduction in olfactory dominance, the proportional data suggest that olfactory-associated structures remain prominent throughout ontogeny. OBL/EL values increase from 42.93% in the juvenile specimen to 49.45–52.35% in adults, while the EL/EW ratio also increases from 3.06 to 3.94–4.09 (Table 2; Supplementary Fig. S1). Together, these patterns suggest coordinated endocast elongation and neuroaxis reorganization during growth, with persistent olfactory prominence rather than sensory replacement.

The cerebrum-bearing region of the encephalic endocast also provides useful comparative information on crocodylian ontogenetic morphology. In *C. siamensis*, this region appears to retain a consistent transverse outline throughout growth, with the greatest width located near the midpoint of the cerebral region rather than at the posterior margin. This condition is consistent with the typical crocodyloid pattern described in comparative endocranial studies and contrasts with the more posteriorly expanded cerebral region reported in many alligatoroids and gavialoids (Pierce et al. 2017; Pligersdorffer et al. 2025; Burke and Mannion 2026). Although the encephalic endocast becomes progressively more elongated during ontogeny, the available specimens suggest that the cerebrum-bearing region in *C. siamensis* changes mainly through proportional elongation rather than a marked posterior shift in maximum width. This differs from the condition reported in *Tomistoma schlegelii*, in which ontogenetic development involves a transition from a midpoint-expanded juvenile cerebral region to a more posteriorly expanded adult condition (Burke and Mannion 2023). Comparisons with

gavialids, including *Gavialis*, further indicate that cerebral-region morphology may follow lineage-specific ontogenetic trajectories among crocodylians (Castillo and Gold 2025; Burke and Mannion 2026).

As individuals transition into subadult and adult stages, overall encephalic endocast size increases and the neuroaxis becomes progressively straighter, consistent with findings across other crocodylians in which adult endocasts are more elongated and linearly organised relative to the endocranial cavity (Jirak and Janacek 2017; Watanabe et al. 2019). Although the olfactory bulb continues to grow in absolute size and scales predictably with body size (Ngwenya et al. 2013; Jirak and Janacek 2017), ontogenetic change may also involve proportional changes in endocast regions corresponding to the optic tectum and cerebellum (George and Holliday 2013; Hu et al. 2021). This pattern may reflect a sensory reorganisation linked to ecological transitions across life stages, rather than sensory replacement or loss. Juvenile crocodilians often occupy structurally complex microhabitats and may rely strongly on chemosensory and other local environmental cues for predator avoidance and prey detection, whereas larger subadults and adults occupy broader aquatic habitats and engage in visually guided predation on larger prey, potentially involving greater reliance on visual cues and coordinated motor responses (Platt et al. 2006; Radloff et al. 2012; Nagloo et al. 2016). This pattern mirrors developmental trends reported in *Alligator mississippiensis*, *Caiman crocodilus*, and *C. niloticus* (Macrini et al. 2007; George and Holliday 2013; Dufeau and Witmer 2015; Allemand et al. 2023), and reflects sensory reorganisation rather than sensory replacement or loss. Given the prolonged growth trajectories and pronounced ecological differences between life stages that characterise crocodilians (Hutton 1987; Schwab et al. 2022), these ontogenetic shifts provide a useful framework for considering stage-specific habitat requirements and behavioral variation in *C. siamensis*, with broader relevance for conservation and management of this critically endangered species (Somaweera et al. 2020; Lourenço-de-Moraes et al. 2023).

**Coordinated Ontogenetic Scaling of the Endosseous Labyrinth**

Ontogenetic changes in the endosseous labyrinth closely parallel those observed in the encephalic endocast, reinforcing the interpretation of coordinated sensory system development governed by proportional scaling (Schwab et al. 2021, 2022; Castillo and Gold 2025). Juvenile specimens possess a short lagena and comparatively reduced semicircular canal curvature, suggesting early-stage differences in vestibular- and auditory-related morphology rather than directly demonstrated functional limitation. Smaller semicircular canal radii are generally associated with lower

sensitivity to angular acceleration in biomechanical models, although this functional relationship was not directly tested here (Van Buskirk et al. 2006; Ifediba et al. 2007; Straka et al. 2014; Essner et al. 2022). A shorter lagena may indicate differences in auditory-related morphology, including potential differences in low-frequency sensitivity, as suggested by comparative studies (Walsh et al. 2009; Manley 2017; Schwab et al. 2020; Pochat-Cottilloux et al. 2024). Comparable early-stage configurations have been documented in hatchlings of *C. niloticus* and *Alligator mississippiensis* and *Gavialis gangeticus*, where smaller canal dimensions and shorter lagenae are associated with ontogenetic differences in vestibular and auditory morphology. (Ifediba et al. 2007; Georgi 2008; Ekdale 2016; Morris et al. 2019; Castillo and Gold 2025).

Subadult individuals show elongation of the lagena and increased thickness of the semicircular canal arcs. These changes are consistent with morphologies associated in previous studies with vestibular and auditory function, and may reflect increasing sensory-related differentiation during ontogeny (Leitch and Catania 2012; Chabert et al. 2015; Carr et al. 2016). Such morphological trends align with ecological transitions documented in subadult crocodiles, which begin to explore wider environments and exhibit more complex foraging behaviors (Platt et al. 2006; Brien et al. 2014; Reber 2020; González-Solórzano et al. 2024).

Compared to juvenile and subadult specimens, adult individuals exhibit proportionally larger lagena dimensions and more pronounced semicircular canal curvature of the semicircular canals (Schwab et al. 2020 2021 2022; Melkersson et al. 2024; Pochat-Cottilloux et al. 2024). In contrast, juvenile specimens are characterized by proportionally prominent olfactory-associated regions, shorter lagenae, and less pronounced semicircular canal curvature (Macrini et al. 2007; Dufeau and Witmer 2015; Castillo and Gold 2025), whereas subadult specimens display intermediate morphological conditions between the juvenile and adult stages (George and Holliday 2013; Schwab et al. 2022; Allemand et al. 2023). The enlarged lagena and increased curvature of the semicircular canals observed in adults are consistent with morphologies previously linked to vestibular and auditory function (Vergne et al. 2009; Manley 2017; Schwab et al. 2020; Pochat-Cottilloux et al. 2024), although direct functional performance was not evaluated here. These morphologies may provide a useful basis for discussing the ecological demands of larger-bodied crocodilians, including aquatic movement, visually guided predatory behavior, and social interactions across broader ecological ranges (Vergne et al. 2009; Manley 2017; Schwab et al. 2020, 2022; Melkersson et al. 2024). Because this study is based on CT-derived osteological morphology and morphometric correlations, functional interpretations should be regarded as cautious inferences rather than direct demonstrations of sensory performance.

**Ontogenetic Sensory Scaling and Ecological Transitions**

The coordinated ontogenetic scaling of encephalic endocast and endosseous labyrinth structures in *C. siamensis* may reflect underlying ecological transitions during growth. Juveniles likely occupy structurally complex, protective microhabitats and rely more heavily on chemosensory cues, a strategy also reported in hatchlings of other crocodylians (Chabert et al. 2015; Dufeau and Witmer 2015; Neenan et al. 2017; González-Solórzano et al. 2024). As individuals increase in size, dietary breadth expands and locomotor demands become more pronounced, potentially associated with increased reliance on visual and locomotor coordination (Morpurgo et al. 1991; George and Holliday 2013; Woodborne et al. 2021; Puértolas-Pascual et al. 2023).

Strong correlations between skull length and labyrinthine parameters further suggest that labyrinthine structures associated with auditory and vestibular functions scale with body size. In particular, the relationship between skull size and lagena length suggests ontogenetic variation in auditory-related morphology, which could have implications for acoustic sensitivity and spatial orientation, although direct functional validation is required (Miller et al. 1993; Radloff et al. 2012; Schwab et al. 2020, 2021; Ajji and Lang 2025). However, this interpretation should be treated cautiously, as recent work by Pochat-Cottilloux et al. (2024) demonstrated that variation in crocodylian endosseous labyrinth morphology is primarily explained by size-related allometry and associated changes in braincase conformation, rather than clear functional or phylogenetic differentiation. Similar allometric scaling has also been reported in other extant crocodylians and fossil crocodylomorphs (Di-Poï et al. 2013; Leitch et al. 2012; Jirak and Janáček 2017; Puértolas-Pascual et al. 2022; Schwab et al. 2022; Burke and Mannion 2023). Our results are consistent with this broader pattern, suggesting that ontogenetic scaling is a major driver of labyrinthine variation in *Crocodylus siamensis*.

The relatively small lagena observed in juvenile *Crocodylus siamensis* should not be interpreted as evidence of reduced hearing capacity, but rather may indicate ontogenetic differences in auditory frequency sensitivity. Inner ear morphology, particularly lagena length, has been shown to correlate with auditory capability and the frequency range of hearing in reptiles and birds (Walsh et al. 2009). This suggests that juvenile individuals may have differed from adults in auditory-related morphology, potentially corresponding to differences in frequency sensitivity. A comparable ontogenetic pattern has been reported in *Alligator mississippiensis*, where juveniles show heightened sensitivity to higher-frequency sounds associated with hatchling vocalizations and parental communication (Dufeau and Witmer 2015).

**Implications for Conservation and Comparative Neurobiology**

The ontogenetic sensory scaling patterns documented in *Crocodylus siamensis* are broadly consistent with developmental trends reported in other crocodylians, including *Alligator mississippiensis*, *Caiman crocodilus*, *Crocodylus niloticus*, and *Gavialis gangeticus*, where neuroanatomical and sensory structures undergo progressive reorganization throughout growth (Macrini et al. 2007; Dufeau and Witmer 2015; Schwab et al. 2022; Castillo and Gold 2025).

These ontogenetic changes likely reflect shifts in habitat use, prey preference, locomotor behavior, and sensory reliance across life stages. Consequently, the sensory scaling patterns documented here have important implications for the conservation and management of *C. siamensis*. Distinct neuroanatomical configurations across ontogeny suggest that juveniles and adults may differ substantially in their sensitivity to environmental disturbances and habitat alteration. (Lang 1981; Hutton 1987; Brien et al. 2014; Radloff et al. 2012; Schwab et al. 2020; Somaweera et al. 2020). Because most specimens were obtained from captive sources, possible effects of captivity-related factors, including diet, husbandry conditions, and developmental environment, cannot be fully excluded. However, the present study was designed to identify broad ontogenetic patterns rather than population-level ecological variation, and all specimens showed consistent scaling trends across growth stages. Future comparisons between wild and captive individuals will be necessary to evaluate the influence of rearing conditions on neuroanatomical development.

In addition to its conservation relevance, this study provides an essential neuroanatomical baseline for comparative research. The three-dimensional reconstructions and quantitative metrics presented here offer reference data for evaluating how captive breeding conditions, environmental stressors, or conservation interventions may influence sensory-related neuroanatomical development. The strong statistical relationships observed between external cranial dimensions and internal neuroanatomical structures are best interpreted as biological scaling patterns associated with ontogenetic development, rather than as a direct consequence of the non-invasive measurement approach. Although these correlations do not directly demonstrate sensory function, they indicate that cranial growth covaries with the development of sensory-related neuroanatomical structures. These coordinated changes suggest that shifts in skull size are accompanied by proportional changes in neuroanatomical investment, reflecting broader developmental and ecological transitions (Ngwenya et al. 2013; Dumoncel et al. 2021; Fokkema et al. 2020; Lourenço-de-Moraes et al. 2023). Thus, non-invasive cranial measurements may serve as a practical morphological proxy for estimating internal neuroanatomical variation, particularly when direct CT-based data are unavailable. Such relationships

may have potential applications for ecological monitoring and comparative behavioral inference, although functional validation using behavioral or physiological data remains necessary in future studies.

## CONCLUSIONS

This study presents the first integrative characterization of endocranial and endosseous labyrinth development in *C. siamensis* across stages based on high-resolution CT data. Both neuroanatomical systems follow predictable allometric trajectories, accompanied by consistent, stage-dependent morphological shifts. Early ontogenetic stages are characterized by strongly curved forebrains, shorter lagenae, and less pronounced semicircular canal curvature, whereas later stages exhibit progressive encephalic endocast elongation, proportional expansion of midbrain and hindbrain regions, and increased differentiation of the inner ear, particularly the lagena and semicircular canals.

The strong covariation observed between skull length and internal neuroanatomical metrics indicates that external cranial dimensions provide a useful first-order framework for tracking relative sensory-related neuroanatomical changes across growth stages. Within the constraints imposed by the rarity and conservation status of this species, these patterns establish a quantitative developmental baseline that is directly relevant to comparative neuroanatomy, behavioral inference, and conservation monitoring in both captive and wild populations of *C. siamensis*.

Beyond its biological and conservation relevance, the developmental framework established in this study may provide a useful foundation for future paleontological investigations. Because cranial cavities and inner ear structures are commonly preserved in fossil crocodylian skulls, even when soft tissues are absent, the ontogenetic patterns documented in *C. siamensis* could serve as a comparative reference for future studies aiming to infer growth stage, sensory-related morphology, and possible ecological differentiation in extinct crocodylians from Thailand and surrounding regions.

Future comparative work integrating extant and fossil crocodylians may further clarify how developmental neuroanatomical patterns evolved through time and may strengthen the use of living crocodylians as analogues for interpreting the fossil record.

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**Authors' contribution:** KL; Substantial contribution in the concept and design of the study, PT and KS; Specimen's collection and identification, KL and PT; Contribution to data analysis and interpretation, KL; Project financing, KL and PT; Contribution to manuscript preparation

**Availability of data and materials:** The data presented in this study are available on request from the corresponding author.

**Consent for publication:** Not applicable.

**Ethics approval consent to participate:** Not applicable.

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**Supplementary Materials**

**Script S1.** R script used for linear regression analysis and graphical visualization of the relationship between dorsal cranial length (DCL) and volume of the endosseous labyrinth in *Crocodylus siamensis*. The script includes model fitting using the base lm() function and visualization using the ggplot2 package. (download)

**Fig. S1.** Relative proportional indices of the encephalic endocast across ontogenetic stages of *Crocodylus siamensis*. OBL/EL (%) represents olfactory bulb length relative to total endocast length, EL/EW represents proportional elongation of the encephalic endocast, and EL/DCL represents endocast length relative to dorsal cranial length. These indices were calculated from the measurements reported in table 2. (download)