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An enlarged endocranial venous system in *Steneosaurus pictaviensis* (Crocodylia: Thalattosuchia) from the Upper Jurassic of Les Lourdines, France

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Abstract – Large endocranial features are revealed in a three-dimensionally preserved specimen of the thalattosuchian crocodile *Steneosaurus pictaviensis*. Structures found on an endocast indicate the presence of the same venous blood system, although much enlarged, as found within the cranial cavity of modern crocodilians. An exceptionally large longitudinal dorsal blood sinus forms an expanded torcular herophili above the junction of the midbrain and hindbrain. The venous canals entering the posterodorsal part of the torcular herophili are the *capiti dorsalis*, which drain blood from the temporal and occipital musculature, entering the braincase in this region as in many extant and extinct Archosauria. © 2000 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

thalattosuchian / Jurassic / endocast / sinus / vein / France

Résumé – Un système veineux endocrânien volumineux chez *Steneosaurus pictaviensis* (Crocodylia : Thalattosuchia) du Jurassique supérieur des Lourdines, France. D'après les moulages endocrâniens, le système veineux, sinus longitudinal, sinus dorsal, sinus latéraux et torcular, se montrent particulièrement développés sur le spécimen étudié de *Steneosaurus pictaviens* (Thalattosuchia). Les gouttières de ce système vasculaire sont comparables à celles des Crocodiliens actuels, mais considérablement élargies au niveau du cervelet et du confluent des sinus transverses. À cet endroit, on observe, de chaque côté, un canal propre aux *venae capiti dorsalis* qui drainent la musculature occipito-supra temporale, comme on le voit chez les Archosauriens fossiles et actuels. © 2000 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

thalattosuchien / Jurassique / moulage endocrânien / sinus / veine / France

Version abrégée

1. Introduction

L'anatomie des crocodiliens n'a pas beaucoup changé au cours des millions d'années de leur évolution. Pour étudier les variations du système nerveux dans une perspective temporelle et écologique, les cerveaux et les boîtes crâniennes d'un crocodile aquatique fossile et d'un crocodile terrestre actuel ont été comparés.

2. Méthode

La position, l'orientation et les proportions de différentes parties cérébrales de crocodiliens (voir appendice) ont été examinées. Tous les crânes fossiles ont été

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préparés à l'acide. Un moulage endocrânien a été réalisé en silicone sur le spécimen LPP.M.35 (*Steneosaurus pictaviensis)*. Pour comparaison, un second moulage a été réalisé sur *Gavialis gangeticus*.

3. Résultats

Les moulages endocrâniens de *Steneosaurus* et *Gavialis* sont globalement similaires, mais il existe quelques différences notables. Le toit de la boîte crânienne de *Steneosaurus* s'élève de quelques millimètres depuis le tiers antérieur des hémisphères cérébraux, jusqu'à la partie postérieure du cervelet. Deux structures tubulaires se détachent postérieurement de cette partie gonflée de la boîte crânienne. Les *figures 1* et *2* montrent les différences entre les moulages endocrâniens. Les flèches étroites sur les *figures 1a* et *2b* indiquent l'élargissement du sinus sanguin au-dessus des hémisphères cérébraux, les flèches épaisses indiquent la région du *torcular herophili*, les *sinus transversii*, de même que la région d'entrée des *vena capiti dorsalis* dans la boîte crânienne. Ces veines entrent dans la boîte crânienne de part et d'autre du plan médian, séparées entre elles de 9 mm. La *figure 2b* illustre les contours de la région dilatée, ainsi que les deux canalicules.

4. Discussion

La région dilatée mise en évidence sur l'endocrâne de *Steneosaurus* abrite les sinus longitudinal dorsal et transverses, ainsi que la connexion des veines *capiti dorsalis* avec ces sinus. Ces trois structures se rencontrent chez la plupart des archosaures [2, 7, 9, 11]. Les crocodiles actuels ne présentent pas de veines *capiti dorsalis* et les sinus sus-décrits sont plus réduits que chez *Steneosaurus* (*figures 1b* et *2a*).

Andrews [1] a noté la présence des veines *capiti dorsalis* dans l'endocrâne de *Steneosaurus* mais ne les a pas décrites de manière détaillée. La production d'un moulage endocrânien de cette espèce permet, pour la première fois, d'étudier ses particularités anatomiques neurovasculaires. Cependant, il est intéressant de constater que des théropodes, comme *Allosaurus* et *Tyrannosaurus*, présentent également une expansion des sinus endocrâniens [8]. Comment expliquer la présence de larges sinus chez *Steneosaurus* et ces théropodes ? Il ne s'agit probablement pas d'une adaptation à la vie aquatique, car les théropodes sont uniquement terrestres. De plus, Colbert [5] a décrit un cervelet dilaté chez les Sebecosuchiens, mais Hopson [8] a montré qu'il ne s'agissait en fait que d'un agrandissement des sinus sanguins, comme il a été observé chez *Steneosaurus*. Les Sebecosuchiens étaient probablement adaptés à une vie terrestre, contredisant de fait tout lien entre sinus volumineux et vie aquatique. Ce caractère vasculaire paraît être variable au sein des crocodiles fossiles ; son statut phylogénétique reste encore obscur. De plus, demeure la possibilité que ce caractère représente un anévrisme méningé pathologique.

Les ichthyosaures, plésiosaures et nothosaures présentent des foramens similaires, mais plus petits et dans une position plus postéro-dorsale dans la boîte crânienne [8].

S'agit-il d'un caractère primitif ? Ces caractères ne sont probablement pas primitifs, car ils ne sont pas aussi dilatés chez Sphenosuchus [11], ni chez les autres archosauriens primitifs [8].

La prochaine étape de cette étude consistera à détailler l'endocrâne des Metriorhynchidae, descendants des Téléosauridae [4], pour détecter une éventuelle tendance évolutive au sein des thalattosuchiens.

5. Conclusion

Pour la première fois, un moulage endocrânien de *Steneosaurus* est décrit. Les structures dilatées observées sont interprétées comme étant le sinus longitudinal dorsal, les sinus transverses et les entrées des *vena capiti dorsalis*. Ses sinus sont plus grands que ceux observés chez les crocodiles actuels, mais ce caractère n'est pas rare, car on le trouve chez d'autres crocodiliens fossiles et quelques théropodes. Cependant, la fonction de cet agrandissement des sinus reste pour l'instant inconnu.

1. Introduction

The gross anatomy of crocodilians has not changed significantly over two hundred million years of evolution. In order to determine whether neural systems in crocodiles have been equally conservative, comparisons were made between the brain and braincase of a fossil aquatic crocodile and a modern terrestrial crocodile. The principal question to be tackled was thus: have there been any detectable neurological developments in the braincase through time and in response to major ecological changes?

So far, only a single description of a natural thalattosuchian endocranial cast, with a comparatively low degree of preservation, has been given [12]. Andrews [1] mentioned a blood vessel that is visible in the endocast featured in the present work, entering the hind-end of the braincase of *Steneosaurus*, but did not describe it in detail. This vessel in *Steneosaurus* has not been commented upon since, except briefly by O'Donoghue [9].

To date no attempts have been made to produce an endocranial cast that would enable further study of this feature. Thanks to the detailed 3-D preservation of a specimen of *Steneosaurus pictaviensis* (LPP.M.35), and the delicate method of acid preparation (dissolving the limestone filling the endocranium), it was possible to clear a braincase of matrix, without damage, so that a high fidelity endocranial cast could be manufactured. Nomenclature is based on Bruner [2].

2. Materials and methods

To evaluate whether any neurological change has occurred in crocodilians over time, this study initially focused on the analysis of brains and braincases of modern and fossil Crocodylia. Data was primarily collected on the relative sizes, positions and orientations of the different parts of the brain, cranial nerves and blood vessels entering and exiting the cranial cavity were traced and identified, and the occurrence of any new features was noted. In this way sufficient data for a comparative study of crocodilian cranial anatomy was assimilated. The crania and brains of various extant Crocodylia (see Appendix) were examined and measured using vernier calibers accurate to 0.1 mm at the Comparative Anatomy Department of the Natural History Museum in Paris, and detailed illustrations of the skulls of adults were made.

A total of four teleosaurid and metriorhynchid skulls which were recovered from 'Les Lourdines', an Upper Jurassic locality in the 'Département de la Vienne' (see Appendix), were investigated in the Geobiology Department of the University of Poitiers, France. These crania were prepared in acid, cleaned, and their nerve foramina rendered visible by mechanical preparation. *Steneosaurus pictaviensis*, the most robust specimen, underwent the greatest degree of treatment, and dissolution of the limestone in and around the skull was continued until all the matrix material was removed from the braincase.

An endocranial mould was made of *Steneosaurus pictaviensis* using Silicone rubber (ELASTOSIL M, Caoutchouc silicone RTV-2 (Room Temperature vulcanisation)) purchased from WACKER silicone. A catalyst (tetra-*N*-propoxysilane) was added to the silicone during the process of making the cast in amounts such that it remained sufficiently pliable to facilitate extraction. For comparison, a second cast was made of the unnumbered *Gavialis gangeticus* specimen from the Biology Department in Poitiers.

3. Results

There are strong similarities between the endocranial casts of *Steneosaurus* and *Gavialis* in terms of the proportions of the cerebral hemispheres, the optic lobes and the medulla oblongata (*tables I–II* and *figures 1– 2*). Note that the pituitary fossa is not evident on the *Steneosaurus* endocast; presumably this area was infilled in the fossil specimen. The *Steneosaurus* cast also has additional material adhering to the base of the anterior portion of the cast; however this is an artefact resulting from the slightly damaged floor of this part of the braincase. Lastly, the fossil cast does not preserve the anterior part of the brain, so the olfactory apparatus is missing. The fossil cast therefore appears shorter than the *Gavialis* endocast.

There are, however, some very important differences. The endocranial roof of *Steneosaurus* in *figure 1a* is raised by 1.5 mm (where indicated by the thicker arrow and by the anterior narrower part of the dashed line in *figure 2b*). This begins on the midline one third of the way back from the front of the cerebral hemispheres and extends posteriorly, widening to a point above the

Table I. Skull measurements (in mm).
Tableau I. Mesures crâniennes (en mm).

Measurements of Skull (to 1 mm)	*Gavialis gangeticus*	*Steneosaurus pictaviensis*
Length (maximum)	720	720
Height (maximum)	120	70
Length supratemporal fenestrae	64	160
Width foramen magnum	29	21
Height foramen magnum	19	13
Width between supratemporal fenestrae (at 58 mm in from the FM)	48	31

Table II. Endocast measurements (in mm).
Tableau II. Mesures des moulages endocrâniens (en mm).

Measurements of the Endocast (to 0.1 mm)	*Gavialis gangeticus*	*Steneosaurus pictaviensis*
Width cerebral hemispheres (maximum)	33.8	27.5
Height cerebral hemispheres	25	24.9
Length cerebral hemispheres (equivalent points)	34	29.5
Total length brain (from equivalent points)	95.2	75.9
Height brain (maximum)	28.5	26.4
Distance between dorsal braincase structures	—	9
Depth into cavities until matrix is reached	—	7.8

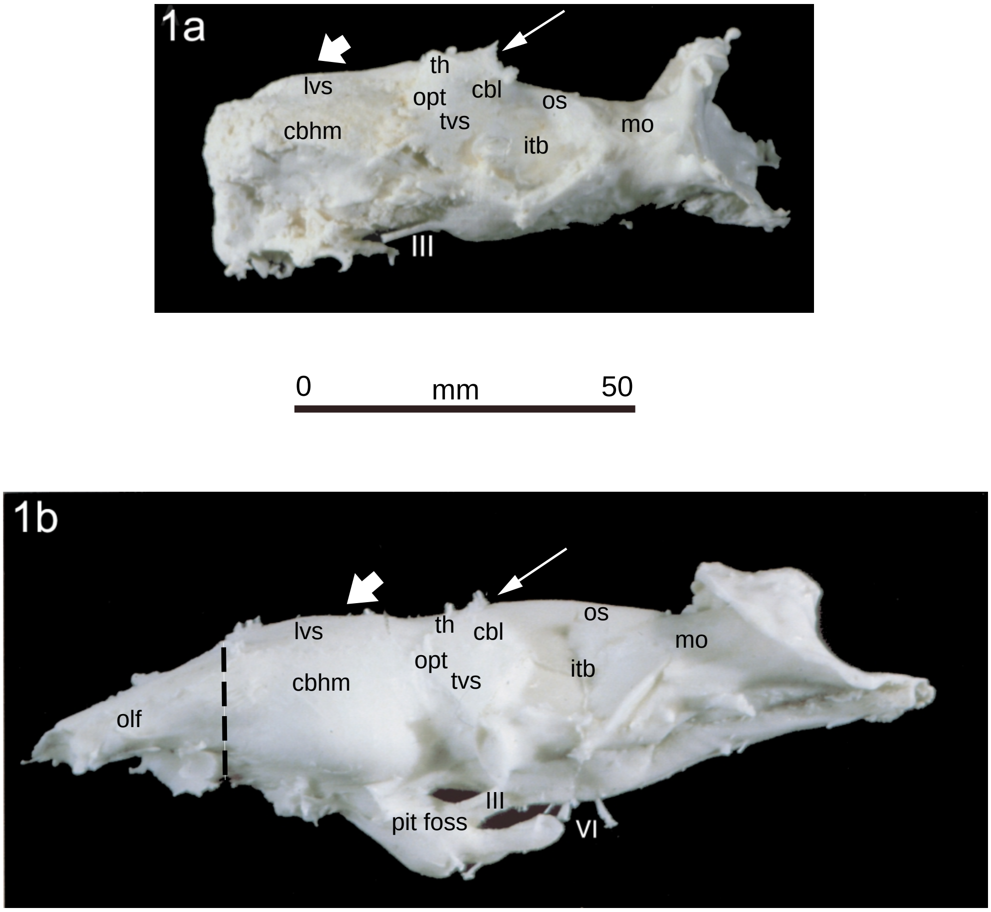

Figure 1. a. Left lateral view of the endocast of *Steneosaurus pictaviensis* (LPP.M.35). **b.** Left lateral view of an endocast of *Gavialis gangeticus*. Arrows indicate equivalent regions. The dashed line in *figure 1b* indicates the anteriormost point of the endocast of *Steneosaurus*. **cbhm**: cerebral hemispheres; **cbl**: cerebellum; **itb**: impression of tympanic bulla; **lvs**: longitudinal venous sinus; **mo**: medulla oblongata; **olf**: olfactory lobes; **os**: occipital sinus; **pit foss**: pituitary fossa; **th**: torcular herophili; **III**: oculomotor nerve; **VI**: abducens nerve.

Figure 1. a. Vue latérale gauche du moulage endocrânien de *Steneosaurus pictaviensis* (LPP > M.35). **b.** Vue latérale gauche du moulage endocrânien de *Gavialis gangeticus*. Les flèches indiquent les régions équivalentes. La ligne pointillée de la *figure 1b* indique la limite antérieure du moulage endocrânien de *Steneosaurus*. **cbhm :** hémisphères cérébraux; **cbl :** cervelet; **itb** : impression de la bulle tympanique; **lvs** : sinus veineux longitudinal; **mo** : moëlle allongée; **olf** : lobes olfactifs; **os** : sinus occipital; **pit foss** : fosse pituitaire; **th** : torcular herophili; **III** : nerf oculo-moteur; **VI** : nerf abducens.

cerebellum, just anterior to the tympanic bullae. Here, indicated by the thinner arrow and by the posterior irregular part of the dashed line in *figure 2b*, are two channels entering the braincase walls above the cerebellar region. These rounded tubular cavities then extend in a posterior direction, and reach approximately 7.8 mm in depth before they are blocked with matrix. These channels are close to the mid-line of the skull, and are separated by just 9 mm (*figure 2b*).

4. Discussion

The extensive elevated area reflects the presence of a large longitudinal dorsal venous sinus in the cranial cavity. The large cavities reflect the entrance of the *vena capiti dorsalis* into the endocranial cavity in *Steneosaurus*. The presence of a longitudinal dorsal blood sinus is found in most reptiles including lizards, crocodilians, most dinosaurs and birds (where they rarely leave such large impressions on the endocranial walls). Concerning the *capiti dorsalis*, O'Donoghue [9] states: 'The entrance of the *capiti dorsalis* through a foramen or notch in the hinder end of the braincase, either in the prootic or supraoccipital, appears to be a constant feature in early Amphibia and Reptilia'. This said that the equivalents of the *vena capiti dorsalis* are generally a lot smaller than those of *Steneosaurus*.

The vena parietalis are also present in *Steneosaurus,* feeding into the *capiti dorsalis* just before they enter the endocranial cavity, the blood then runs into the longitudinal sinus [2, 9]. The vena parietalis, which drain the supratemporal musculature, lead into the skull through

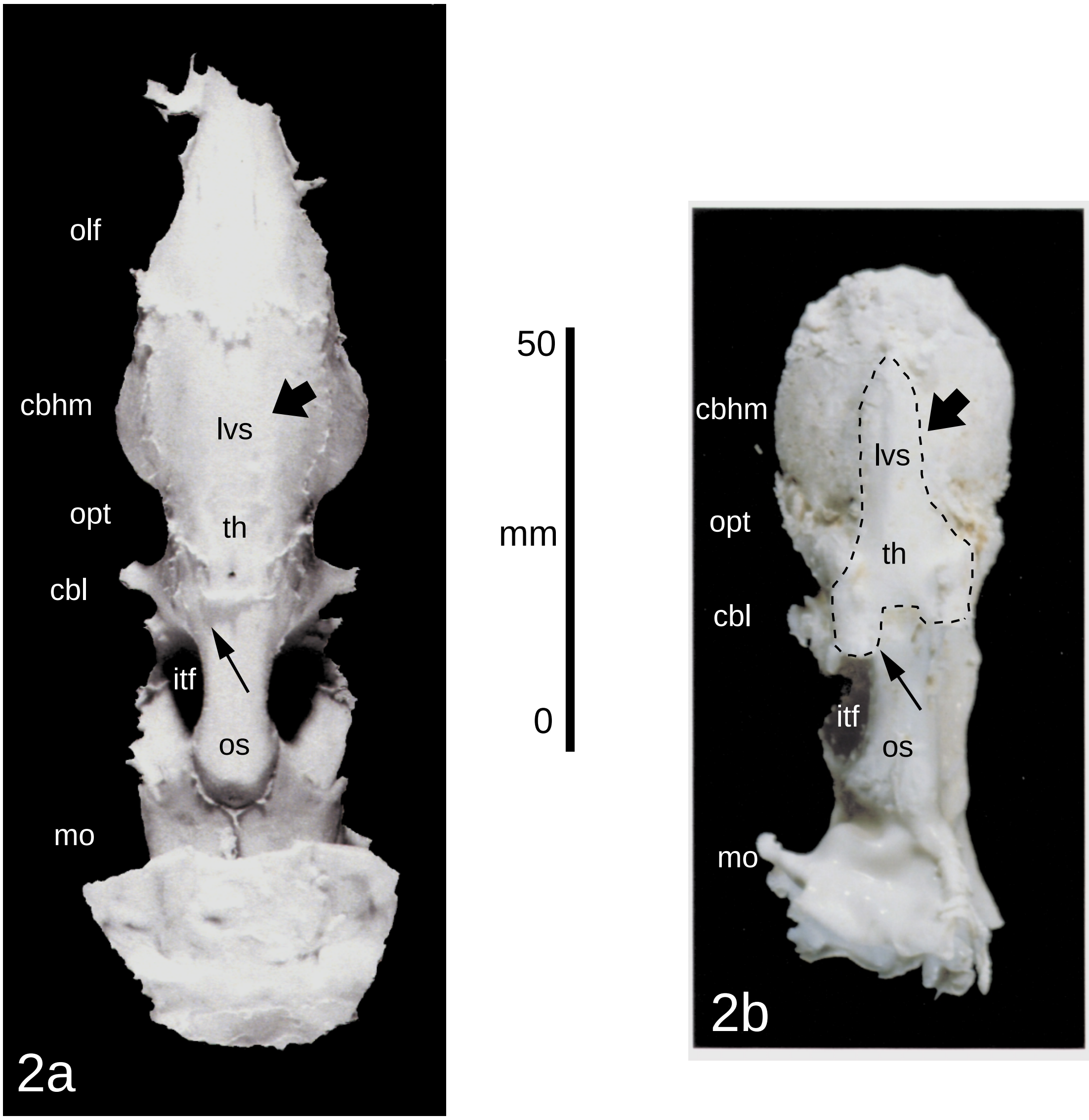

Figure 2. a. Dorsal view of the endocast of *Gavialis gangeticus*. **b.** Dorsal view of the endocast of *Steneosaurus pictaviensis* (LPP.M.35). Arrows indicate equivalent regions. The dashed line in *figure 2b* highlights the enlarged endocranial area of *Steneosaurus*.

Figure 2. a. Vue dorsale du moulage endocrânien de *Gavialis gangeticus*. **b**. Vue dorsale du moulage endocrânien de *Steneosaurus pictaviensis (LPP.M.35)*. Les flèches indiquent les régions équivalentes. La ligne pointillée de la *figure 2b* montre la région endocrânienne élargie de *Steneosaurus*.

foramina in the medioposterior corner of the supratemporal fenestra.

Modern Crocodylia have a much less prominent sinus arrangement than that seen in *Steneosaurus* (*figures 1a* and *2b*). The longitudinal dorsal blood sinus starts far forward in the endocranial cavity and runs back to form the torcular herophili at the boundary between the optic lobes and the cerebellum (i.e. where the endocranial roof reaches a high point) in *Steneosaurus*, this then gives off a pair of *sinus traversii* laterally and a *sinus occipitalis* posteriorly [6]. They have only small remnants of the blood vessels that entered the cranial cavity in this posterodorsal position [11]. The blood draining from the occipitotemporal regions via equivalent vessels in these and other archosaurians then generally exits the endocranial cavity through the trigeminal foramen (in the case of the middle cerebral vein [2, 7]), or the metotic fissure (in the case of the posterior cerebral vein in *Sphenodon* [9]). In the case of the posterior cerebral vein in more derived reptiles such as the adult crocodile, the blood vessels exit the foramen magnum [11], or both the exits mentioned above for the posterior cerebral vein are used.

In theropods, such as *Allosaurus fragilis* and *Tyrannosaurus rex*, large dorsal blood sinuses are present in similar regions of the skull, and large vascular vessels enter the braincase in the same position as the *capiti dorsalis* in *Steneosaurus* (label ‘vc’ [8], *figure 1*). The hypothesized drainage routes out of the brain are through the middle and posterior cerebral veins, which exit through the trigeminal foramen and metotic foramen or foramen magnum respectively as in archosaurian relatives. Similar blood sinuses also exist in other early archosaurs such as *Sphenosuchus* [11], and *Erythrosuchus* and *Xilousuchus* [7]. The drainage route for these sinuses is hypothesized to be through the same pathways, though these sinuses do not leave any impression on the endocranial roof.

What was the function of these enlarged parts of the cranial venous system? It seems unlikely that they were marine adaptations as *Allosaurus* and *Tyrannosaurus* are terrestrial. Moreover, crocodilians with aquatic adaptations including the Eocene Dyrosauridae [10], and the extant *Crocodylus porosus*, lack this feature. Interestingly, the Eocene Sebecosuchia, which are thought to have been terrestrial, are reported to have had an expanded cerebellum [5], although Hopson [8] states that this was an expanded blood sinus, as the author believes was the case in *Steneosaurus*. If Sebecosuchia also had an enlarged sinus [3], this suggests that there was a tendency towards development of this structure several times in crocodylian history.

Other marine reptiles, including ichthyosaurs, plesiosaurs and nothosaurs have similarly positioned vascular vessels entering the cranial cavity [8], but expansion is normally less pronounced both in these vessels and in the blood sinus.

Are expanded sinuses a primitive character? This is unlikely, given that primitive archosaurians including both extant forms such as *Sphenodon* [9], and extinct taxa such as *Sphenosuchus* [11], and *Pholidosaurus meyeri* [8] do not possess expanded sinuses or venous canals.

An examination of the Metriorhynchidae would be of interest as they are thought to have evolved from the Teleosauridae [4]. Theoretically, they should also have large blood sinuses and *capiti dorsalis*, but appropriate material is not currently available.

5. Conclusion

The endocranial characteristics of *Steneosaurus* described here include an expanded longitudinal blood sinus, torcular herophili, *sinus traversi* and *capiti dorsalis*, some of the main components of the venous system of the head, and the drainage system of the occipitotemporal musculature. This enlargement is revealed here in detail for the first time due to the exceptional preservation of the specimen and the delicate technique of acid preparation. The large size of these sinuses is rare, but not exceptional, because similar features are found in the non-avian Theropoda and some fossil Crocodylia. Further work is needed to clarify their function.

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Appendix

Crocodilian skulls. The Laboratoire d'anatomie comparée in Paris: *Gavialis gangeticus* (1944-249), *Alligator mississippiensis* (1910-17), *Crocodylus porosus* (on display at the Museum national d'histoire naturelle in Paris) and *Crocodylus niloticus* (1963-22). **Crocodilian brains.** The Laboratoire d'anatomie comparée in Paris: *Alligator mississippiensis* (1945-93), *Crocodylus porosus* (1932-58), *Osteolaemus tetrapis* (1963-50).

Thalattosuchian skulls. The University of Poitiers: two Teleosaurs: *Steneosaurus pictaviensis* (LPP.M.35) and *Steneosaurus edwardsi* (LPP.M.21), and two metriorhynchids: *Metriorhynchus brachyrhynchus* (LPP.M.22), and one juvenile Metriorhynchid (LPP.M.23).

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