


Braincase anatomy of extant Crocodylia, with new insights into the development and evolution of the neurocranium in crocodylomorphs

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Abstract

Present-day crocodylians exhibit a remarkably akinetic skull with a highly modified braincase. We present a comprehensive description of the neurocranial osteology of extant crocodylians, with notes on the development of individual skeletal elements and a discussion of the terminology used for this project. The quadrate is rigidly fixed by multiple contacts with most braincase elements. The parabasisphenoid is sutured to the pterygoids (palate) and the quadrate (suspensorium); as a result, the basiptyergoid joint is completely immobilized. The prootic is reduced and externally concealed by the quadrate. It has a verticalized buttress that participates in the canal for the temporal vasculature. The ventrolateral processes of the otoccipitals completely cover the posteroventral region of the braincase, enclose the occipital nerves and blood vessels in narrow bony canals and also provide additional sutural contacts between the braincase elements and further consolidate the posterior portion of the crocodylian skull. The otic capsule of crocodylians has a characteristic cochlear prominence that corresponds to the lateral route of the perilymphatic sac. Complex internal structures of the otoccipital (extracapsular buttress) additionally arrange the neurovascular structures of the periotic space of the cranium. Most of the braincase elements of crocodylians are excavated by the paratympanic pneumatic sinuses. The braincase in various extant crocodylians has an overall similar structure with some consistent variation between taxa. Several newly observed features of the braincase are present in *Gavialis gangeticus* and extant members of Crocodylidae to the exclusion of alligatorids: the reduced exposure of the prootic buttress on the floor of the temporal canal, the sagittal nuchal crest of the supraoccipital projecting posteriorly beyond the postoccipital processes and the reduced paratympanic pneumaticity. The most distinctive features of the crocodylian braincase (fixed quadrate and basiptyergoid joint, consolidated occiput) evolved relatively rapidly at the base of Crocodylomorpha and accompanied the initial diversification of this clade during the Late Triassic and Early Jurassic. We hypothesize that profound rearrangements in the individual development of the braincases of basal crocodylomorphs underlie these rapid evolutionary modifications. These rearrangements are likely reflected in

the embryonic development of extant crocodylians and include the involvement of neomorphic dermal anlagen in different portions of the developing chondrocranium, the extensive ossification of the palatoquadrate cartilage as a single expanded quadrate and the anteromedial inclination of the quadrate.

KEYWORDS

anatomy, braincase, computed tomography, Crocodylia, Crocodylomorpha, CT scan, development, evolution

1 | INTRODUCTION

Depending on the systematic reviews used, present-day crocodylians comprise 23 to 28 species of semiaquatic ambush predators in Africa, Asia, Australia and the Americas (Grigg & Kirshner, 2015; Hekkala et al., 2011; McAliley et al., 2006; Murray et al., 2019; Oaks, 2011; Shirley et al., 2014). They represent the only surviving lineage of the once ecologically and taxonomically diverse clade Crocodylomorpha (Clark, 1986, 1994; Nesbitt, 2011; Walker, 1990). Crocodylomorphs evolved during the Triassic and were the only pseudosuchian archosaurs to survive the end-Triassic extinction (Nesbitt, 2011). Present-day crocodylians, along with their closest extant sister-taxon, Aves, constitute the only two extant archosaurian lineages.

The highly modified akinetic skull is the hallmark of extant crocodylians and their extinct relatives (Iordansky, 1973; Langston, 1973; Pol et al., 2013). The solid braincase, palate and posterior aspect of the skull are among the key changes that occurred during the evolution of crocodylomorphs and are related to an increase in bite force (Erickson et al., 2012; Langston, 1973; Pol et al., 2013). These processes co-occurred with the initial radiation of crocodylomorphs in the Late Triassic–Early Jurassic and have been related to the ecological and evolutionary success of the clade from the early Mesozoic onward (Leardi et al., 2017, 2020; Pol et al., 2013; Walker, 1990). Thus, the anatomy of the braincase is a prominent topic in crocodylian evolution and biology.

Various aspects of the braincase structure of crocodylians have been studied over the past three centuries (e.g. Brochu, 1999; Brühl, 1862; Cuvier, 1824; Dufeu & Witmer, 2015; Holliday & Witmer, 2009; Iordansky, 1973; Kälin, 1955; Langston, 1973; Miall, 1878; Müller, 1967; Owen, 1850; Walker, 1990). Despite an enormous amount of previous research, a comprehensive up-to-date description of the braincase anatomy of extant crocodylians has been lacking. Furthermore, the braincase nomenclature of crocodylomorphs is complex, convoluted and varies considerably between previously published studies (e.g., Busbey & Gow, 1984; Clark, 1986; Dufeu & Witmer, 2015; Iordansky, 1973; Leardi et al., 2017, 2020; Owen, 1850; Walker, 1990; Wu & Chatterjee, 1993; see Table 2). This terminological instability complicates the study and anatomical comparison of the complex structure of the neurocranium. It likely accounts for the often brief and superficial descriptions of the braincase in many fossil crocodylomorphs, insufficient sampling of neurocranial characters in existing phylogenetic analyses and the misidentification of certain structures in published studies (e.g. quadrate primary head in Clark, 1986, 1994; some of the complex structures of the otic and periotic regions in Busbey & Gow,

1984; Turner & Buckley, 2008: fig. 10; Witmer et al., 2008; paratympanic pneumatic recesses—see Table 2; File S2).

In this study, we aim to provide a comprehensive description of the braincase osteology of extant crocodylians. The application of CT scanning and 3D modelling allows examination and illustration of the intricate structure of the region in as much detail as possible. A unified nomenclature for various skeletal features is presented. In addition, we comment on the embryonic development of individual skeletal elements and paratympanic pneumatic recesses based on both published accounts and CT datasets. These developmental observations provide a deeper knowledge of the anatomy of the fully ossified neurocranium and facilitate discussion of the processes underlying the evolution of the unique braincase in crocodylomorphs.

2 | MATERIALS AND METHODS

2.1 | Institutional abbreviations

CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; DVZ M, morphological collection of Department of Vertebrate Zoology of Saint Petersburg State University, Saint Petersburg, Russia; ENS R, specimen identifier in the catalogue of European Synchrotron Radiation Facility repository, Grenoble, France; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; LFAC, specimen identifier in the catalogue of European Synchrotron Radiation Facility repository, Grenoble, France; MB.R., Museum für Naturkunde, Berlin, Germany; OUV, Ohio University Vertebrate Collection, Athens, Ohio, USA; PIN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; RVC-JRH, John R. Hutchinson collection, Royal Veterinary College, University of London, London, UK; TMM, Texas Memorial Museum, University of Texas at Austin, Austin, Texas, USA; UF, University of Florida, Florida Museum of Natural History, Gainesville, Florida, USA; ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia; ZMMU MSU R, Zoological museum of Moscow State University, Moscow, Russia.

2.2 | Specimens

The braincases of 75 crocodylian crania were analysed (see File S1 for a complete list of taxa examined). The sample comprises all currently recognized extant genera (*Alligator*, *Caiman*, *Crocodylus*, *Gavialis*,

Mecistops, *Melanosuchus*, *Osteolaemus*, *Paleosuchus* and *Tomistoma*) and a total of 18 species covering all present-day lineages of Crocodylia (Figures 1 and 2; File S1). Most of the studied species are represented by at least two specimens (and up to 20 for some taxa), allowing some consideration of intraspecific variability. *Alligator mississippiensis*, *Caiman crocodilus*, *Crocodylus niloticus*, *Osteolaemus tetraspis* and *Paleosuchus palpebrosus* are represented by embryonic, hatchling and juvenile specimens in order to assess ontogenetic changes. No living animals were used or euthanized specifically for this study.

2.3 | Methods

The braincase anatomy of crocodylians was studied using two principal methods: osteological observations on articulated and disarticulated skulls and CT scanning. In the course of the present study, skulls of several representatives of nine crocodylian species were X-ray CT scanned (Figure 1; Table 1). CT and high-resolution CT scans were obtained at local medical centres using Toshiba Aquilion 64 and Philips iCT medical tomographers. Micro-CT scanning was undertaken at the

Saint Petersburg State University Research Centre for X-ray Diffraction Studies (Saint Petersburg, Russia) using a Skyscan 1172. Selected scan parameters for the specimens used in this study are presented in Table 1.

The rest of the sample includes CT scan data for present-day crocodylians that are available online at Digimorph (<http://digimorph.org/>), OSF CrocBase (osf.io/6zamj), ESRF database (<http://paleo.esrf.fr/>), Dryad (<https://doi.org/10.5061/dryad.mt64k>) and Morphosource (<https://www.morphosource.org/>) (see File S1). These were either downloaded and examined on a personal PC or analysed directly online.

Data acquired from CT scans were imported into the visualization software Amira 6.3.0 (FEI-VSG Company) and manually segmented. Measurements on the 3D models were performed using Amira 6.3.0. All imagery in the Results section of this study is based on the digital models of the segmented skulls. Photorealistic 3D visualization (Figure 1) was done using Cinematic Rendering Syngo.via VB20 software (SIEMENS Healthineers). No dissections were performed; the soft-tissue contents of the crocodylian braincase were reviewed using the literature and CT scans of intact heads. Aspects of the embryonic development of crocodylian skull were acquired through the analysis of the relevant literature and CT data.



FIGURE 1 3D photorealistic images of crocodylian crania used in this study, in dorsal view. (a) *Alligator mississippiensis* (DVZ M 4/13); (b) *Caiman yacare* (ZMMU MSU R-6967); (c) *Crocodylus novaeguineae* (DVZ M 9/13); (d) *Gavialis gangeticus* (ZIN 7249); (e) *Tomistoma schlegelii* (ZMMU MSU R-13859); (f) *Mecistops cataphractus* (DVZ M 6/13). Scale bars each equal 5 cm

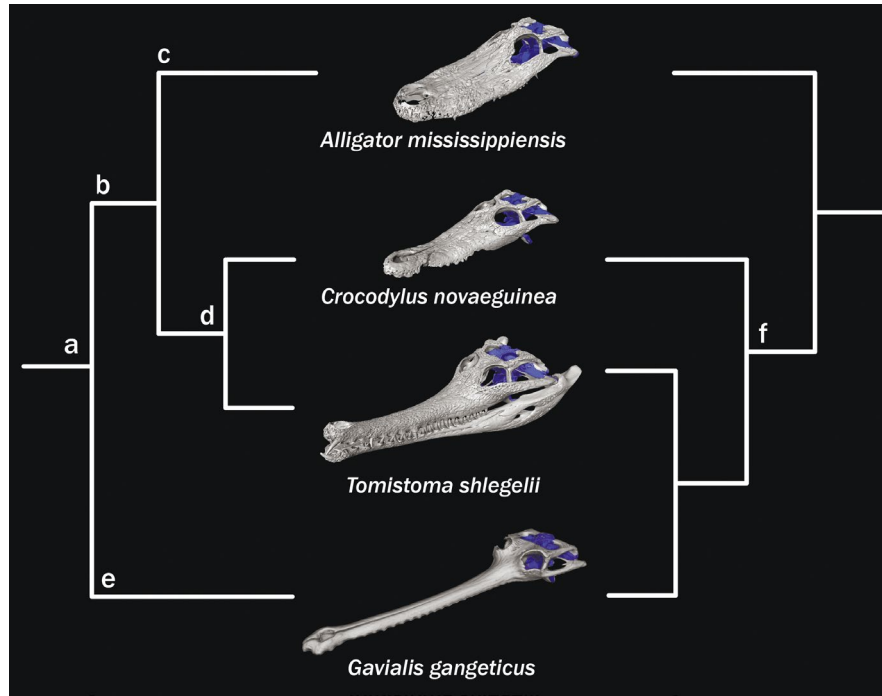


FIGURE 2 Phylogenetic framework of present-day crocodylians. Key taxa used in this study are mapped onto the two phylogenetic schemes (left—traditional morphology based; right—molecular based), with the braincase region highlighted in blue. a: Crocodylia; b: Breviostres; c: Alligatoridae; d: Crocodylidae; e: Gavialidae; f: Longirostres. Skulls not to scale

TABLE 1 CT-scanning parameters for specimens used in the study

Taxon	Specimen	Matrix type of scan	Scan parameters	Stack size
<i>Alligator mississippiensis</i>	DVZ M 4/13 (articulated skull)	High-resolution CT scan (1024 × 1024)	164 μA, 140 kV, slice thickness 0.67 mm	837 slices
<i>Alligator sinensis</i>	DVZ M 2/13 (articulated skull)	CT scan (512 × 512)	300 μA, 120 kV, slice thickness 0.5 mm	663 slices
<i>A. sinensis</i>	DVZ M 3/13 (disarticulated skull)	High-resolution CT scan (1024 × 1024)	164 μA, 140 kV, slice thickness 0.67 mm	494 slices
<i>Caiman crocodilus (hatchling)</i>	PIN comparative collection, unnumbered (disarticulated skull)	Micro-CT scan (4000 × 4000)	200 μA, 44 kV	2416 slices
<i>Caiman yacare</i>	ZMMU MSU R-6967 (partially disarticulated skull)	High-resolution CT scan (1024 × 1024)	72 μA, 140 kV, slice thickness 0.67 mm	422 slices
<i>Crocodylus novaeguineae</i>	DVZ M 9/13 (articulated skull)	High-resolution CT scan (1024 × 1024)	164 μA, 140 kV, slice thickness 0.67 mm	631 slices
<i>Osteolaemus tetraspis</i>	DVZ M 7/13 (disarticulated skull with nearly complete braincase)	CT scan (512 × 512)	200 μA, 120 kV, slice thickness 0.5 mm	464 slices
<i>Mecistops cataphractus</i>	DVZ M 6/13 (articulated skull)	High-resolution CT scan (1024 × 1024)	151 μA, 140 kV, slice thickness 0.67 mm	1000 slices
<i>Gavialis gangeticus</i>	ZIN 7249 (articulated skull)	CT scan (512 × 512)	250 μA, 135 kV, slice thickness 1.0 mm	571 slices
<i>Tomistoma schlegelii</i>	ZMMU MSU R-13859 (articulated skull)	High-resolution CT scan (1024 × 1024)	82 μA, 140 kV, slice thickness 0.67 mm	1469 slices
<i>T. schlegelii</i>	ZMMU MSU R-9296 (articulated skull)	High-resolution CT scan (1024 × 1024)	82 μA, 140 kV, slice thickness 0.67 mm	1267 slices

2.4 | Phylogenetic framework

We use Crocodylia and “crocodylian” in reference to the crown group that comprises the last common ancestor of *Gavialis*

gangeticus, *C. niloticus* and *A. mississippiensis* and all of its descendants (Brochu, 1999, 2003) (Figure 2). Extant crocodylians are generally divided into three main clades: Alligatoridae, Crocodylidae and Gavialidae (Benton & Clark, 1988; Brochu,

1999, 2003). The higher level relationships among Crocodylia remain a matter of continuing debate. The most contentious issue concerns the phylogenetic position of *Gavialis* (Figure 2). Most unconstrained morphological analyses recover *Gavialis* and its closest relatives (Gavialidae) as distantly related to other crocodylians (Brevirostres) (Brochu, 1997, 1999, 2003; Brochu & Storrs, 2012; Narváez et al., 2015; Norell, 1989; Tarsitano et al., 1989). By contrast, molecular phylogenies find overwhelming support for a sister-taxon relationship between *Gavialis* and *Tomistoma* (Densmore, 1983; Gatesy et al., 2003; Janke et al., 2005; Oaks, 2011). In the latter hypothesis, *Gavialis*, *Tomistoma* and all traditional crocodylids form a clade (Longirostres), and alligatorids are only distantly related to that clade (Harshman et al., 2003) (Figure 2). The unresolved phylogenetic position of *Gavialis* affects definition of higher level clades among Crocodylia (Brochu, 1997, 1999, 2003). Recently, the hypothesis of Longirostres received additional support from the geometric morphometric analysis of the braincase (Gold et al., 2014), tip-dated Bayesian approach (Lee & Yates, 2018) and constrained parsimony analysis of morphological data (Iijima & Kobayashi, 2019). In the text, we use informal clade names (“alligatorids”, “crocodylids” and “gavialids”) in reference to traditional groups in sense of Brochu (1999, 2003) unless stated otherwise.

Crocodylomorpha is regarded as a monophyletic taxon that comprises present-day crocodylians and all taxa more closely related to them than to other pseudosuchian archosaurs (Leardi et al., 2017; Nesbitt, 2011). Non-crocodyliform crocodylomorphs are paraphyletic, as opposed to the monophyletic Crocodyliformes (Clark et al., 2004; Leardi et al., 2017, 2020; Nesbitt, 2011). Among crocodylomorphs, thalattosuchians have an unresolved phylogenetic position, having been variously interpreted as basal crocodylomorphs, basal crocodyliforms or relatively derived crocodyliforms nested within Neosuchia (Benton & Clark, 1988; Herrera et al., 2018; Leardi et al., 2020; Wilberg, 2015). In this study, we follow Wilberg (2015) and consider Thalattosuchia relatively basal crocodylomorphs, lying outside Crocodyliformes.

3 | STATEMENT OF TERMINOLOGY

3.1 | General comment

Terminology stands above all other issues discussed in this study. Various aspects of the braincase of crocodylians have been the subject of numerous studies over the past three centuries (see Section 1). As a result, a great variety of terms has been proposed and used. In this section, we present our terminology in detail and list changes made to previously used terms before proceeding to the osteological description.

The ultimate goal of our terminological approach was to develop an anatomical nomenclature for the crocodylian braincase that (1) will be clear and unified across the variety of sources; (2) will allow broader comparison with numerous crocodylomorphs

and non-crocodylomorph archosauriforms and emphasize homology and (3) will be up-to-date and exclude historical terms that imply a false statement of homology. We utilize a strictly phylogenetic concept of homology, whereby homologous structures in different taxa must have been inherited from the last common ancestor of these taxa.

We are aware that some of the applied terms may be contentious as we have changed or avoided using some established and widely employed names. However, we believe that terms should not be based on tradition or convenience; they should not reflect a false statement of homology. We hope that this study will facilitate further detailed research on the braincase anatomy of crocodylomorphs and the discussion of the most useful osteological terminology for this clade.

3.2 | Terminology

Osteological terminology used in this study in general follows Lordansky (1973), Clark (1986), Walker (1990), Brochu (1999) and Holliday and Witmer (2009). Along with such terms, we propose new anatomical names for several osteological structures that either have not been properly described or have a convoluted and misleading nomenclature historically (see Table 2; File S2). Due to space limitations of this study, the lengthy detailed discussion of each term is provided in File S2. The principal terms used in this study are summarized in Table 2.

We use the traditional directional terms “anterior”, “posterior”, “dorsal” and “ventral” rather than their veterinary equivalents “rostral”, “caudal”, “superior” or “inferior”. However, some terms consistently used in previous contributions (e.g. anterior superior and inferior processes of the prootic) deviate from this principle and are employed in their original formulation.

Throughout the text, we use age categories like hatchling, juvenile and adult. These categories are not precise but are useful for descriptive purposes. Our observations suggest that the braincase osteology and paratympanic pneumatic system of crocodylians appear anatomically similar immediately after hatching and after 1 or 2 years of post-hatching life. The pronounced changes occur later in ontogeny and likely coincide with what Tarsitano (1985) termed “cranial metamorphosis”. Thus, in terms of this study, the hatchling age category comprises individuals that are several days or months in age. The juvenile age category covers the period from several months to the first 1–2 years of post-hatching life.

The nomenclature of the paratympanic pneumatic cavities is especially complex (see Table 2; File S2). Overall, it follows Owen (1850), Müller (1967), Walker (1990) and Dufeu and Witmer (2015). Terms borrowed from the mammalian (e.g. mastoid antrum, Eustachian canal) and avian nomenclature (e.g. anterior, posterior and dorsal/superior recesses) are not used in these study because they might be confusing and imply false homology. Recent studies suggest that the tympanic middle ear of mammals evolved independently from that of diapsids (Kitazawa et al., 2015; Thompson

TABLE 2 Summary of the proposed terminology (see detailed discussion in File S2)

Present study	Source	Synonyms in previous studies
Temporal and occipital aspects of the skull		
Temporal canal	Walker (1990)	Temporoorbital canal (Sedlmayr, 2002)
Postquadrate foramen	Walker (1990)	Superior tympanic recess (Wu & Chatterjee, 1993: fig. 7C) Antrum pneumaticum dorsale (Whetstone & Whybrow, 1983)
Anterior temporal foramen	Walker (1990)	Temporoorbital foramen (Leardi et al., 2020) Temporo-orbital foramen (Barrios et al., 2018; Herrera et al., 2018; Kley et al., 2010)
Posttemporal fenestra	lordansky (1973)	Post-temporal fenestra (Clark, 1986; Walker, 1990)
Laterosphenoid		
Laterosphenoid	The term has priority for archosauriforms in general and crocodylomorphs in particular (Clark et al., 1993)	Alisphenoid (Miall, 1878; Owen, 1850) Pleurospenoid (Bellairs & Kamal, 1981)
Anterior process of laterosphenoid	Used for crocodylomorphs for the first time; term sensu Clark et al. (1993) and Sobral et al. (2016)	Laterosphenoid anterolateral lamina (Kley et al., 2010)
Slender process	Used for crocodylomorphs for the first time; term sensu Clark et al. (1993) and Sobral et al. (2016)	—
Laterosphenoid body	Holliday and Witmer (2009)	—
Postorbital process		
Caudal bridge		
Lateral bridge of laterosphenoid	Holliday and Witmer (2009)	Laterosphenoid bridge (Brochu, 1999; lordansky, 1973; Walker, 1990)
Capitate process	lordansky (1973) and Holliday and Witmer (2009)	
Antotic crest (laterosphenoid buttress)	Sensu Holliday and Witmer (2009)	Cotylar crest (Clark et al., 1993; Kley et al., 2010)
Trigeminal foramen (internal) and maxillomandibular foramen (external)	Sensu Holliday and Witmer (2007, 2009)	Foramen ovale (Busbey & Gow, 1984; lordansky, 1973)
Prootic		
Prootic	Miall (1878), lordansky (1973), Bellairs and Kamal (1981)	Petrosal (Brühl, 1862; Owen, 1850)
Prootic buttress	Walker (1990)	—
Dorsal lamina of prootic (as part of the prootic buttress)	New term	—
Anterior inferior process	Used for crocodylomorphs for the first time; terms sensu Evans (1986, 2008), Sobral et al. (2016).	—
Anterior superior process		
Lateral lamina of the prootic	New term for the structure that corresponds to the prootic-basisphenoid flange of basal crocodylomorphs (e.g. Walker, 1990) and crista prootica (otosphenoidal crest) of other diapsids (e.g. Evans, 2008)	—
Anterior bridge	New term	—
Inner ear and otic capsule		
Fenestra ovalis	Baird (1960, 1970), Wever (1978), Walker (1990), Gower and Weber (1998)	Fenestra vestibuli (=oval window) (Witmer et al., 2008: fig. 6.5)
Fenestra pseudorotunda	Walker (1990), Gower and Weber (1998)	Fenestra cochleae (=round window) (Witmer et al., 2008: fig. 6.5; note that this structure is at the same time misidentified with perilymphatic foramen)

(Continues)

TABLE 2 (Continued)

Present study	Source	Synonyms in previous studies
Cochlear duct	Baird (1960, 1970), Wever (1978)	Cochlea (Bona et al., 2013; Sobral & Müller, 2016; Witmer et al., 2008) Lagena (Bona et al., 2017; Leardi et al., 2020)
Cochlear recess	Walker (1990)	Lagenar/cochlear recess (Gower, 2002)
Lagena (ventral-most part of the cochlear duct)	Baird (1960, 1970), Wever (1978)	—
Lagenar recess (ventral-most part of the cochlear recess)	Walker (1990)	—
Cochlear prominence	Walker (1990)	—
Perilymphatic loop	Modified from Walker (1990) to increase clarity of anatomical description	Includes crista interfenestralis of Walker (1990) and Gower and Weber (1998)
Crista interfenestralis	Walker (1990) and Gower and Weber (1998)	—
Otoccipital ledge	Modified from Walker (1990)	Opisthotic ledge (Walker, 1990)
Perilymphatic foramen	Baird (1960) and Walker (1990)	Fenestra cochleae (=round window) (Witmer et al., 2008: fig. 6.5)
Recessus scalae tympani	Baird (1960, 1970) and Rieppel (1985)	—
Perilymphatic (periotic) sac	Baird (1960)	—
Otic bulla	The term refers to the endocranial bulge of the otic capsule, which is not directly related to the tympanic membrane/cavity	Bulla tympani (Iordansky, 1973) Tympanic bulla (Kley et al., 2010)
Otoccipital		
Otoccipital	In reference to a single braincase element with complex embryonic origin and corresponding to exoccipital and opisthotic of basal diapsids	Exoccipital (Miall, 1878) Exoccipital and opisthotic (Busbey & Gow, 1984; Iordansky, 1973; Walker, 1990)
Ventrolateral process of otoccipital	New term for a portion of otoccipital of crocodylomorphs with a specific embryonic origin (dermal juxtaotic laminae) and evolutionary history, distinct from paroccipital process	Ventrolateral part of the otoccipital (Clark, 1986) Ventrolateral flange of the otoccipital (Herrera et al., 2018) Part of paroccipital process (e.g. Leardi et al., 2020)
Extracapsular buttress	New term for a portion of otoccipital that has dual embryonic origin (from cartilaginous subcapsular process and dermal juxtaotic lamina)	Subcapsular process (Busbey & Gow, 1984; Clark, 1986) Subcapsular buttress (Leardi et al., 2020; Walker, 1990)
Anterovertebral process	New term	'Exoccipital' (probably part of the subcapsular buttress) (Walker, 1990: p. 97)
Metotic foramen	Sensu Walker (1990)	Fissura metotica (Iordansky, 1973) Metotic fissure (Kley et al., 2010) Jugular foramen (Bellairs & Kamal, 1981)
Foramen vagi (external)	Iordansky (1973)	Metotic foramen (Barrios et al., 2018; Bona et al., 2017) Foramen jugulare externum (Müller, 1967) Jugular foramen (Lessner & Holliday, 2020)
Internal vagal foramen	New terms	—
Internal glossopharyngeal foramen		—
Paroccipital process	Iordansky (1973), Clark (1986), Walker (1990)	—
Occipital arch	New term for part of otoccipital that corresponds to eponymous embryonic cartilaginous arch (after Bellairs & Kamal, 1981)	Exoccipital (Walker, 1990)
Supraoccipital		
Supraoccipital	Generally used term for a single ossification with complex development	Supraoccipital and epiotic (Edinger, 1938; Miall, 1878; Walker, 1990)

(Continues)

TABLE 2 (Continued)

Present study	Source	Synonyms in previous studies
Anterior lamina	Newly proposed terms for general divisions of supraoccipital	—
Posterior lamina		Posterior surface/projection (e.g. Kley et al., 2010; Leardi et al., 2020)
Dorsal lamina		—
Capsular portion of the supraoccipital	Consistent with the capsular portions of prootic and otoccipital	Epiotic (Edinger, 1938; Miall, 1878; Walker, 1990) ? Anterior pyramidal projection (Leardi et al., 2020)
Otoccipital strut	Newly proposed term for a bony strut that projects posterodorsally from foramen of posterior semicircular canal and is formed by supraoccipital and otoccipital	—
Postoccipital process	Kálin (1933) and Iordansky (1973)	Lateral flange of supraoccipital (Leardi et al., 2020)
Sagittal nuchal crest	A combined term proposed to ensure consistent terminology among previous studies	Nuchal crest (Kley et al., 2010; Turner, 2006) Vertical ridge (Clark, 1986) Supraoccipital sagittal crest (Barrios et al., 2018)
Parabasisphenoid		
Parabasisphenoid	In reference to a single braincase element with complex embryonic origin (includes dermal parasphenoid); as in Gower (2002), Kley et al. (2010), Nesbitt (2011), Sobral et al. (2016)	Basisphenoid (Brochu, 1999; Clark, 1986; Iordansky, 1973; Leardi et al., 2020; Miall, 1878; Walker, 1990)
Parabasisphenoid rostrum (cultriform process)	Generally used term (e.g. Bellairs & Kamal, 1981; Iordansky, 1973; Sobral et al., 2016; Walker, 1990)	—
Hypophyseal fossa	Generally used term (e.g. Clark, 1986; Iordansky, 1973; Leardi et al., 2020)	Pituitary fossa (Bellairs & Kamal, 1981; Miall, 1878; Walker, 1990)
Parabasisphenoid body	Iordansky (1973)	—
Descending lamina	Brochu (2004)	Narrow strip posterior to the posterior margin of the pterygoids (Iordansky, 1973: p. 228)
Posterolateral alar process	Newly proposed term	Lateral exposure of parabasisphenoid, posterior to pterygoid and quadrate (Brochu, 1999; Iordansky, 1973; Miall, 1878)
Basioccipital		
Basioccipital	Generally used term (e.g. Bellairs & Kamal, 1981; Brochu, 1999; Iordansky, 1973; Miall, 1878; Walker, 1990)	—
Basioccipital tuberosities	Iordansky (1973)	Basioccipital tubera (Brochu, 1999)
Basioccipital plate	Iordansky (1973)	—
Quadrate		
Quadrate head	Sensu Walker (1990) and Leardi et al. (2020)	—
Otic process	Sensu Leardi et al. (2020)	Posterodorsal process (Wu & Chatterjee, 1993)
Main body of quadrate (quadrate body)	Generally used term (Clark, 1986; Kley et al., 2010; Leardi et al., 2020; Walker, 1990)	—
Anterodorsal process	Walker (1990) and Wu and Chatterjee (1993)	—
Anteromedial process	Newly proposed term for the part of quadrate with distinct embryonic origin (dermal lamina palatoquadrati anterior)	Primary quadrate head (Clark, 1994) Orbital process (Leardi et al., 2020)
Pterygoid process	Generally used term (e.g. Herrera et al., 2018; Kley et al., 2010; Leardi et al., 2020)	Pterygoid ramus of quadrate (Busbey & Gow, 1984; Clark, 1986; Walker, 1990; Wu & Chatterjee, 1993)
Otic buttress	After Montefeltro et al. (2016)	—

(Continues)

TABLE 2 (Continued)

Present study	Source	Synonyms in previous studies
Posterodorsal process	Newly proposed term for dorsoventrally short but anteroposteriorly elongated projection from the dorsal surface of the quadrate	—
Paratympanic pneumaticity		
Median pharyngeal recess (unpaired)	Sensu Witmer (1997), Nesbitt (2011), Dufeu and Witmer (2015)	Median Eustachian canal and basisphenoid branch of median Eustachian canal (Miall, 1878; Owen, 1850) Median Eustachian canal and its anterior median branch (Mea) (Colbert, 1946; Walker, 1990) Mediane Eustachische Öffnung, canalis anterior, canalis posterior (Müller, 1967) Hypophyseal–basicranial tube and its anterior branches (Tarsitano, 1985) Sub-basisphenoid recess (Leardi et al., 2020; Walker, 1990) Median pharyngeal system (Dufeu & Witmer, 2015)
Median pharyngeal canal and foramen (unpaired)	Dufeu and Witmer (2015)	Median Eustachian canal and foramen (Clark, 1986; Colbert, 1946; Miall, 1878; Owen, 1850; Walker, 1990) Hypophyseal–basicranial canal and foramen (Tarsitano, 1985)
Parabasisphenoid recess (paired)	Dufeu and Witmer (2015)	Basisphenoid diverticulum (Dufeu & Witmer, 2015) Corresponds in part to: Basisphenoid branch of median Eustachian canal (Miall, 1878; Owen, 1850) Anterior branch of median Eustachian canal (Mea) (Colbert, 1946; Walker, 1990) Canalis anterior (Müller, 1967)
Precarotid recess (paired, with median communication in some taxa)	Walker (1990) and Leardi et al. (2020)	Anterior pneumatic recess (Wu & Chatterjee, 1993)
Postcarotid recess (paired, with median communication in some specimens/taxa)		
Rostral recess (unpaired)		
Subcarotid recess (paired)	Dufeu and Witmer (2015)	—
Basioccipital recess (paired cavities plus unpaired median communication with median pharyngeal canal)	Walker (1990) and Dufeu and Witmer (2015)	Corresponds in part to: Basioccipital branch of median Eustachian canal (Miall, 1878; Owen, 1850) Posterior branch of median Eustachian canal (Mep) (Colbert, 1946; Walker, 1990) Canalis posterior (Müller, 1967)
Pharyngotympanic cavity (recess) (paired)	Dufeu and Witmer (2015)	Middle ear cavity (Tucker, 2017; Walker, 1990) Tympanic cavity (Colbert, 1946; Owen, 1850; Tarsitano, 1985; Walker, 1990) Cavum tympani (Müller, 1967)
Pharyngotympanic canal (paired)	Dufeu and Witmer (2015) and Tucker (2017)	Lateral Eustachian canal (e.g. Clark, 1986; Colbert, 1946; Miall, 1878; Owen, 1850; Tarsitano, 1985; Walker, 1990) Tuba Eustachii (Müller, 1967)
Rhomboidal recess (paired)	Owen (1850), Walker (1990) and Leardi et al. (2020)	—

(Continues)

TABLE 2 (Continued)

Present study	Source	Synonyms in previous studies
Recessus epitubaricus (paired)	Dufeau and Witmer (2015)	Rhomboidal recess (Iordansky, 1973) Corresponds in part to: lateral branch of the anterior branch of the median Eustachian canal (Meal) (Colbert, 1946; Walker, 1990)
Pharyngotympanic fossa on the lateral surface of prootic (paired)	Newly proposed term	Corresponds in part to: lateral branch of the anterior branch of the median Eustachian canal (Meal) (Colbert, 1946; Walker, 1990) The depressed areas at the sides of the prootics, in front of and lateral to the prootic parts of the cochlear prominences (prootic recesses) (Walker, 1990: p. 75)
Infundibular recess (paired) Quadrate recesses (paired)	Dufeau and Witmer (2015)	Quadrate pneumaticity (e.g. Busbey & Gow, 1984; Clark, 1986; Leardi et al., 2017)
Intertympanic recess (paired during early ontogeny in extant taxa and in adults of some basal non-crocodyliform crocodylomorphs; unpaired in adults of extant taxa)	Tarsitano (1985) and Dufeau and Witmer (2015)	Mastoid antrum (Clark, 1986; Hasse, 1873; Leardi et al., 2020; Müller, 1967; Walker, 1990; Wu & Chatterjee, 1993) Transverse pneumatic canal (Busbey & Gow, 1984; Clark, 1986; Iordansky, 1973)
Prootic facial recess (paired)	A combined term proposed to enchain consistent terminology among previous studies	Facial antrum (Leardi et al., 2020; Walker, 1990; Wu & Chatterjee, 1993) Prootic diverticulum (Dufeau & Witmer, 2015)
Laterosphenoid recess (paired)	Müller (1967)	Diverticulum zum Laterosphenoid Müller (1967) Rostral extension of the prootic diverticulum (Dufeau & Witmer, 2015) ? Trigeminal recess (Leardi et al., 2020; Wu & Chatterjee, 1993)
Otoccipital recess (paired)	Müller (1967) and Dufeau and Witmer (2015)	Divertikel des adulten Exoccipitale (Müller, 1967) Otoccipital diverticulum (Dufeau & Witmer, 2015) ? Posterior pneumatic recess (Leardi et al., 2020; Wu & Chatterjee, 1993)
Pterygoid recess (paired)	Dufeau and Witmer (2015)	—

& Tucker, 2013; Tucker, 2017); thus, mammalian terms should not be applied to the structures in crocodylomorphs. Furthermore, the last common ancestor of birds and crocodylomorphs did not have the elaborated pneumatic system; consequently, most paratympanic recesses in these two clades are likely not homologous (see Gower, 2002; Gower & Weber, 1998; Nesbitt, 2011; Sobral et al., 2016).

The terms “diverticulum”, “sinus”, “recess” and “antrum” are used somewhat interchangeably in the literature. In this study, we make the following distinction between them. A pneumatic diverticulum is an epithelial extension (“pocket”) filled with air (soft-tissue structure). A pneumatic recess or antrum is a cavity or a marked depression on the bone generated by the pneumatic diverticulum (skeletal structure). A pneumatic sinus is a combined structure present in a living animal or a fresh corpse; it comprises the diverticulum occupying the recess. As we have mostly worked with skeletal material, we refer to the reconstructed structures as pneumatic recesses.

It should be taken into account that dried crocodylian skulls often appear to be more pneumatic and bear a large number of variously sized internal cavities. These cavities are often filled with soft tissues in a living animal or a fresh corpse. These cavities, along

with the paratympanic pneumatic recesses, are the result of bone resorption (Dufeau & Witmer, 2015; Hua & de Buffrenil, 1996; and citations therein). We differentiate the paratympanic pneumatic recesses (originating from the epithelial diverticula of the pharynx and connected to other paratympanic pneumatic recesses) and the resorption cavities (not related directly to the pharynx diverticula or, at least, lacking connections with the rest of the paratympanic system in a given specimen).

4 | RESULTS

4.1 | Crocodylian braincase: overview

The braincase of crocodylians is a complex structure that incorporates elements of various embryonic origins. The neurocranium (=endocranium) is composed of several mostly endochondral ossifications. The olfactory region of the neurocranium in present-day crocodylians remains cartilaginous throughout ontogeny and is represented by the trough-like planum suprasettale lying atop the interorbital septum (Ali et al., 2008; Iordansky, 1973). Small ossifications in the interorbital septum have occasionally been reported (Bellairs

& Kamal, 1981). The orbitotemporal region of the neurocranium is represented by the paired laterosphenoids. Three ossifications form the otic capsule: the paired prootics, the paired otoccipitals and the single supraoccipital. The unpaired parabasisphenoid (=fused basi- and parasphenoid) and basioccipital make up the floor of the neurocranium.

Several dermal ossifications (e.g. fused frontals, parietals and pterygoids) are sutured to the neurocranial elements and participate in the formation of the braincase. A separate dermal ossification (postparietal or dermo-supraoccipital) has occasionally been reported in crocodylians (e.g. Lordansky, 1973; Mook, 1921). Based on recent studies, however, a separate dermal postparietal is present only in the late embryonic stages of crocodylians; the unpaired central element reported by Mook (1921) is best considered a derivative from the perichondrally ossifying trabecular bone of the developing supraoccipital (Klembara, 2001; Rieppel, 1993).

The derivatives of the palatoquadrate cartilage represent the splanchnocranium and are integrated into the lateral wall of the crocodylian braincase (Klembara, 2004). The compound quadrate ossification sutures with almost all of the aforementioned braincase bones. A certain portion of the palatoquadrate cartilage (columella prootica; Klembara, 2004) fuses with the pila antotica and the taenia marginalis of the crocodylian chondrocranium and ultimately ossifies as the laterosphenoid (Klembara, 2004).

Consequently, the braincase of the adult crocodylian is composed of 10 types of individual elements and a total of 15 separate bones: the unpaired parabasisphenoid, basioccipital, supraoccipital, frontal, parietal and the paired laterosphenoids, prootics, otoccipitals, pterygoids and quadrates (Figures 3–23). Of these, the structure of some elements of the skull roof and the palate (frontal, parietal, pterygoids) is well known (e.g. Brochu, 1999; Lordansky, 1973), and we will only provide some relevant anatomical comments. We focus on the description of the neurocranial and splanchnocranial components of the crocodylian braincase that have received less attention in the previous literature.

4.2 | General features of the crocodylian braincase

The braincase of the extant crocodylians is highly modified and anatomically divergent from the general diapsid condition. The *lateral aspect* of the braincase constitutes the orbitotemporal region of the skull (laterosphenoid) and the medial wall of the temporal fossa and the adductor chamber (Figure 3). The epipterygoid is absent in the orbitotemporal region of extant crocodylians (Holliday & Witmer, 2009). The quadrate forms most of the medial wall of the adductor chamber and provides the main attachment site for the adductor muscles (Busbey, 1989; Holliday & Witmer, 2007; Lordansky, 1964, 1973; Lessner & Holliday, 2020; Schumacher, 1973). The integration of the splanchnocranial elements (namely, the quadrate) into the lateral wall of the braincase is a characteristic feature of Crocodylia (Lordansky, 1973; Langston, 1973). The quadrate is sutured to most of the neurocranial elements of the braincase and also

to the pterygoid, parietal, squamosal and quadratojugal (Figure 3). This obscures many elements of the neurocranium in lateral view (i.e. prootic, most of otoccipital and parabasisphenoid) and results in the rigidly fixed quadrate in the crocodylian skull.

The quadrate of crocodylians is notably inclined anteromedially relative to the condition of other extant diapsids (Figure 3) (Lordansky, 1973; Walker, 1990). Its otic process contacts the prootic, a characteristic condition of crocodylomorphs and a synapomorphy of this clade (Clark et al., 2004; Nesbitt, 2011; Walker, 1990; Wu & Chatterjee, 1993). In addition, the mandibular condyles are displaced posteriorly and dorsally relative to the occipital condyle, as compared to the condition in other extant diapsids (Figures 3, 4 and 6) (Lordansky, 1973). The progressive anteromedial inclination of the quadrate during the evolutionary history of crocodylomorphs has been correlated with the acquisition of the quadrate–prootic contact and the disposition of the mandibular condyles (Lordansky, 1973: p. 236; Walker, 1990: p. 104); however, these correlations require further testing using geometric morphometric techniques and an explicit phylogenetic framework. The anteromedial inclination of the crocodylian quadrate also results in the reorganization of the meatal chamber of crocodylians (=outer ear cavity). The meatal chamber appears as a deep recess bounded by the quadrate ventrally, the squamosal dorsally and posteriorly and the postorbital and the quadratojugal anteriorly (Lordansky, 1973; Montefeltro et al., 2016).

The akinetic structure of the skull is a distinguishing feature of Crocodylia among extant diapsids (Lordansky, 1973; Langston, 1973; Pol et al., 2013; Walker, 1990). In addition to various sutural contacts of the quadrate with the adjacent elements, the plesiomorphically synovial basipterygoid joint is absent (Holliday & Witmer, 2008). The basipterygoid processes of the parabasisphenoid exist in the crocodylian chondrocranium only during early embryological stages (Klembara, 1993). The subsequent progressive ossification of the embryonic skull results in the firm suturing between the parabasisphenoid and the pterygoid (Bellairs & Kamal, 1981; Klembara, 1993). In addition, the ascending processes of the pterygoids contact the laterosphenoids and, in some taxa (e.g. *Alligator* spp., *Caiman* spp., *Tomistoma schlegelii*, *Gavialis gangeticus*), the prootics (Figure 3). These contacts cover almost the entire lateral surface of the parabasisphenoid (except for its rostrum and a narrow exposure of the alar processes posteriorly) and additionally fix the braincase of crocodylians.

The *posterior (occipital) aspect* of skull is formed mainly by the four occipital elements (paired otoccipitals and single supra- and basioccipital) (Figure 4). The parabasisphenoid and the pterygoid are slightly exposed ventrally. The foramen magnum is bounded by the basioccipital and otoccipitals; the supraoccipital does not participate in its margin (Figure 4). The parietal is exposed as a thin median strip of bone dorsal to the supraoccipital. Each otoccipital forms a continuous contact with the corresponding squamosal. The otoccipitals have ventrolateral processes that provide additional sutural contacts between the braincase elements. This results in the highly consolidated structure of the posterior part of the crocodylian cranium (Pol et al., 2013).

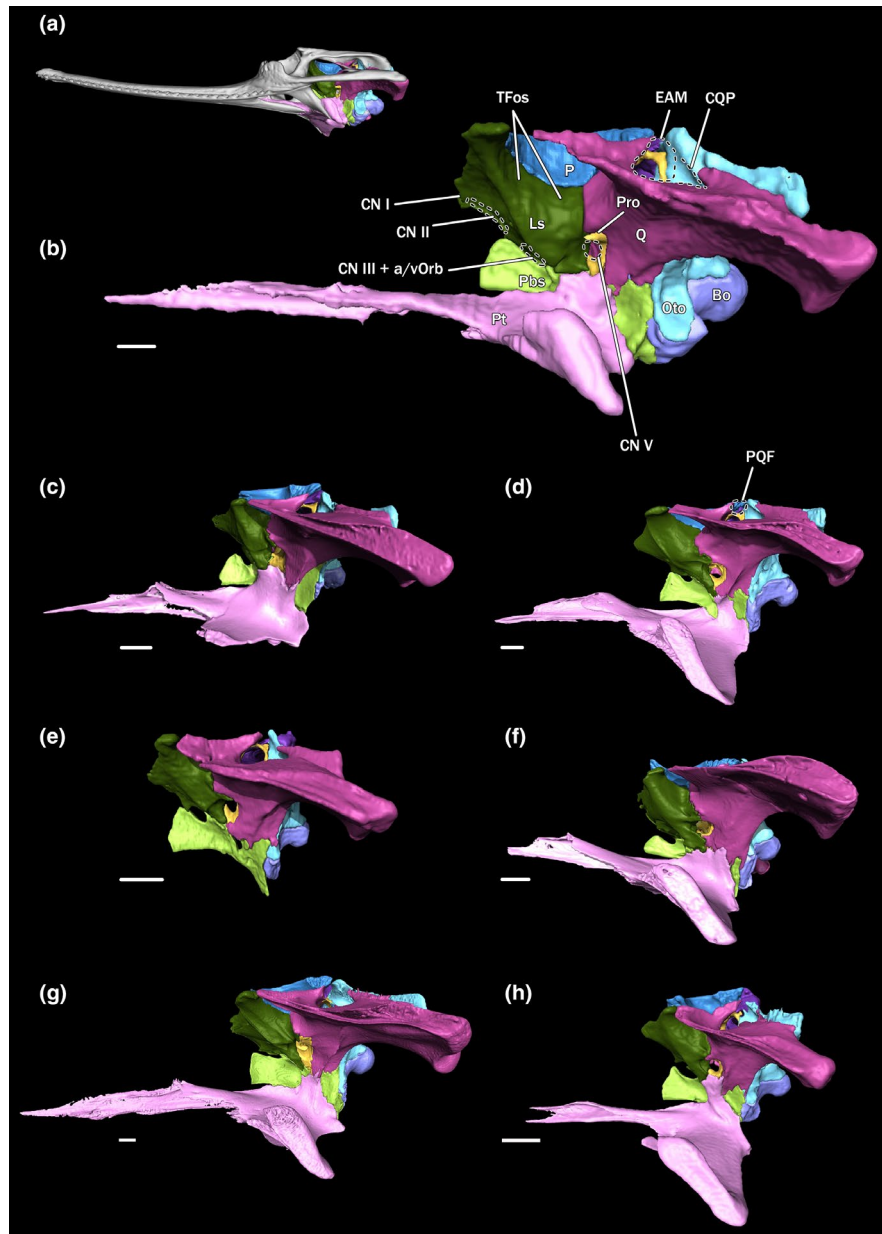


FIGURE 3 Lateral aspect of the braincase of crocodylians in left lateral view. (a) Inset showing the region of interest illustrated in (b–h). Note that pterygoids of some specimens are incomplete or missing. (a, b) *Gavialis gangeticus* (ZIN 7249); (c) *Alligator mississippiensis* (DVZ M 4/13); (d) *Mecistops cataphractus* (DVZ M 6/13); (e) *Osteolaemus tetraspis* (DVZ M 7/13); (f) *Crocodylus novaeguineae* (DVZ M 9/13); (g) *Tomistoma schlegelii* (ZMMU MSU R-13859); (h) *Caiman yacare* (ZMMU MSU R-6967). Bo, basioccipital; CN I–CN V, cranial nerve foramina; CN III + a/vOrb, common foramen for oculomotor nerve and orbital artery and vein; CQP, cranioquadrate passage; EAM, external auditory meatus; Ls, laterosphenoid; Oto, otoccipital; P, parietal; Pbs, parabasisphenoid; PQF, postquadrate foramen; Pro, prootic; Pt, pterygoid; Q, quadrate; TFos, temporal fossa. Scale bars each equal 1 cm

The aforementioned modifications result in the reorganization of the neurovascular passages in the posterior portion of the cranium in crocodylians relative to the condition in other diapsids (Benton & Clark, 1988; Clark, 1986; Porter et al., 2016; Walker, 1972, 1990). The neurovascular structures pass through canals within the otoccipital. These canals open on the posterior surface of the otoccipital in several foramina (Figure 4b). A prominent feature of the crocodylian braincase is the presence of the cranioquadrate passage (cranioquadrate canal). The posttemporal fenestrae are reduced and almost closed.

The *cranioquadrate passage* is a bony canal for the hyomandibular branch of the facial nerve (CN VII_{hm}) and the stapedia artery and vein (Figure 5) (Iordansky, 1973; Lessner & Holliday, 2020; Porter et al., 2016; Sedlmayr, 2002; Shiino, 1914). These neurovascular structures are typically not enclosed in bone in most diapsids (e.g. Evans, 2008; Porter & Witmer, 2015; Walker, 1990: fig. 49). The rotation and the extensive suturing of the quadrate to the lateral wall of the braincase in crocodylians results in the formation of a narrow canal for the aforementioned neurovascular structures. The cranioquadrate passage is formed by the quadrate laterally and the

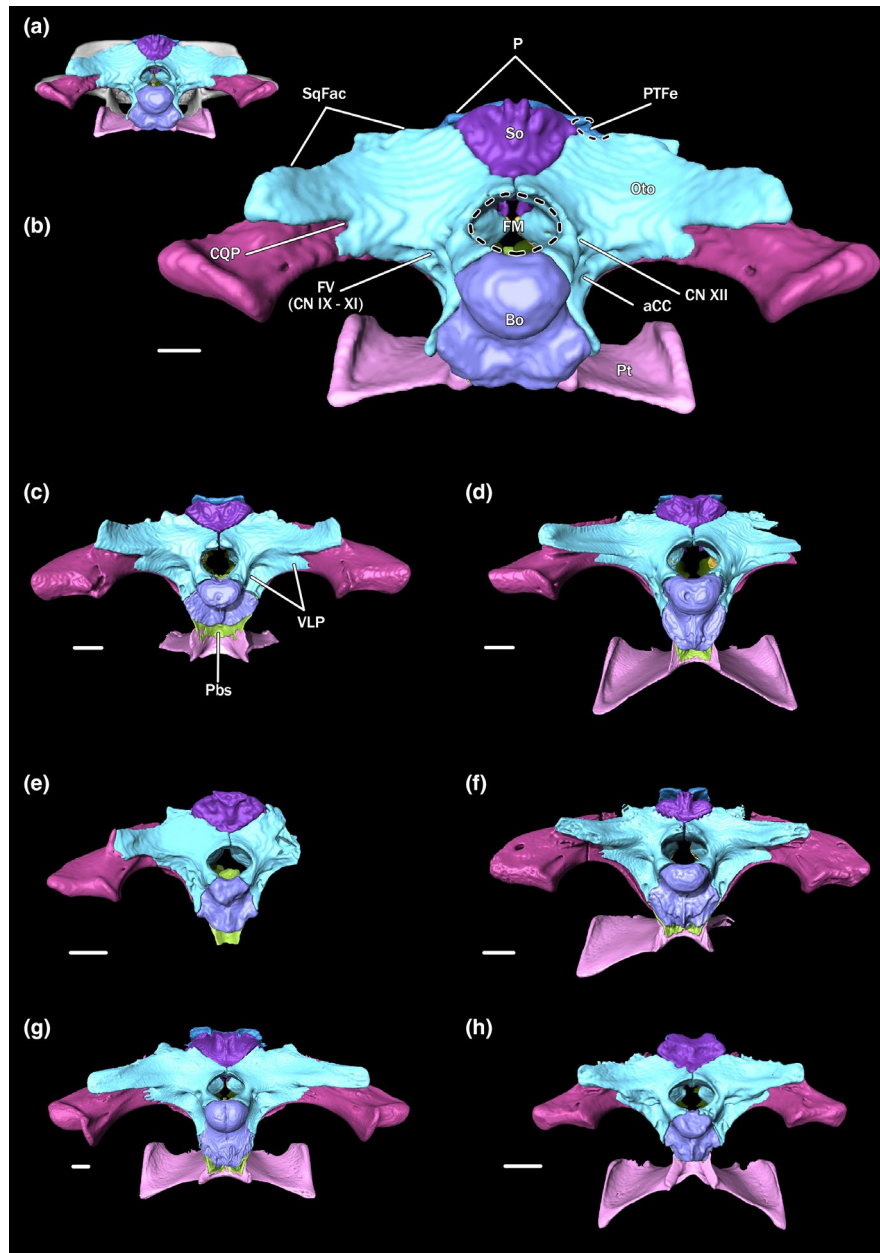


FIGURE 4 Occipital aspect of the braincase of crocodylians in posterior view. (a) Inset showing the region of interest illustrated in (b–h). Note that some specimens are incomplete. (a, b) *Gavialis gangeticus* (ZIN 7249); (c) *Alligator mississippiensis* (DVZ M 4/13); (d) *Mecistops cataphractus* (DVZ M 6/13); (e) *Osteolaemus tetraspis* (DVZ M 7/13); (f) *Crocodylus novaeguineae* (DVZ M 9/13); (g) *Tomistoma schlegelii* (ZMMU MSU R-13859); (h) *Caiman yacare* (ZMMU MSU R-6967). aCC, foramen for cerebral carotid artery; Bo, basioccipital; CN IX–CN XII, cranial nerve foramina; CQP, cranioquadrate passage; FM, foramen magnum; FV, foramen vagi; VLP, ventrolateral process; Oto, otoccipital; P, parietal; Pbs, parabasisphenoid; Pt, pterygoid; PTFe, posttemporal fenestra; So, supraoccipital; SqFac, squamosal facet. Scale bars each equal 1 cm

otoccipital medially; corresponding grooves are present on the isolated bones. The cranioquadrate passage extends anteromedially from the occipital surface of the skull and opens deep within the meatal chamber, posterior to the external auditory meatus (Figures 3a and 5c) (Montefeltro et al., 2016). At its anteromedial end, the cranioquadrate passage is connected to the temporal canal medially via the postquadrate foramen and to the extracapsular space anteriorly (Figure 5d). The extracapsular space is a deep groove limited by the extracapsular buttress of the otoccipital (see Section 4.5). This

groove represents a passage for numerous neurovascular structures comprising CN IX, CN X, the ramus communicans of sympathetic nerve and associated vasculature (Figure 5d,e) (Lessner & Holliday, 2020; Porter et al., 2016; Sedlmayr, 2002; Shiino, 1914; Walker, 1990). The *postquadrate foramen* of crocodylians is deep within the meatal chamber, posterior to the external auditory meatus and medial to the dorsal otic incisure of the squamosal (Figures 3d and 5c,d) (Montefeltro et al., 2016; Walker, 1990). The postquadrate foramen is bounded anteriorly by the quadrate, posteriorly by the otoccipital,

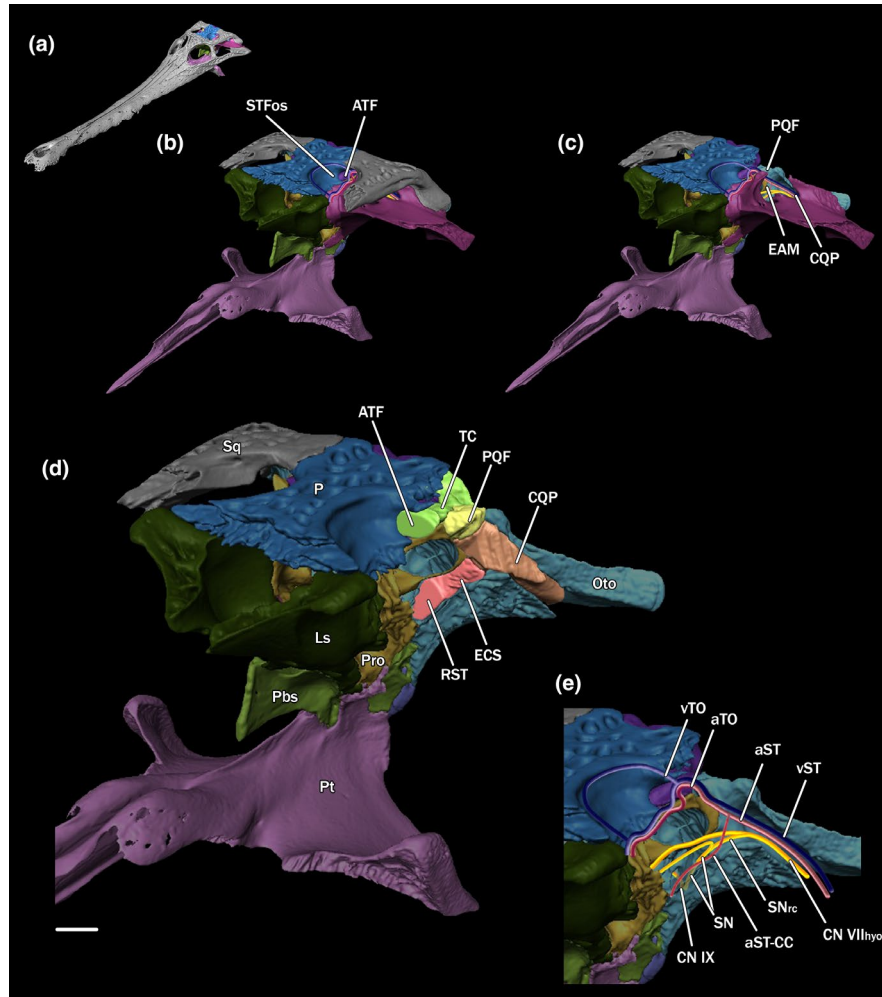


FIGURE 5 Anatomy of the cranioquadrate passage, temporal fossa and periotic region of crocodylians. (a–e) *Mecistops cataphractus* (DVZ M 6/13), in oblique anterodorsal and slightly lateral view. (a) Inset showing the region of interest illustrated in (b–e); (b) braincase with both squamosals in situ; (c) braincase with left squamosal detached; (d) braincase with left squamosal and quadrate detached; (e) inset from (d) showing details of periotic region. aST, stapedial artery; aST-CC, arterial branch between stapedial and cerebral carotid arteries; ATF, anterior temporal foramen; aTO, temporoorbital artery; CN VII_{hyo}, hyomandibular branch of facial nerve; CN IX, glossopharyngeal nerve; CQP, cranioquadrate passage; EAM, external auditory meatus; ECS, extracapsular space; Ls, laterosphenoid; Oto, otoccipital; P, parietal; Pbs, parabasisphenoid; PQF, postquadrate foramen; Pro, prootic; Pt, pterygoid; RST, recessus scala tympani; SN, sympathetic nerve; SN_{rc}, ramus communicans of sympathetic nerve; Sq, squamosal; STFos, supratermporal fossa; TC, temporal canal; vST, stapedial vein; vTO, temporoorbital vein. Scale bar equals 1 cm

ventrally by the prootic and the supraoccipital and dorsally by the squamosal. It provides the passage for the main branches of the stapedial vessels (temporoorbital artery and vein) into the temporal canal (Figure 5e) (Porter et al., 2016; Sedlmayr, 2002; Walker, 1990).

The *temporal canal* is a bony canal for the temporoorbital artery and vein in crocodylians (Figure 5d) (Porter et al., 2016; Sedlmayr, 2002; Walker, 1990). The temporal canal is enclosed by the parietal and the squamosal dorsally and by the prootic, the supraoccipital and the quadrate ventrally (Figures 5 and 6). The temporal canal opens anteriorly into the supratermporal fossa via the anterior temporal foramen (=temporoorbital foramen), laterally via the postquadrate foramen, and posteriorly on the occipital surface of the skull via the posttemporal fenestra (Figures 4–6). Together, the cranioquadrate passage and the temporal canal provide a continuous route for the

stapedial/temporoorbital artery and vein from the occipital surface of the skull into the supratermporal fossa (Figure 5) (Holliday et al., 2020; Porter et al., 2016; Sedlmayr, 2002). The cranioquadrate passage and the temporal canal are not pneumatized in extant crocodylians (Dufeu & Witmer, 2015; Walker, 1990; this study). In addition, these structures are separated from the external auditory meatus by soft tissue (suspensory plate; see Montefeltro et al., 2016). Thus, the cranioquadrate passage should not be considered and visualized as a part of the paratympanic pneumaticity, as it has been done in various recent studies (e.g. Bona et al., 2013, 2017; Serrano-Martínez et al., 2019).

The *posttemporal fenestrae* are limited by the parietal, squamosal and supraoccipital; the otoccipitals make a minor contribution to the ventral edges (Figure 4b). Iordansky (1973) noted

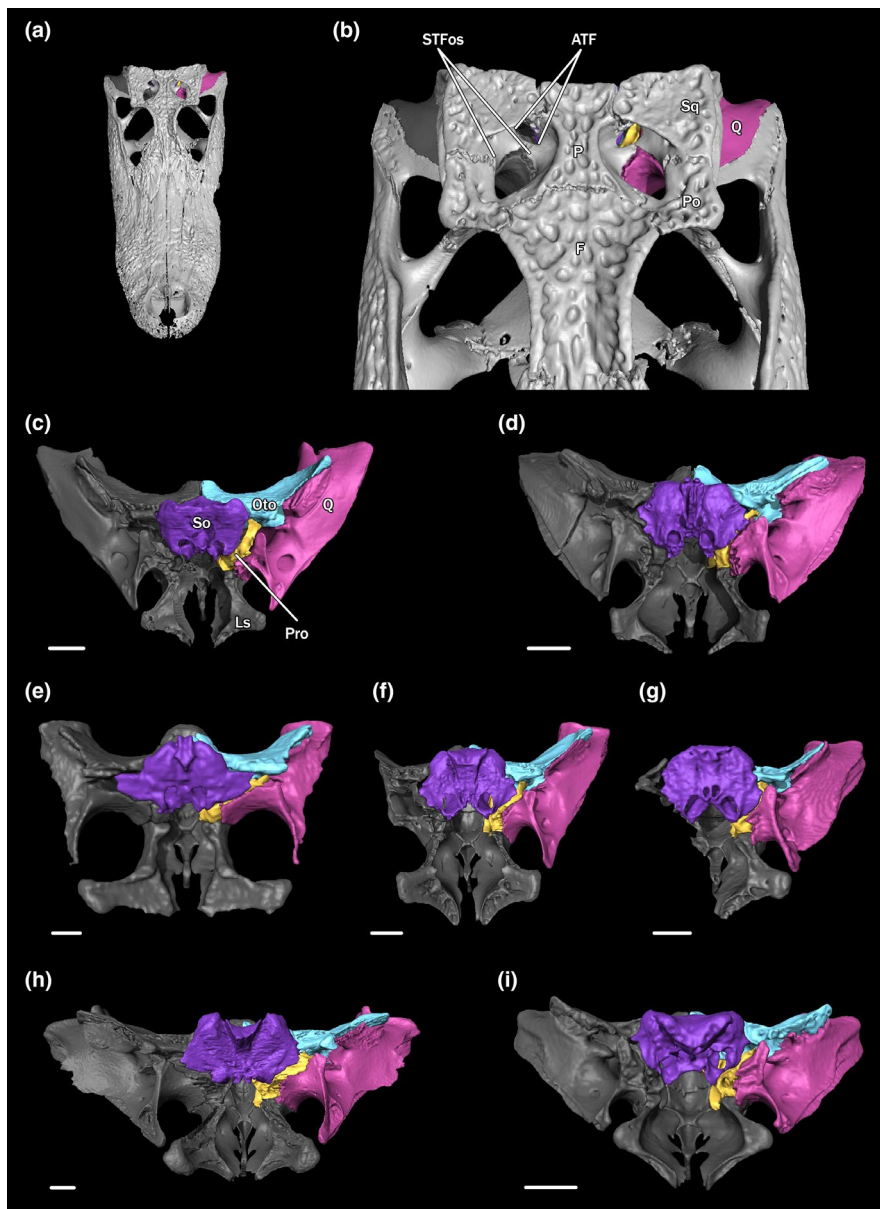


FIGURE 6 Anatomy of the temporal canal of crocodylians. (a) Inset showing the region of interest; (b) close-up of the skull roof in oblique anterodorsal view; (c–i) crocodylian braincases with the skull roof detached and the bones forming the floor of the left temporal canal rendered in colour. Note that some specimens are incomplete. (a–c) *Alligator mississippiensis* (DVZ M 4/13); (d) *Crocodylus novaeguineae* (DVZ M 9/13); (e) *Gavialis gangeticus* (ZIN 7249); (f) *Mecistops cataphractus* (DVZ M 6/13); (g) *Osteolaemus tetraspis* (DVZ M 7/13); (h) *Tomistoma schlegelii* (ZMMU MSU R-13859); (i) *Caiman yacare* (ZMMU MSU R-6967). ATF, anterior temporal foramen; F, frontal; Ls, laterosphenoid; Oto, otocipital; P, parietal; Po, postorbital; Pro, prootic; Q, quadrate; So, supraoccipital; Sq, squamosal; STFos, supratemporal fossa. Scale bars each equal 1 cm

that the posttemporal fenestrae of crocodylians are reduced to narrow slits and filled with cartilage in life. However, Walker (1990: p. 88) summarized evidence for the presence of a small vein that enters the posttemporal fenestrae in crocodylians. Our detailed observations of crocodylian skulls show that the posttemporal fenestrae are slit-like (especially medially), occupying little space between the bones bordering them. In addition, we observed the squamosal–supraoccipital contact deep within the posttemporal fenestrae in individual skulls of some crocodylians (e.g. *G. gangeticus*, *C. crocodilus*, *Mecistops cataphractus*,

Crocodylus spp.). If present, this contact blocks the fenestra anteriorly, and only a tiny rounded notch (1–2 mm in diameter) remains at the ventromedial margin of the posttemporal fenestra, between the edges of the supraoccipital, squamosal and otocipital. This notch leads into the temporal canal. In addition, our observations of the original CT scan data of crocodylians with injected vessels (Porter et al., 2017) revealed that small veins are occasionally present posteriorly within the temporal canal and drain into the stapedia vein anteriorly. However, no major vessels enter the posttemporal fenestrae from the occipital surface

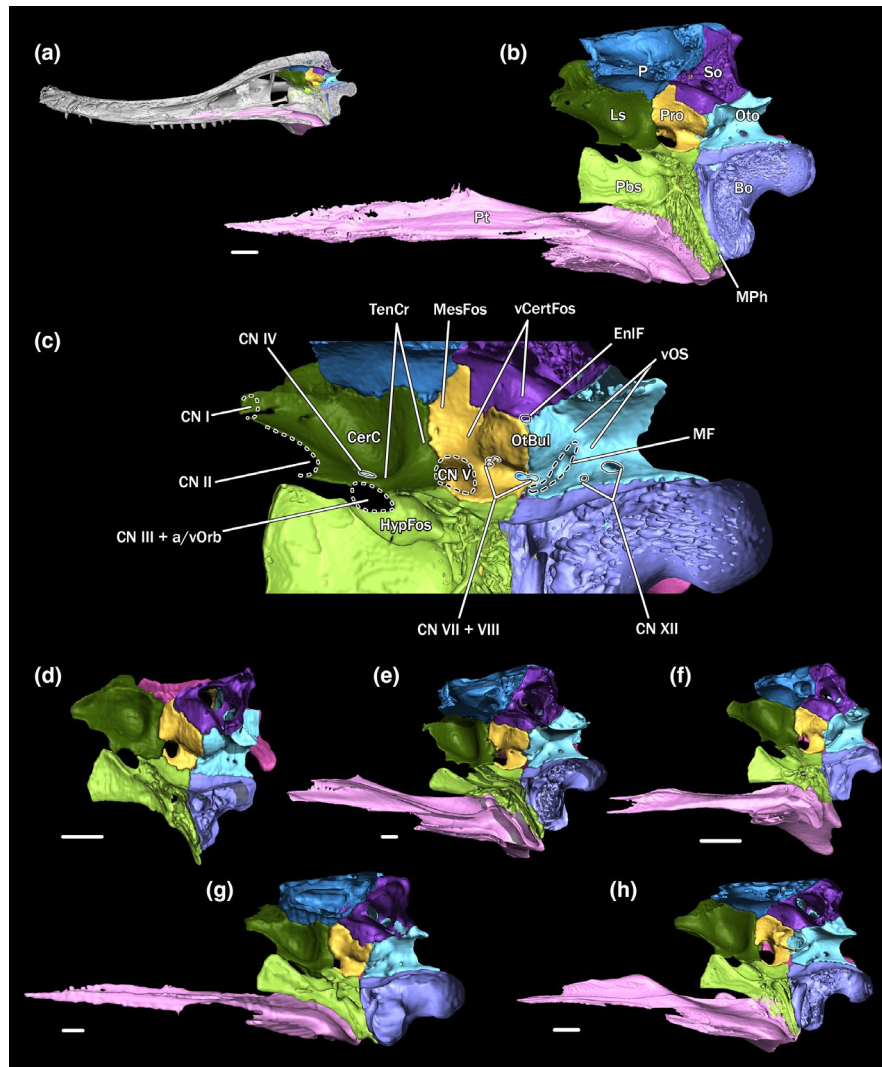


FIGURE 7 Endocranial aspect of the braincase of crocodylians in right medial view. (a) Inset showing the region of interest illustrated in (b–h); (c) close-up of (b) showing the details of the endocranial anatomy. Note that some specimens are incomplete. (a–c) *Tomistoma schlegelii* (ZMMU MSU R-13859); (d) *Osteolaemus tetraspis* (DVZ M 7/13); (e) *Crocodylus novaeguineae* (DVZ M 9/13); (f) *Caiman yacare* (ZMMU MSU R-6967); (g) *Gavialis gangeticus* (ZIN 7249); (h) *Mecistops cataphractus* (DVZ M 6/13). Bo, basioccipital; CerC, cerebral cavity; CN I–CN XII, cranial nerve foramina; CN III + a/vOrb, common foramen for oculomotor nerve and orbital artery and vein; EnIF, endolymphatic foramen; HypFos, hypophyseal fossa; Ls, laterosphenoid; MesFos, mesencephalic fossa; MF, metotic foramen; MPh, median pharyngeal foramen; OtBul, otic bulla; Oto, otoccipital; P, parietal; Pbs, parabasisphenoid; Pro, prootic; Pt, pterygoid; So, supraoccipital; TenCr, tentorial crest; vCertFos, fossa for cerebellotectal venous sinus; vOS, depression for occipital venous sinus. Scale bars each equal 1 cm

based on the dataset of Porter et al. (2017). We conclude that the posttemporal fenestrae in extant crocodylians are greatly reduced, and no vessels corresponding to the transverso-occipital vein of some diapsids appear to enter them (see also Kuzmin et al., 2020: p. 136).

The *endocranial cavity* of crocodylians is enclosed by the frontal, parietal and supraoccipital dorsally, the parabasisphenoid and basioccipital ventrally and by the laterosphenoid, prootic and otoccipital laterally (Figure 7). The frontal and the laterosphenoid form the osseous borders of the olfactory tract (CN I). The medial surface of the laterosphenoid is strongly concave. This concavity corresponds to the cerebral cavity, dorsally bounded by the frontal and the parietal. The cerebral cavity is bordered posteriorly by the blunt vertical

tentorial crest of the laterosphenoid (Figure 7c). A slight depression formed by the laterosphenoid, parietal and prootic corresponds to the mesencephalic fossa, which contains the optic lobes of the brain. Posterior to this, a prominent fossa arches posterodorsally over the otic capsule. This fossa corresponds to the course of the cerebello-tectal venous sinus of Porter et al. (2016) (=recessus lateralis of longitudinal sinus in Hopson, 1979; rostral petrosal sinus in Sedlmayr, 2002). This venous sinus is a large transverse tributary of the dorsal longitudinal venous sinus (Porter et al., 2016; Sedlmayr, 2002). The otic capsules of crocodylians are fully ossified and protrude medially into the endocranial cavity as large otic bullae. Each otic bulla is formed by the prootic, supraoccipital and otoccipital. A small endolymphatic foramen is located at the Y-shaped triple junction of

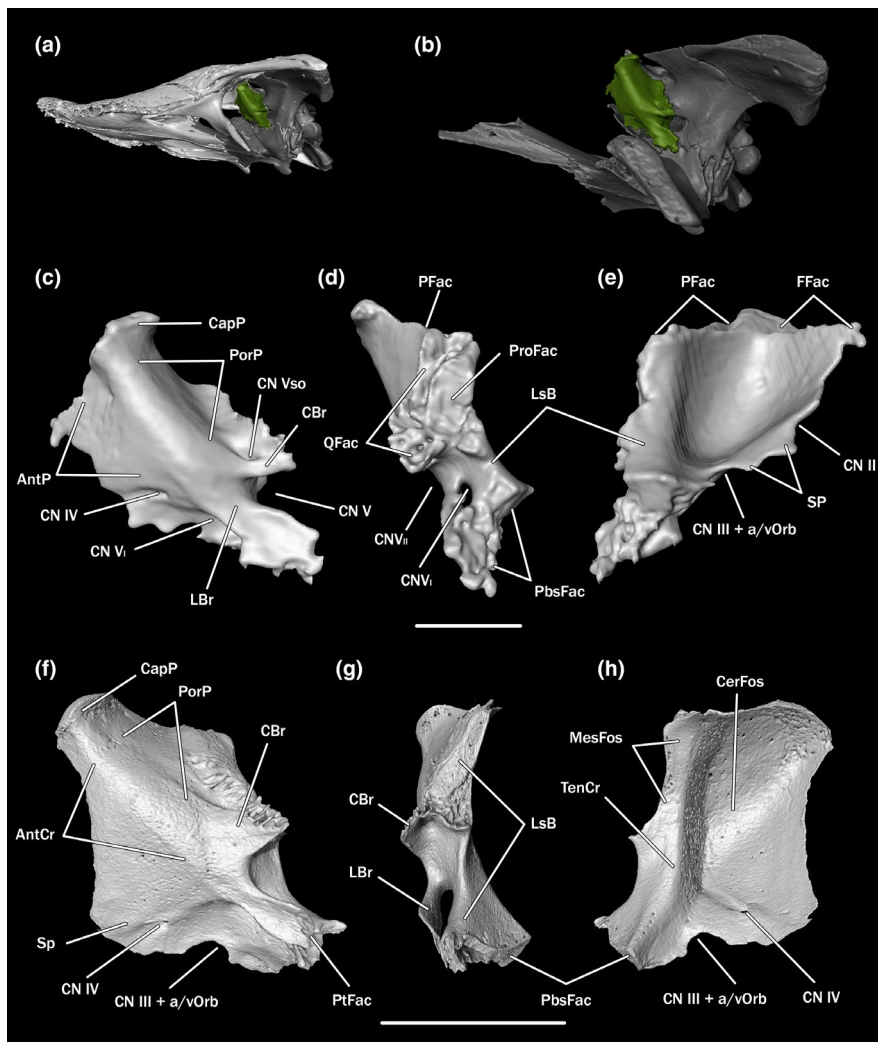


FIGURE 8 Anatomy of the laterosphenoid of crocodylians. (a, b) Insets showing the region of interest on *Crocodylus novaeguineae* (DVZ M 9/13). (c–e) Laterosphenoid of *C. novaeguineae* (DVZ M 9/13) in (c), left lateral, (d) posterior and (e) medial views. (f–h) Laterosphenoid of hatchling *Caiman crocodilus* (PIN comparative collection, unnumbered) in (f), left lateral, (g) posterior and (h) medial views. AntCr, antotic crest; AntP, anterior process; CapP, capitate process; CBr, caudal bridge; CerFos, cerebral fossa; CN II, foramen for optic nerve; CN III + a/vOrb, common foramen for oculomotor nerve and orbital artery and vein; CN IV, foramen for trochlear nerve; CN V, foramen and fossa for the trigeminal nerve; CN V_i, CN V_{ii}, CN V_{so}, foramina for ophthalmic, maxillary and supraorbital branches of the trigeminal nerve; FFac, frontal facet; LBr, lateral bridge; LsB, laterosphenoid body; MesFos, mesencephalic fossa; PbsFac, parabasisphenoid facet; PFac, parietal facet; ProFac, prootic facet; PorP, postorbital process; PtFac, pterygoid facet; QFac, quadrate facet; SP, slender process; TenCr, tentorial crest. Upper scale bar (for c–e) equals 1 cm; lower scale bar (for f–h) equals 5 mm

these elements. The anatomy of the otic capsule of the inner ear is characteristic of crocodylians among extant diapsids (see Sections 4.4 and 4.5).

Numerous neurovascular foramina pierce the endocranial surface (Figure 7c) (Iordansky, 1973; Lessner & Holliday, 2020). The endocasts of crocodylians are well known (e.g. Beyrand et al., 2019; Hopson, 1979; Jirak & Janacek, 2017; Lessner & Holliday, 2020; Watanabe et al., 2019; Witmer et al., 2008) and will not be described in this study. However, it is worth mentioning that the brain of adult crocodylians fills only up to about 50% of the volume of the endocranial cavity (Watanabe et al., 2019). Voluminous endocranial vessels leave relevant osteological correlates on the braincase bones (Figure 7c) (Porter et al., 2016; Sedlmayr, 2002).

The braincase of the present-day crocodylians is characterized by the presence of an elaborate system of paratympanic pneumatic cavities (see Section 4.10). The basicranium undergoes substantial cranial metamorphosis in the post-hatchling development, resulting in the verticalized state of the braincase floor (Tarsitano, 1985; see Sections 4.7 and 4.8).

4.3 | Laterosphenoid

A single ossification (laterosphenoid) is present in the orbitotemporal region of the braincase of extant crocodylians. The definitive laterosphenoid of crocodylians is a complex ossification that

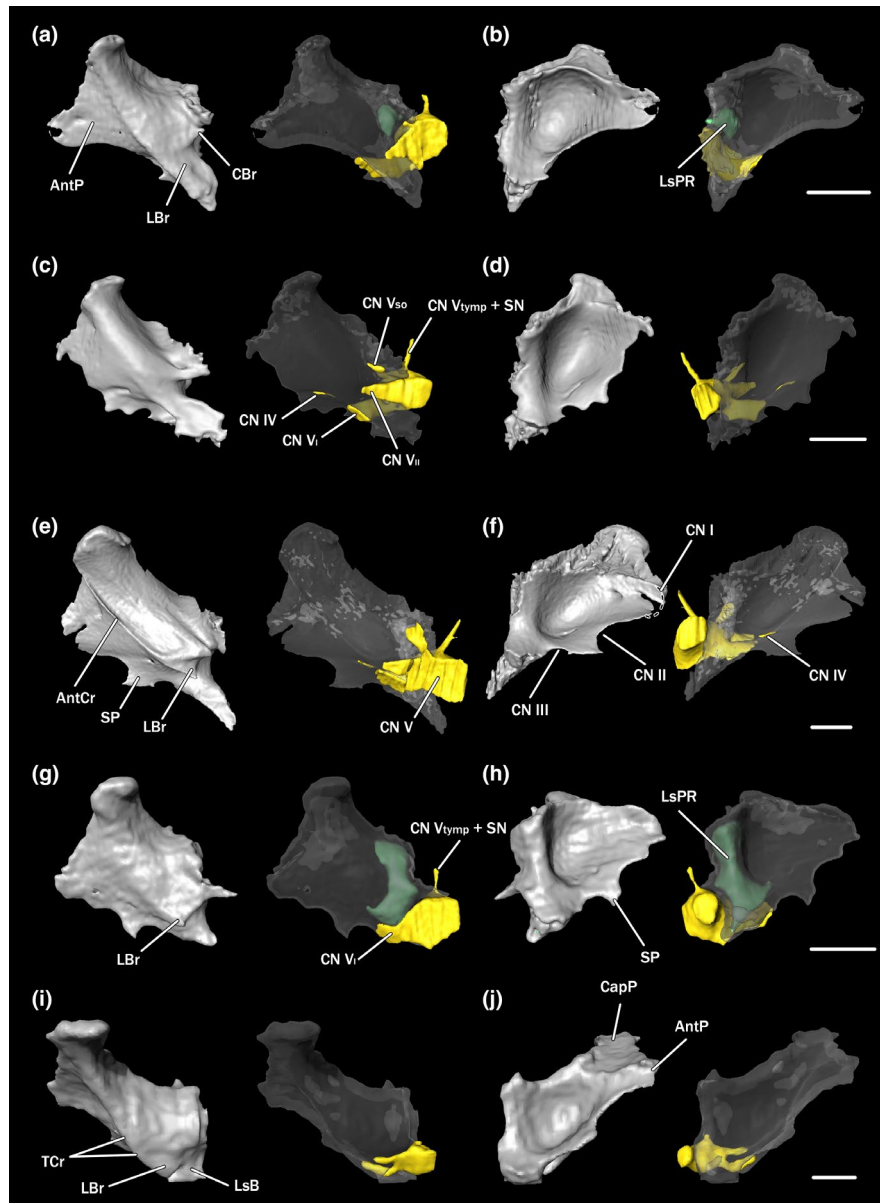


FIGURE 9 Comparison of crocodylian laterosphenoids. (a, c, e, g, i) In left lateral view; (b, d, f, h, j) in medial view. Each pair comprises CT-based models of non-transparent skeletal element and semitransparent element with digital endocasts of relevant neurovascular and pneumatic structures. (a, b) *Alligator mississippiensis* (DVZ M 4/13); (c, d) *Crocodylus novaeguineae* (DVZ M 9/13); (e, f) *Tomistoma schlegelii* (ZMMU MSU R-13859); (g, h) *Osteolaemus tetraspis* (DVZ M 7/13); (i, j) *Gavialis gangeticus* (ZIN 7249). AntCr, antotic crest; AntP, anterior process; CapP, capitate process; CBr, caudal bridge; CN I–CN V, cranial nerves; CN V_I, CN V_{II}, CN V_{so}, CN V_{tymp}, ophthalmic, maxillary, supraorbital and tympanic branches of the trigeminal nerve; LBr, lateral bridge; LsB, laterosphenoid body; LsPR, laterosphenoid pneumatic recess; SN, sympathetic nerve; SP, slender process; TCr, tensor crest. Scale bars each equal 1 cm

incorporates several cartilaginous structures of the embryo: the pila antotica, the pila metoptica, part of the taenia medialis and the columella prootica; the latter is derived from the palatoquadrate cartilage (Bellairs & Kamal, 1981; Bhullar & Bever, 2009; Klembara, 2004; Sobral et al., 2016). The laterosphenoid is sutured to the frontal and parietal dorsally, to the prootic posteriorly, to the quadrate posterolaterally and to the parabasisphenoid and pterygoid ventrally (Figures 3, 7 and 8). The laterosphenoid of the studied osteolaemines either does not contact the pterygoid ventrally (e.g. *O. tetraspis*) or contacts it only briefly (*Voay robustus*), due to

the sutural contact between the quadrate and parabasisphenoid ventral to the laterosphenoid (Figure 3e). The capitate process of the laterosphenoid fits into a socket on the ventral surface of the postorbital, forming a synovial but immobile joint (Holliday & Witmer, 2008; Iordansky, 1973).

The laterosphenoid may be subdivided into the following portions: (1) the body that contacts the prootic, quadrate and parabasisphenoid and forms the anterior border of the trigeminal fossa; (2) the postorbital and capitate processes that form the temporal surface; (3) the anterior process that forms the orbital surface

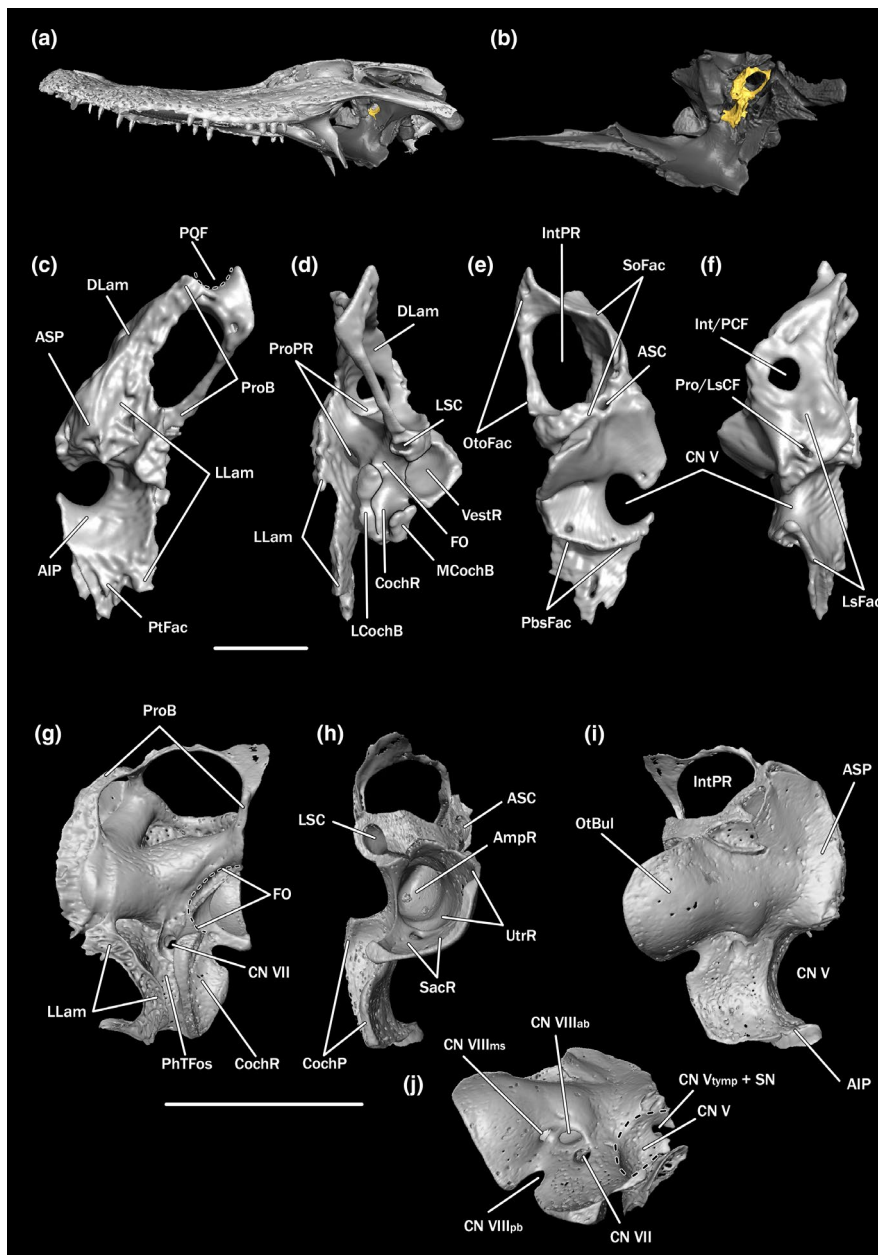


FIGURE 10 Anatomy of the prootic of crocodylians. (a, b) Insets showing the region of interest on *Alligator mississippiensis* (DVZ M 4/13). (c–f) Prootic of *A. sinensis* (DVZ M 3/13) in (c), left lateral, (d) posterior, (e) medial and (f) anterior views. (g–j) Prootic of hatchling *Caiman crocodilus* (PIN comparative collection, unnumbered) in (g), left lateral, (h) posterior, (i) medial and (j) ventral views. AIP, anterior inferior process; AmpR, ampullary recess; ASC, anterior semicircular canal; ASP, anterior superior process; CN V–CN VII, cranial nerve foramina; CN V_{tymp} +SN, foramen for tympanic branch of the trigeminal nerve and sympathetic nerve; CN VIII_{ab}, CN VIII_{pb}, CN VIII_{ms}, foramina for anterior, posterior and macula sacculi branches of the vestibulocochlear nerve; CochP, cochlear prominence; CochR, cochlear recess; DLam, dorsal lamina; FO, fenestra ovalis; IntPR, intertympanic pneumatic recess; Int/PCF, foramen for communication of intertympanic and parietal pneumatic recesses; LCoChB, lateral bulge of the cochlear prominence; LLam, lateral lamina; LSC, lateral semicircular canal; LsFac, laterosphenoid facet; MCoChB, medial bulge of cochlear prominence; OtBul, otic bulla; OtoFac, otoccipital facet; PbsFac, parabasisphenoid facet; PhTFos, pharyngotympanic pneumatic fossa; POF, postquadrate foramen; Pro/LsCF, foramen for communication of prootic and laterosphenoid pneumatic recesses; ProB, prootic buttress; ProPR, prootic facial pneumatic recess; PtFac, pterygoid facet; QFac, quadrate facet; SacR, saccular recess; SoFac, supraoccipital facet; UtrR, utricular recess; VestR, vestibular recess. Upper scale bar (for c–f) equals 1 cm; lower scale bar (for g–j) equals 5 mm

and (4) smaller processes—the lateral and caudal bridges and the slender process. The *laterosphenoid body* is a vertical pillar that separates the passages for the oculomotor (CN III) and trigeminal (CN V) nerves. It is sutured to the parabasisphenoid ventrally and

is transversally expanded dorsally, at the contact with the prootic and the quadrate (Figure 8d,e,g). The lateral and posterior aspects of the laterosphenoid body border complex neurovascular structures of the orbitotemporal region (Holliday & Witmer, 2009). The

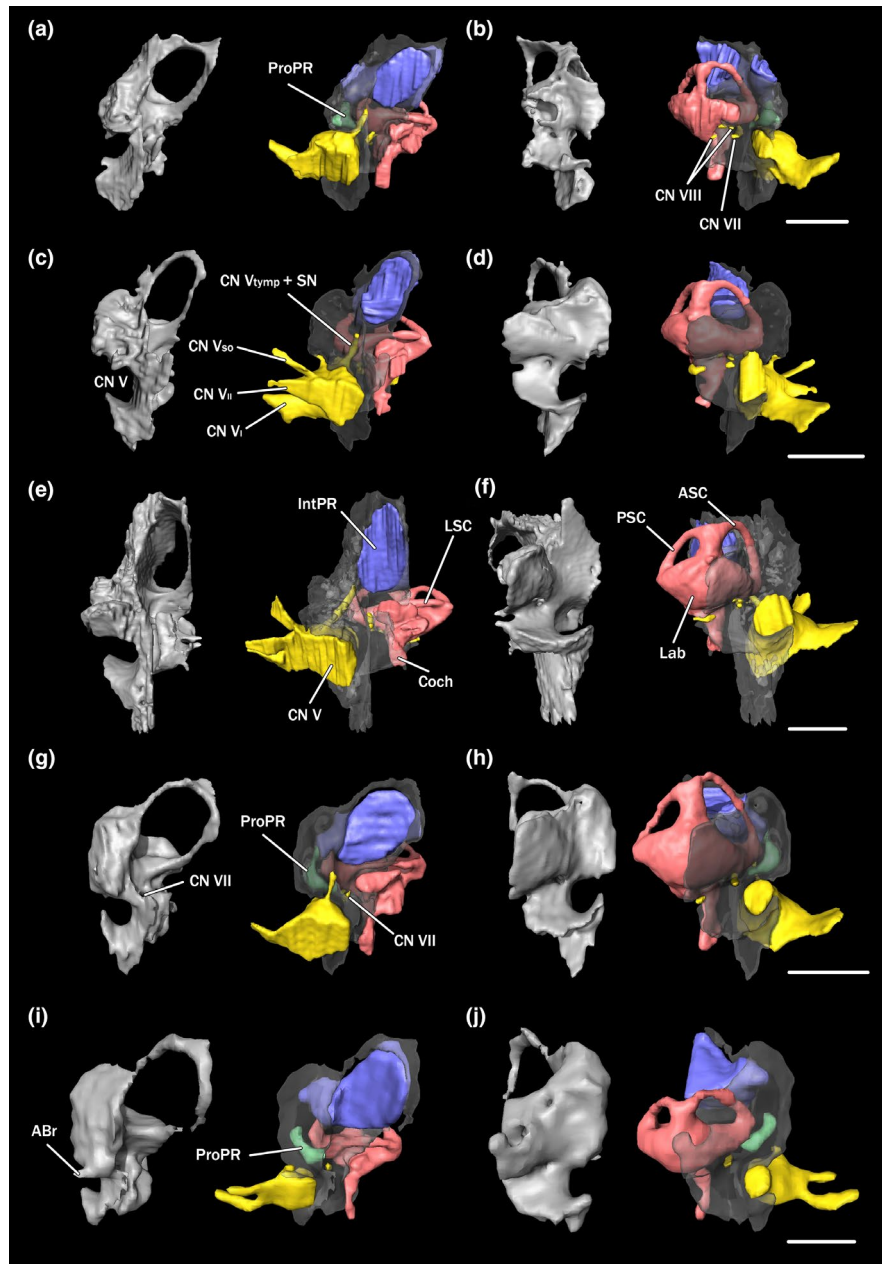


FIGURE 11 Comparison of crocodylian prootics. (a, c, e, g, i) In left lateral view; (b, d, f, h, j) in medial view. Each pair comprises CT-based models of non-transparent skeletal element and semitransparent element with digital endocasts of relevant neurovascular and pneumatic structures. (a, b) *Alligator mississippiensis* (DVZ M 4/13); (c, d) *Crocodylus novaeguineae* (DVZ M 9/13); (e, f) *Tomistoma schlegelii* (ZMMU MSU R-13859); (g, h) *Osteolaemus tetraspis* (DVZ M 7/13); (i, j) *Gavialis gangeticus* (ZIN 7249). ABr, anterior bridge; ASC, anterior semicircular canal; CN V–CN VII, cranial nerves; CN V_I, CN V_{II}, CN V_{so}, CN V_{tymp}, ophthalmic, maxillary, supraorbital and tympanic branches of the trigeminal nerve; Coch, cochlear duct; IntPR, intertympanic pneumatic recess; Lab, endosseous labyrinth; LSC, lateral semicircular canal; ProPR, prootic facial pneumatic recess; PSC, posterior semicircular canal; SN, sympathetic nerve. Scale bars each equal 1 cm

laterosphenoid body forms the anterior margin of the large trigeminal fossa in crocodylians (CN V; Figure 8c,d). The lateral surface of the laterosphenoid body either makes up the short ophthalmic passage together with the lateral bridge (for the ophthalmic branch of the trigeminal nerve (CN V_I), trigeminal artery and associated veins) or bears a groove for corresponding neurovascular elements (Figures 8c,d and 9) (Holliday & Witmer, 2009; Lessner & Holliday, 2020; Porter et al., 2016; Sedlmayr, 2002). The medial surface of

the laterosphenoid body forms the blunt tentorial crest that separates the cerebral and mesencephalic fossae on the endocranial surface (Figure 8e,h). The laterosphenoid body is occasionally pneumatized by the paratympanic diverticula. The corresponding pneumatic cavity is here termed the laterosphenoid pneumatic recess (Figure 9).

The *lateral and caudal bridges* of the laterosphenoid further subdivide the neurovascular structures of the trigeminal region

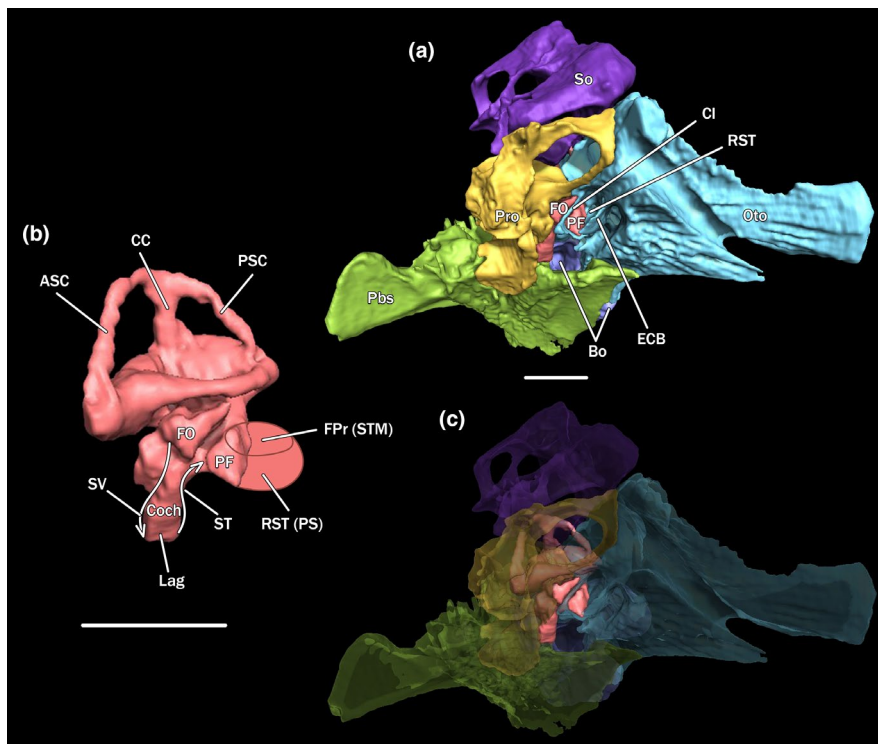


FIGURE 12 Anatomy of the otic capsule of crocodylians. (a) Oblique anterolateral view of the partial braincase of *Alligator mississippiensis* (DVZ M 4/13), with the endocast of the endosseous labyrinth in situ; only bones that participate in the otic capsule are shown. (c) Same, bones rendered semitransparent. (b) Enlarged endocast of the left endosseous labyrinth of *A. mississippiensis* (DVZ M 4/13) with superimposed perilymphatic sac. Arrows show routes of the perilymphatic extensions around the cochlear duct. ASC, anterior semicircular canal; Bo, basioccipital; CC, crus communis; Cl, crista interfenestralis; Coch, cochlear duct; ECB, extracapsular buttress; FO, fenestra ovalis; FPr (STM), fenestra pseudorotunda that forms margins for attachment of the secondary tympanic membrane; Lag, lagena; Oto, otoccipital; Pbs, parabasisphenoid; PF, perilymphatic foramen; Pro, prootic; PSC, posterior semicircular canal; RST (PS), recessus scala tympani that contains extracapsular portion of the perilymphatic sac; So, supraoccipital; ST, scala tympani; SV, scala vestibuli. Scale bars each equal 1 cm

(Holliday & Witmer, 2009). If present, the lateral bridge encloses the ophthalmic passage (for CN V_I) medially and has a prominent groove for the maxillary branch of the trigeminal nerve (CN V_{II}) on its lateral surface (Figures 8c–g and 9). Portions of the temporal musculature originate on the lateral surface of the lateral bridge, ventral to the groove for CN V_{II} (*M. pseudotemporalis profundus*; Holliday & Witmer, 2007, 2009; Lessner & Holliday, 2020). The lateral bridge develops as a small bony outgrowth of the laterosphenoid during later embryological stages (splint of bone lateral to CN V_I in Bellairs & Kamal, 1981). The caudal bridge separates a small branch (supraorbital nerve) from the rest of CN V_{II} (Figures 8c,f and 9) (Holliday & Witmer, 2009).

The lateral and caudal bridges of the laterosphenoid are variably developed in extant crocodylians (Figures 3 and 9; Holliday & Witmer, 2009; Iordansky, 1973). Our observations show that the lateral bridge is generally present in most crocodylian species and reaches the pterygoid ventrally (e.g. *Alligator* spp., *Caiman* spp., *P. palpebrosus*, *Melanosuchus niger*, *Crocodylus* spp.). It is relatively robust in *A. mississippiensis* and *C. crocodilus* and thin in *Crocodylus* spp. In the latter, this feature presents some degree of intra- and interspecific variability. In some specimens of *Crocodylus* spp., the laterosphenoid bridge is reduced to a short

projection with a free ventral end or it is a short process sutured to the body of the laterosphenoid (without reaching pterygoid). However, most (around 80%) of the studied specimens belonging to seven extant species of *Crocodylus* have a complete and long lateral bridge of the laterosphenoid that contacts the pterygoid ventrally.

On the contrary, the lateral bridge appears to be consistently reduced and lacks a ventral contact with the pterygoid in some representatives of *Crocodylidae* (*T. schlegelii*, *M. cataphractus*, *O. tetraspis* and *V. robustus*) and *Gavialidae* (*G. gangeticus* and extinct *G. bengawanicus*) (Figure 9). In these taxa, the bridge is either incomplete ventrally or short, making contact with the laterosphenoid body ventrally and not reaching the pterygoid. In *Gavialis*, the presence of the ventral contact with the pterygoid varies among the studied specimens: ZIN 7249 and TMM M-5490 lack the contact on both sides and ZIN 50 and UF 11898 show a small contact only on one side of the skull. Contra the observations of Holliday and Witmer (2009), the lateral bridge is already fully developed in hatchlings and juveniles of those taxa that have it as adults: for example, *C. crocodilus* (PIN comparative collection, unnumbered), *Crocodylus* sp. (DVZ M 10/13), *C. niloticus* (RVC-JRH-NNC11) and *A. mississippiensis* (TMM M-6723, OUV 10606) (Figure 8f,g). Both hatchlings and

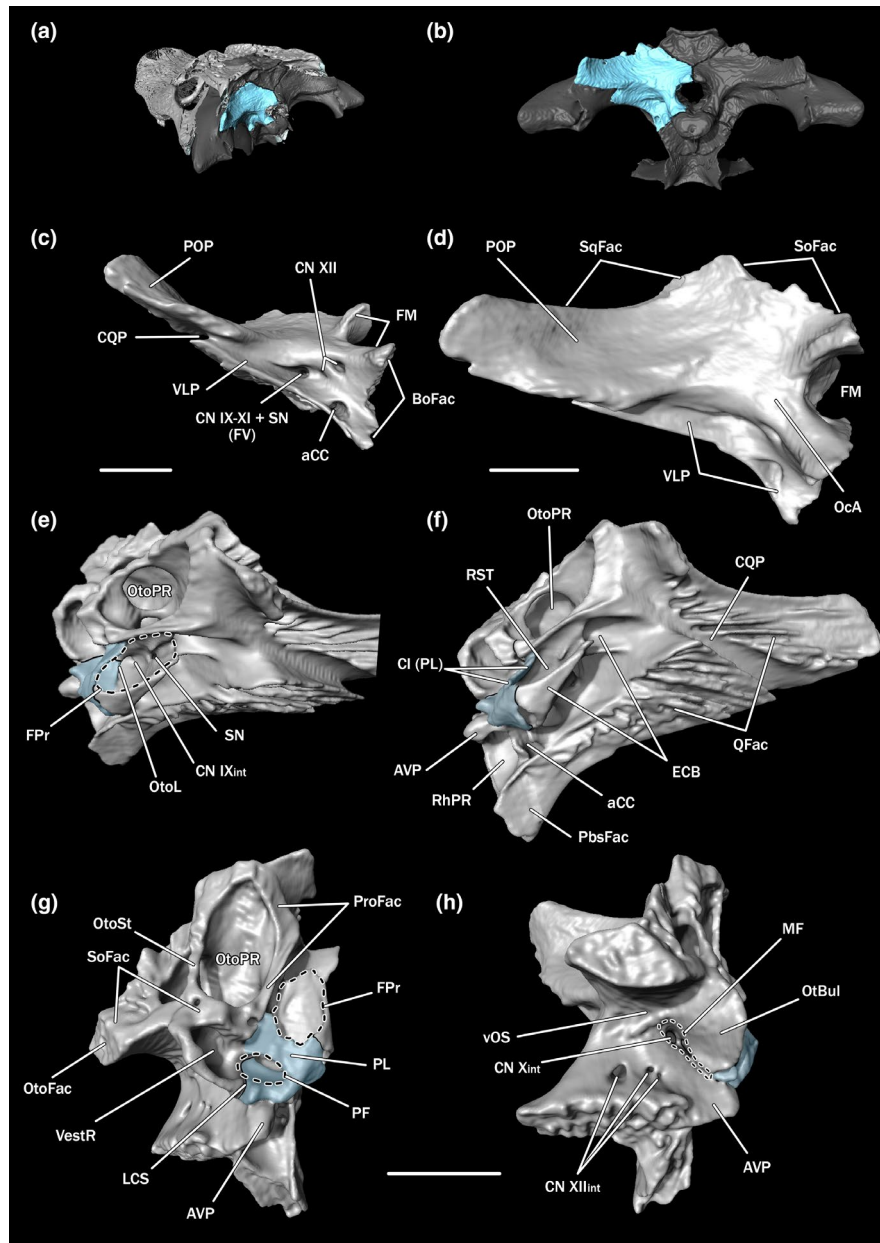


FIGURE 13 Anatomy of the otoccipital of crocodylians. (a, b) Insets showing the region of interest on *Alligator mississippiensis* (DVZ M 4/13). (c–h) Otoccipital of *A. sinensis* (DVZ M 3/13) in (c) ventral, (d) posterior, (e) oblique anterodorsal, (f) anterior, (g) oblique anteromedial and (h) medial views. Perilymphatic loop highlighted in blue. aCC, foramen for cerebral carotid artery; AVP, anteroventral process; BoFac, basioccipital facet; CI (PL), crista interfenestralis of the perilymphatic loop; CN IX–CN XII, external cranial nerve foramina; CN IX_{int}–CN XII_{int}, internal cranial nerve foramina; CQP, cranioquadrate passage; ECB, extracapsular buttress; FM, foramen magnum; FPr, fenestra pseudorotunda; FV, foramen vagi; LCS, loop-closure suture; MF, metotic foramen; OcA, occipital arch; OtBul, otic bulla; OtoFac, otoccipital facet; OtoL, otoccipital ledge; OtoPR, otoccipital pneumatic recess; OtoSt, otoccipital strut; PbsFac, parabasisphenoid facet; PF, perilymphatic foramen; PL, perilymphatic loop; POP, paroccipital process; ProFac, prootic facet; QFac, quadrate facet; RhPR, rhomboidal pneumatic recess; RST, recessus scala tympani; SN, foramen for sympathetic nerve; SoFac, supraoccipital facet; SqFac, squamosal facet; VestR, vestibular recess; VLP, ventrolateral process; vOS, depression for occipital venous sinus. Scale bars each equal 1 cm

adults of *O. tetraspis* (e.g. RVC-JRH-FDC4) lack the developed lateral bridge. Thus, the presence and the degree of development of the lateral bridge are more consistent and less subjected to variability (either intra- or interspecific) among species of present-day crocodylians than previously reported.

Brochu (1999: character 115) noted that, in both extant species of *Alligator*, the pterygoid contributes a short ascending process to the lateral bridge of the laterosphenoid. No such process was observed by us in the studied sample for both species of *Alligator* for all age categories (see File S1 for details of the studied specimens).

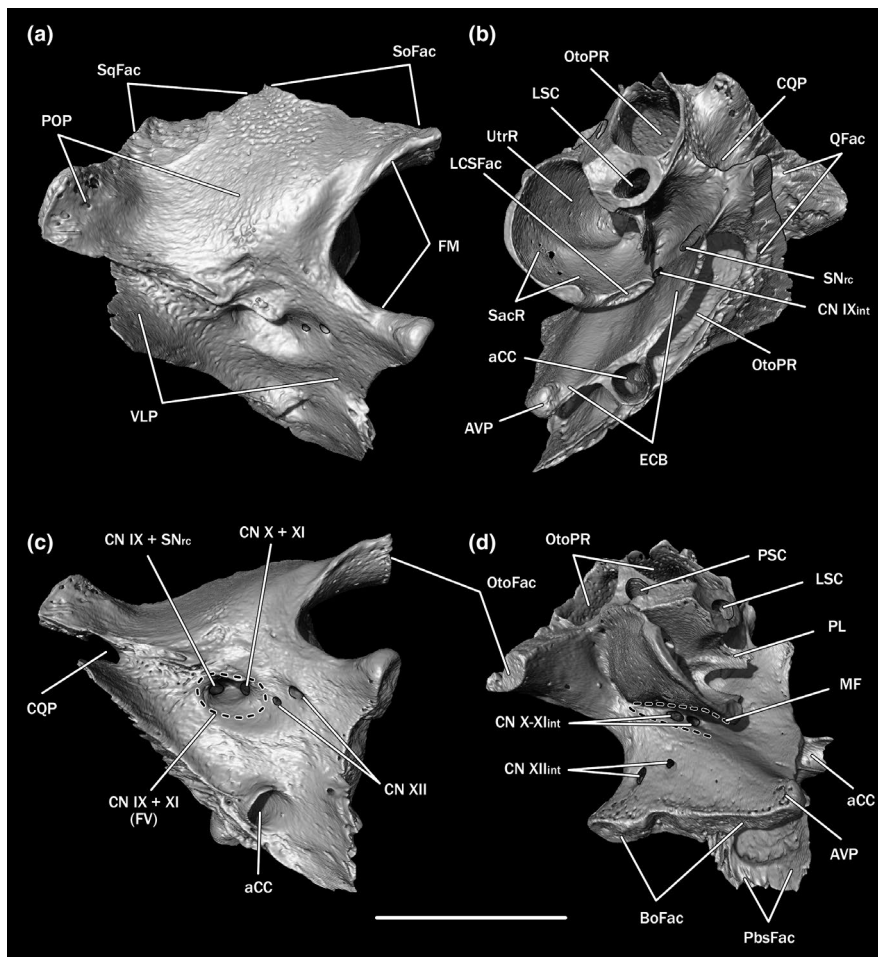


FIGURE 14 Anatomy of the otoccipital of crocodylians. (a–d) Left otoccipital of hatchling *Caiman crocodilus* (PIN comparative collection, unnumbered) in (a) posterior, (b) anterior, (c) oblique ventral and (d) medial views. Note that perilymphatic loop is incomplete. aCC, foramen for cerebral carotid artery; AVP, anteroventral process; BoFac, basioccipital facet; CN IX + XI (FV), common external foramen vagi for posterior cranial nerves and sympathetic nerve; CN IX + SN, external foramen for glossopharyngeal nerve and sympathetic nerve; CN X + XI, external foramen for vagus and accessory nerves; CN XII, external foramina for hypoglossal nerves; CN IX_{int}–CN XII_{int}, internal cranial nerve foramina; CQP, cranioquadrate passage; ECB, extracapsular buttress; FM, foramen magnum; LCSFac, facet for loop-closure suture; LSC, lateral semicircular canal; MF, metotic foramen; OtoFac, otoccipital facet; OtoPR, otoccipital pneumatic recess; PbsFac, parabasisphenoid facet; PL, perilymphatic loop; POP, paroccipital process; PSC, posterior semicircular canal; QFac, quadrate facet; SacR, saccular recess; SN, foramen for sympathetic nerve; SoFac, supraoccipital facet; SqFac, squamosal facet; UtrR, utricular recess; VLP, ventrolateral process. Scale bars each equal 5 mm

More observations are needed to assess the inter- and intraspecific variability of this feature.

Among the studied taxa, the caudal bridge is absent in *Osteolaemus* and *Caiman latirostris* and small in *A. mississippiensis* (Figure 9). In *Gavialis*, the corresponding process (anterior bridge) is formed by the prootic but not the laterosphenoid (Figure 11i). The caudal bridge is fully developed in the studied hatchlings of *C. crocodilus* (Figure 8f,g) but is incipient in *Crocodylus* sp. and *A. mississippiensis*.

The *postorbital process* forms the concave temporal surface of the laterosphenoid and terminates in the *capitate process* distally (Figure 8c,f). The postorbital process is the main site of origin of temporal muscles (Busbey, 1989; Holliday & Witmer, 2007, 2009; Lordansky, 1964; Lessner & Holliday, 2020; Schumacher, 1973). The arched antotic crest (=laterosphenoid buttress) separates

the postorbital and anterior processes of the laterosphenoid, dividing the temporal and orbital aspects of the bone (Figures 8f and 9e). Its thickened ventral part is termed the tensor crest (Figure 9i) and serves as the attachment site of ocular musculature (*M. tensor periorbitae*; Holliday & Witmer, 2007, 2009; Sedlmayr, 2002). The cotylar crest is present on the lateral surface of the postorbital process of adult and larger sized individuals of various crocodylian taxa: for example, *A. mississippiensis* (DVZ 5/13), *Crocodylus porosus* (DVZ 8/13), *G. gangeticus* (ZIN 50) and *T. schlegelii* (ZMMU MSU R-13859). In most of these taxa, the cotylar crest is blunt and oblique; it extends parallel to the antotic crest (Figure 9e). In *Alligator*, it is a crescentic crest that forms the dorsal margin of the groove for CN V_{II} and is anteriorly confluent with the tensor/antotic crest (Holliday & Witmer,

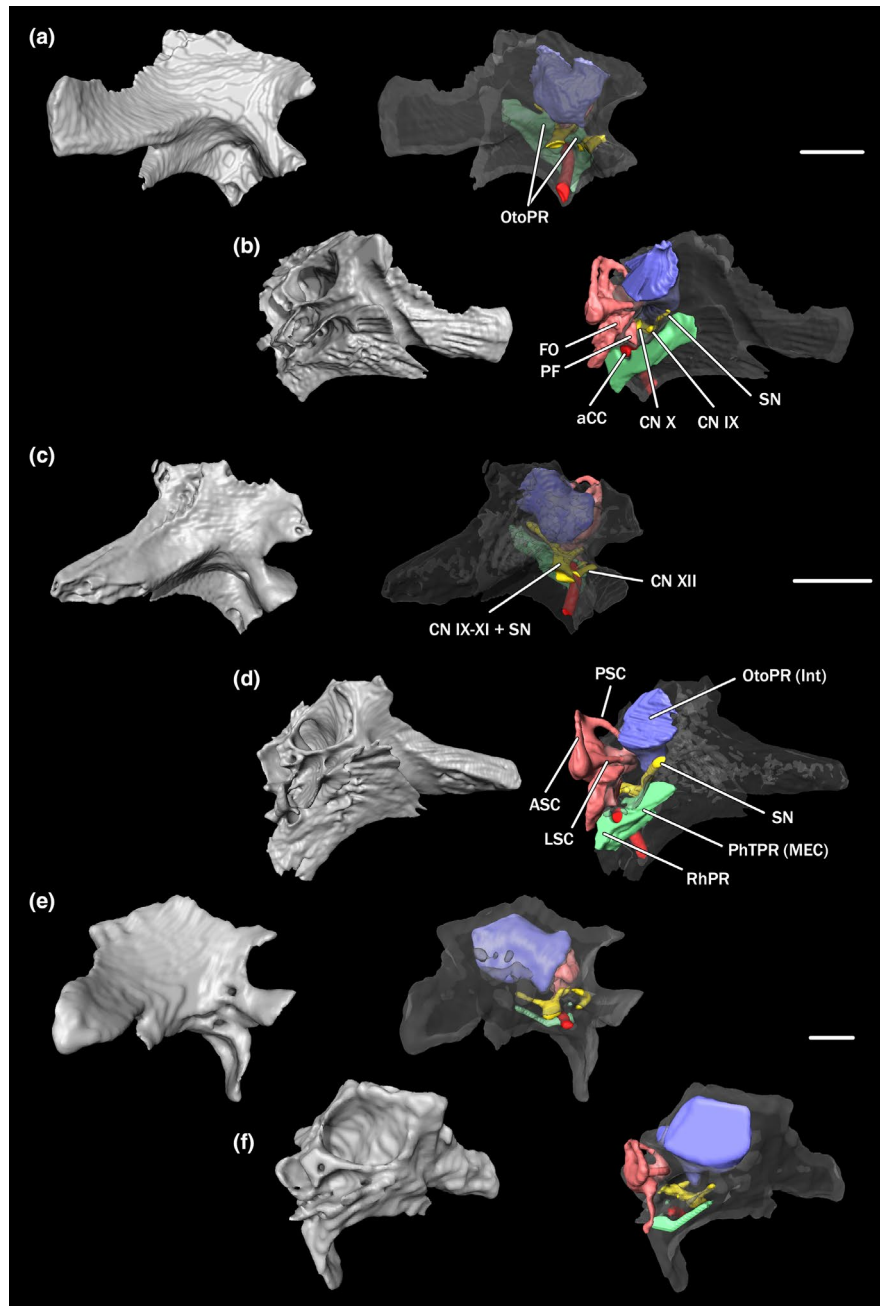


FIGURE 15 Comparison of left crocodylian otoccipitals. (a, c, e) In posterior view; (b, d, f) in anterior view. Each pair comprises CT-based models of non-transparent skeletal element and semitransparent element with digital endocasts of relevant neurovascular and pneumatic structures. (a, b) *Alligator mississippiensis* (DVZ M 4/13); (c, d) *Crocodylus novaeguineae* (DVZ M 9/13); (e, f) *Gavialis gangeticus* (ZIN 7249). aCC, cerebral carotid artery; ASC, anterior semicircular canal; CN IX–CN XII, cranial nerves; FO, fenestra ovalis; LSC, lateral semicircular canal; OtoPR, otoccipital pneumatic recess; OtoPR (Int), intertympanic portion of otoccipital pneumatic recess; PF, perilymphatic foramen; PhTPR, pharyngotympanic (middle ear) cavity; PSC, posterior semicircular canal; RhPR, rhomboidal pneumatic recess; SN, sympathetic nerve. Scale bars each equal 1 cm

2009: fig. 3). This crest is an important osteological correlate of the temporal musculature (*M. pseudotemporalis superficialis*; Holliday & Witmer, 2007, 2009).

The *anterior process* forms the entire orbital aspect of the bone (Figures 8c and 9). Its anterior margin is extremely thin and frequently broken off in dried skulls. In the studied hatchlings of several taxa (*A. mississippiensis*, *C. crocodilus*, *Crocodylus* sp.), the anterior

process is not fully ossified (Figure 8f,h). This suggests that complete ossification of the anterior process occurs only later in the ontogeny of crocodylians. In *G. gangeticus*, the anterior margin of the anterior process is at the same level with the capitata process of the laterosphenoid (Figure 9i,j) (Brochu, 1999: character 130, state 0). This is a distinctive condition among extant taxa. However, the feature has a broader distribution among extinct crocodylians, being present in

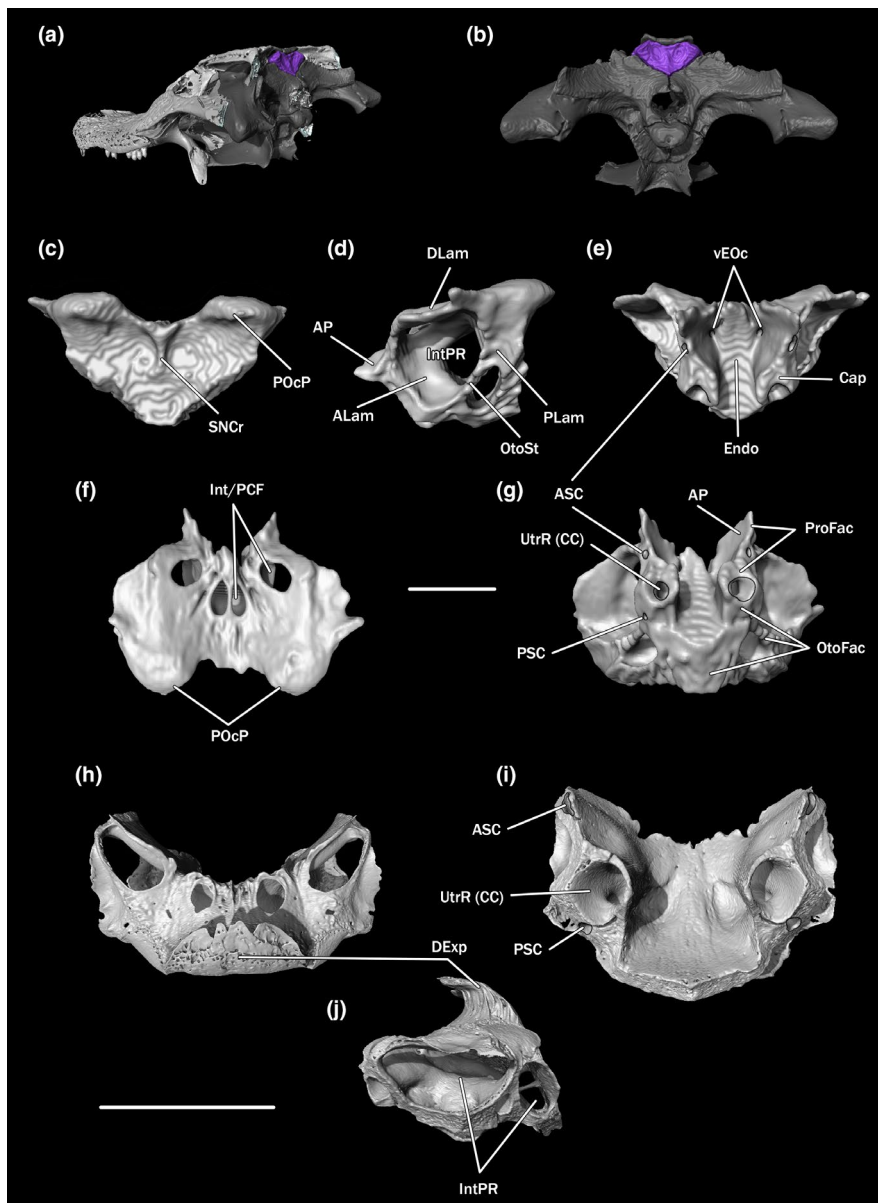


FIGURE 16 Anatomy of the supraoccipital of crocodylians. (a, b) Insets showing the region of interest on *Alligator mississippiensis* (DVZ M 4/13). (c–g) Supraoccipital of *A. sinensis* (DVZ M 3/13) in (c) posterior, (d) left lateral, (e) anterior, (f) dorsal and (g) ventral views. (h–j) supraoccipital of hatchling *Caiman crocodilus* (PIN comparative collection, unnumbered) in (h), dorsal, (i) ventral, and (j) left lateral views. ALam, anterior lamina; AP, anterior process; ASC, anterior semicircular canal; Cap, capsular portion; DExp, dorsal exposure; DLam, dorsal lamina; Endo, endocranial surface; IntPR, intertympanic pneumatic recess; Int/PCF, foramen for communication of intertympanic and parietal pneumatic recesses; OtoFac, otoccipital facet; OtoSt, otoccipital strut; PLam, posterior lamina; POCp, postoccipital process; ProFac, prootic facet; PSC, posterior semicircular canal; SNCr, sagittal nuchal crest; UtrR (CC), utricular recess (crus communis); vEOc, foramen for external occipital vein. Upper scale bar (for c–g) equals 1 cm; lower scale bar (for h–j) equals 5 mm

fossil gavialoids (e.g. *Thoracosaurus borissaki*: CCMGE 1/3373) and tomistomines (e.g. *Paratomistoma courti*: Brochu & Gingerich, 2000).

The anterior processes of the contralateral laterosphenoids meet anteriorly in the fully ossified braincase. Together with the frontal, they encircle the foramen for passage of the olfactory tract (CN I). Posterior and ventral to this contact, the anterior margins of both laterosphenoids are incised and jointly form the single median foramen for passage of the optic nerves (CN II) (Figures 7c, 8e and 9).

In the fully ossified braincase, a short *slender process* descends from each laterosphenoid to contact the rostrum of the parabasisphenoid ventrally (Figures 7d,g,h and 9). This process is located between the foramen for CN II anteriorly and the foramina for CN III and IV posteriorly; it apparently corresponds to the embryonic pila metoptica (Bellairs & Kamal, 1981; Bhullar & Bever, 2009: fig. 1). In crocodylians, the slender process forms the anterior margin of a large foramen that corresponds to the embryonic fenestra metoptica (Bellairs

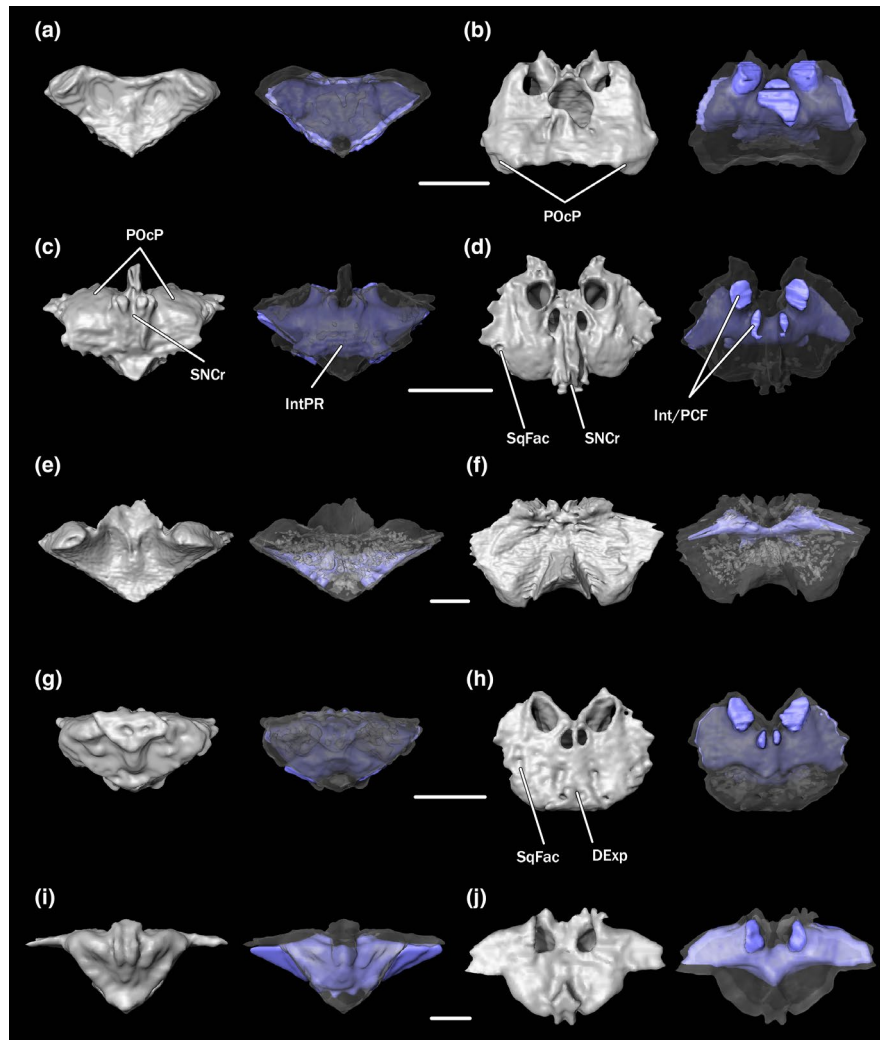


FIGURE 17 Comparison of crocodylian supraoccipitals. (a, c, e, g, i) In posterior view; (b, d, f, h, j) in dorsal view. Each pair comprises CT-based models of non-transparent skeletal element and semitransparent element with digital endocasts of relevant neuro-vascular and pneumatic structures. (a, b) *Alligator mississippiensis* (DVZ M 4/13); (c, d) *Crocodylus novaeguineae* (DVZ M 9/13); (e, f) *Tomistoma schlegelii* (ZMMU MSU R-13859); (g, h) *Osteolaemus tetraspis* (DVZ M 7/13); (i, j) *Gavialis gangeticus* (ZIN 7249). DEExp, dorsal exposure; IntPR, intertympanic pneumatic recess; Int/PCF, foramen for communication of intertympanic and parietal pneumatic recesses; POcP, postoccipital process; SNCr, sagittal nuchal crest; SqFac, squamosal facet. Scale bars each equal 1 cm

& Kamal, 1981). The oculomotor nerve (CN III) and the orbital artery and vein pass through this foramen (Figures 7c and 8f–h; Lordansky, 1973; Lessner & Holliday, 2020; Porter et al., 2016). In the completely ossified laterosphenoids, the separate passage for CN III is present as a well-marked notch or an individual opening (Figure 9d,f). The canal for the trochlear nerve (CN IV) pierces the anterior process of the laterosphenoid just dorsal to that of the foramen for CN III (Figure 9c–f) (Lessner & Holliday, 2020).

4.4 | Prootic

The prootic is the anterior ossification of the otic capsule. It ossifies endochondrally but also includes a separate dermal ossification (lamina prootici anterior in Klembara, 2004). This additional embryonic

anlage corresponds to the lateral lamina of the fully ossified element. The prootic of crocodylians is notably anteroposteriorly short. It is largely obscured on the lateral surface of the braincase by neighbouring bones (Figure 3). In *G. gangeticus* and *T. schlegelii*, the prootic is relatively more exposed on the lateral surface than in other extant crocodylians (Figure 3b,g) (Brochu, 1999: fig. 41; Lordansky, 1973).

The prootic sutures to the laterosphenoid anteriorly, the quadrate laterally, the supraoccipital posterodorsally, the parabasisphenoid and pterygoid ventrally and the parietal dorsally (Figures 3, 6, 7 and 10a,b). It has complex contacts with the otoccipital posteriorly: sutural junctions between several parts occur along with abutting contacts at the region of the otic capsule. The crocodylian prootic may be subdivided into the following parts: (1) the capsular portion; (2) the superior and inferior anterior processes; (3) the lateral lamina and (4) the prootic buttress.

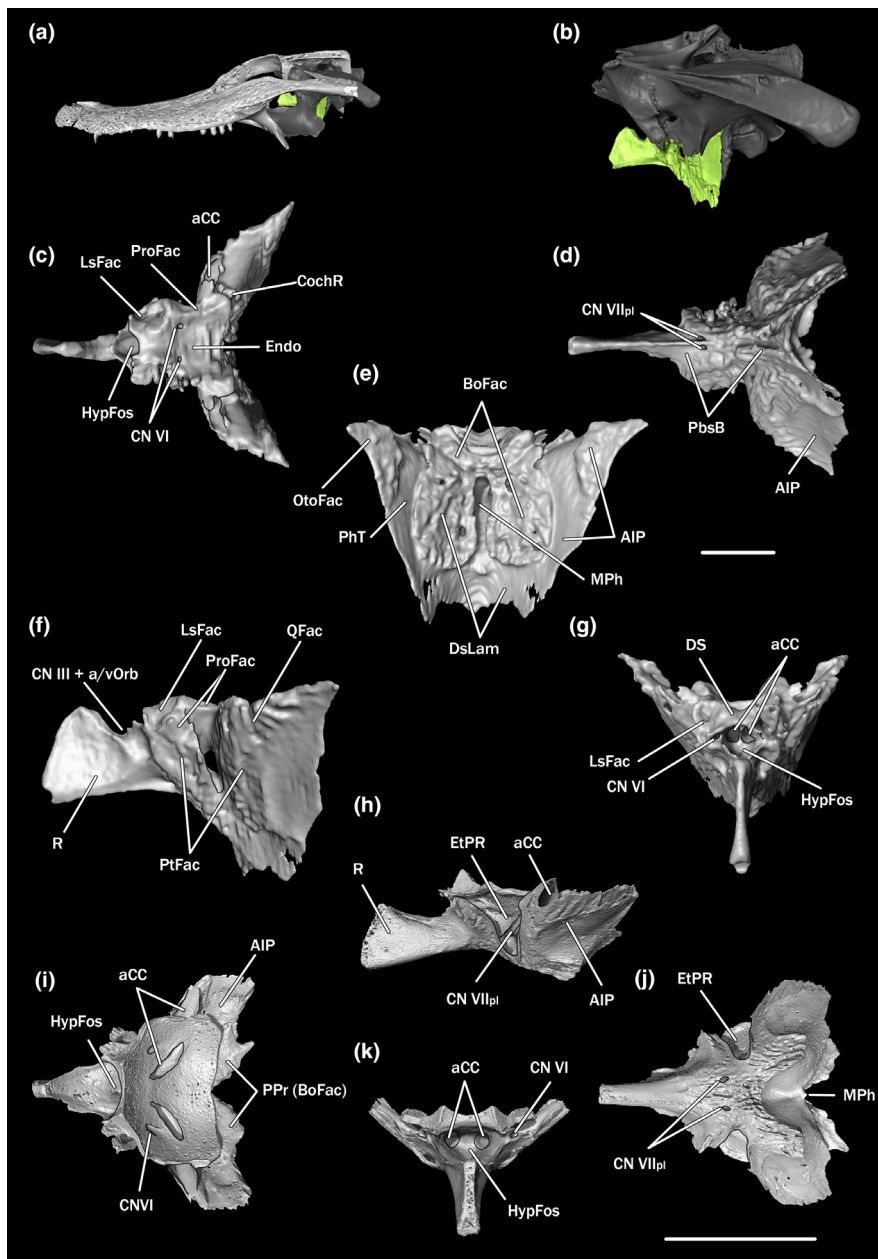


FIGURE 18 Anatomy of the parabasisphenoid of crocodylians. (a, b) Insets showing the region of interest on *Alligator mississippiensis* (DVZ M 4/13). (c–g) Parabasisphenoid of *A. mississippiensis* (DVZ M 4/13) in (c), dorsal, (d) ventral, (e) posterior, (f) left lateral and (g) anterior views. (h–k) parabasisphenoid of hatchling *Caiman crocodilus* (PIN comparative collection, unnumbered) in (h) left lateral, (i) dorsal, (j) ventral and (k) anterior views. aCC, foramen for cerebral carotid artery; AIP, alar process; BoFac, basioccipital facet; CN III +a/vOrb, common foramen for oculomotor nerve and orbital artery and vein; CN VI, foramen for abducens nerve; CN VII_{pl}, foramen/groove for palatine branch of the facial nerve; CochR, cochlear recess; DS, dorsum sellae; DsLam, descending lamina; Endo, endocranial surface; EtPR, pneumatic recessus epitubaricus; HypFos, hypophyseal fossa; LsFac, laterosphenoid facet; MPh, median pharyngeal canal/foramen; OtoFac, otoccipital facet; PbsB, body of parabasisphenoid; PhT, groove of pharyngotympanic canals; PPr (BoFac), posterior projection (basioccipital facet); ProFac, prootic facet; PtFac, pterygoid facet; QFac, quadrate facet; R, rostrum. Upper scale bar (for c–g) equals 1 cm; lower scale bar (for h–k) equals 5 mm

The capsular portion of the prootic forms the anterior third of the otic capsule and the bony framework around various inner ear structures. The spacious vestibular recess contains the vestibular component of the inner ear (Figures 10d,h, 11 and 12). The vestibular recess of the prootic is internally subdivided by blunt ridges in several studied hatchling and adult specimens (Figure 10h). The

resulting cavities correspond to individual portions of the endolymphatic labyrinth (namely, the ampullae of the anterior and lateral semicircular canals, the recessus utriculi and the anterior portion of the saccule; Baird, 1960, 1970; Retzius, 1884). The anterior and lateral semicircular canals pierce the roof of the capsular portion (Figure 11). On the prootic of hatchling crocodylians, these canals

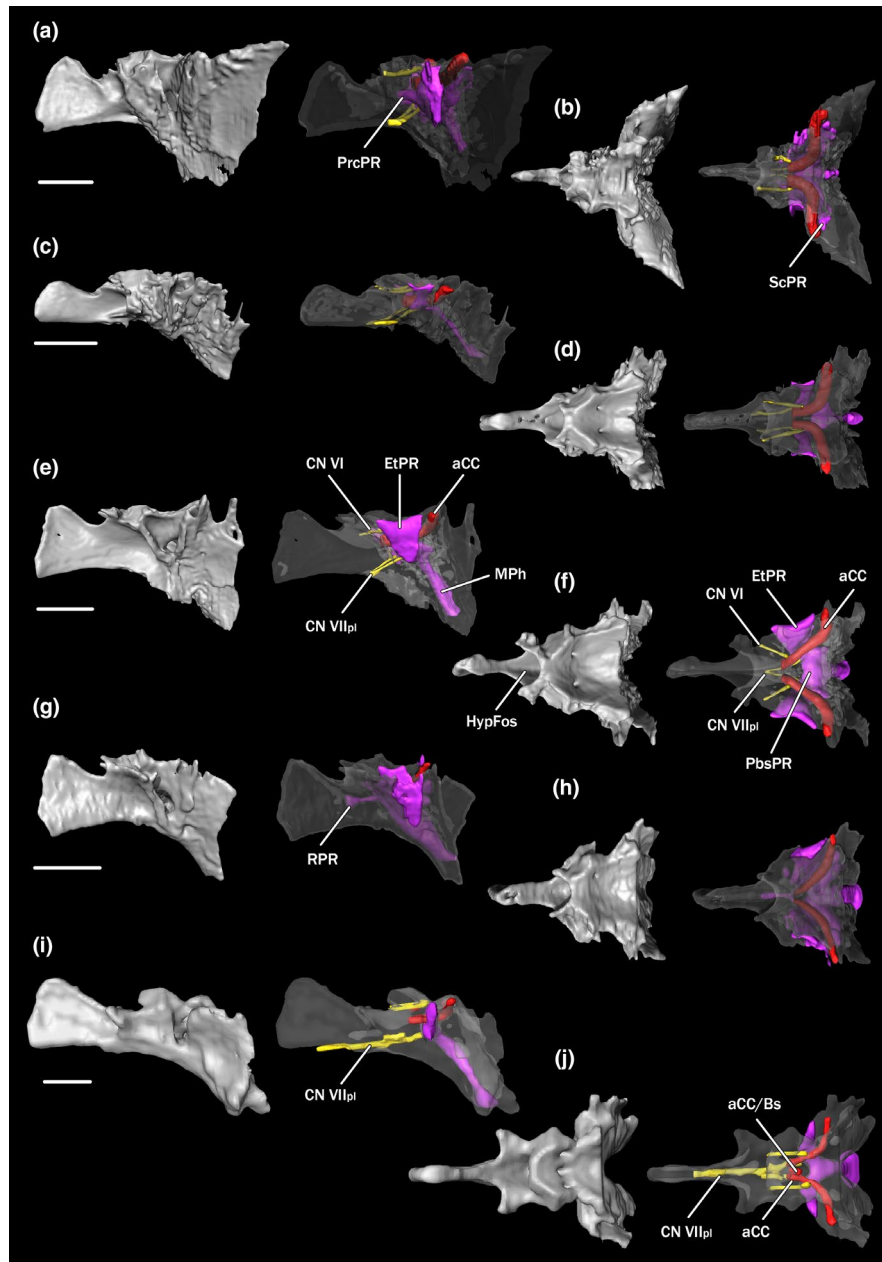


FIGURE 19 Comparison of crocodylian parabasisphenoids. (a, c, e, g, i) In left lateral view; (b, d, f, h, j) in dorsal view. Each pair comprises CT-based models of non-transparent skeletal element and semitransparent element with digital endcasts of relevant neurovascular and pneumatic structures. (a, b) *Alligator mississippiensis* (DVZ M 4/13); (c, d) *Crocodylus novaeguineae* (DVZ M 9/13); (e, f) *Mecistops cataphractus* (DVZ M 6/13); (g, h) *Osteolaemus tetraspis* (DVZ M 7/13); (i, j) *Gavialis gangeticus* (ZIN 7249). aCC, cerebral carotid artery; aCC/Bs, arterial branch between cerebral carotid and basilar arteries; CN VI, abducens nerve; CN VII_{pl}, palatine branch of the facial nerve; EtPR, pneumatic recessus epitubaricus; HypFos, hypophyseal fossa; MPh, median pharyngeal pneumatic canal; PbsPR, parabasisphenoid pneumatic recess; PrcPR, precarotid pneumatic recess; RPR, rostral pneumatic recess; ScPR, subcarotid pneumatic recess. Scale bars each equal 1 cm

prominently protrude on the external (lateral) surface, as compared to the condition in adult individuals (Figure 10g). This suggests negative allometric growth of the semicircular canals relative to the bony otic capsule. Georgi (2008) reported the negative allometric growth of the semicircular canals relative to the skull length, shape changes of the canals during growth, as well as different growth rates among the three canals in *A. mississippiensis*. He suggested

constant remodelling of the inner surface of the otic capsule in this taxon during growth.

Ventrolateral to the vestibular recess, there is the *cochlear prominence* of the prootic (Figure 10d,h). It is represented by two bulges that frame the cochlear recess. Each of the bulges contacts the otoccipital posteriorly: the medial bulge contacts the anteroventral process of the otoccipital and the lateral bulge

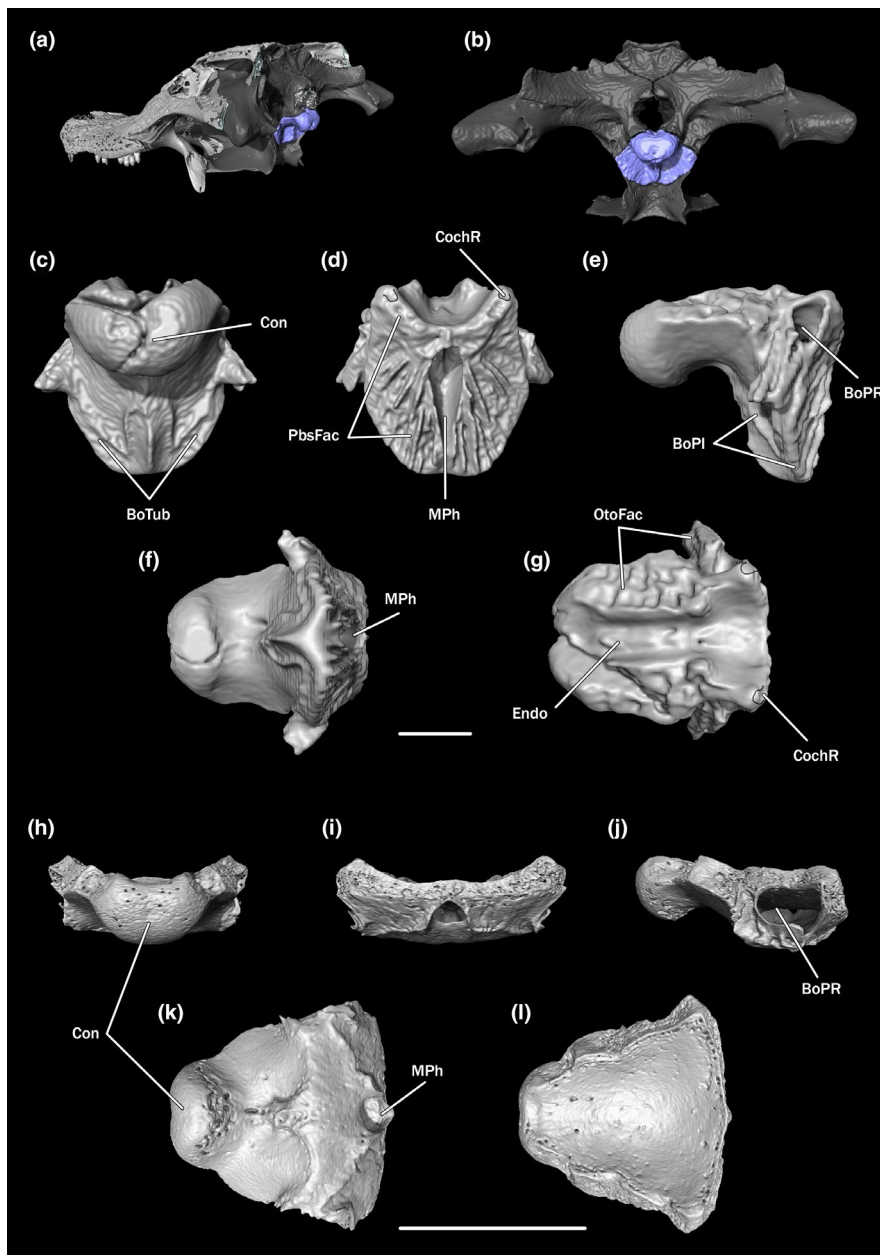


FIGURE 20 Anatomy of the basioccipital of crocodylians. (a, b) Insets showing the region of interest on *Alligator mississippiensis* (DVZ M 4/13). (c–g) Basioccipital of *A. sinensis* (DVZ M 3/13) in (c) posterior, (d) anterior, (e) right lateral, (f) ventral and (g) dorsal views. (h–l) Basioccipital of hatchling *Caiman crocodilus* (PIN comparative collection, unnumbered) in (h), posterior, (i) anterior, (j) right lateral, (k) ventral and (l) dorsal views. BoPI, basioccipital plate; BoPR, basioccipital pneumatic recess; BoTub, basioccipital tuberosities; CochR, cochlear recess; Con, occipital condyle; Endo, endocranial surface; MPh, median pharyngeal pneumatic canal; OtoFac, otoccipital facet; PbsFac, parabasisphenoid facet. Upper scale bar (for c–g) equals 1 cm; lower scale bar (for h–l) equals 5 mm

abuts the perilymphatic loop (Figure 10d). The cochlear recess of crocodylians is markedly dorsoventrally elongated and bent (Figure 10d,g,h). It contains the correspondingly long and geniculate cochlear duct of the inner ear (Figure 12), a distinctive feature of crocodylians among extant diapsids (see Section 4.5 for a detailed comment on the anatomy of inner ear). The ventralmost part of the cochlear recess contains the lagena of the cochlear duct and thus is termed the *lagena recess* (Baird, 1960,

1970; Walker, 1990). The capsular portion is deeply notched just dorsal to the cochlear prominence. This notch is circumscribed by a ridge and corresponds to the anterior outline of the *fenestra ovalis* (Figures 10d,g,h and 12).

The capsular portion of the prootic bulges into the endocranial cavity and forms the anteroventral portion of the *otic bulla* (=bullae tympani in lordansky, 1973). On the endocranial surface, the prootic contacts the supraoccipital posterodorsally along an oblique suture

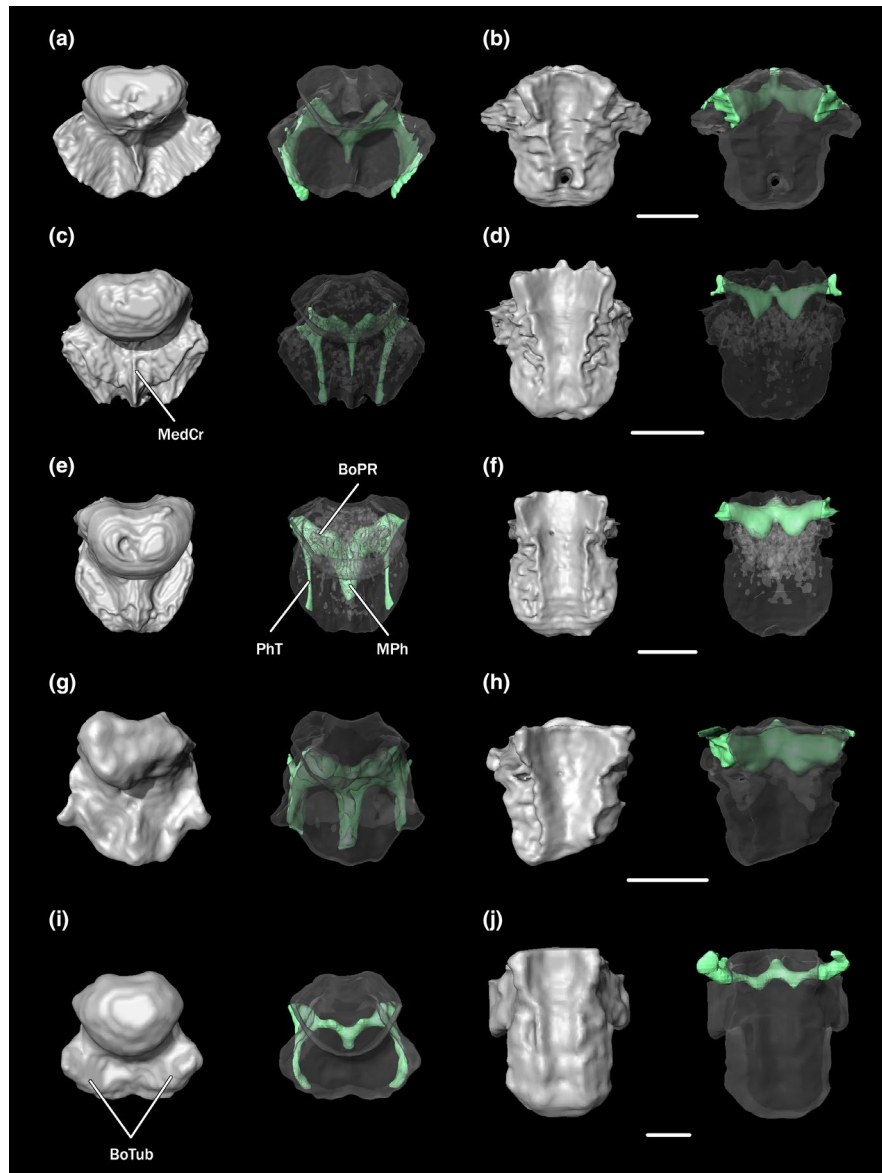


FIGURE 21 Comparison of crocodylian basioccipitals. (a, c, e, g, i) In posterior view; (b, d, f, h, j) in dorsal view. Each pair comprises CT-based models of non-transparent skeletal element and semitransparent element with digital endocasts of relevant pneumatic structures. (a, b) *Alligator mississippiensis* (DVZ M 4/13); (c, d) *Crocodylus novaeguineae* (DVZ M 9/13); (e, f) *Mecistops cataphractus* (DVZ M 6/13); (g, h) *Osteolaemus tetraspis* (DVZ M 7/13); (i, j) *Gavialis gangeticus* (ZIN 7249). BoPR, basioccipital pneumatic recess; BoTub, basioccipital tuberosities; MedCr, medial crest; MPh, median pharyngeal pneumatic canal; PhT, pharyngotympanic canal. Scale bars each equal 1 cm

and the otoccipital posteriorly along a vertical suture (Figure 7). The small endolymphatic foramen is present at a point where the three bones converge on the surface of the tympanic bulla (Figure 7c). The medial surface of the prootic is generally pierced by four small foramina that transmit several branches of cranial nerves (Figures 7c, 10j and 11b) (Iordansky, 1973; Lessner & Holliday, 2020). These foramina are from anterior to posterior: the opening for the facial nerve (CN VII); the foramen for the anterior branch of the vestibulo-cochlear nerve (CN VIII), which supplies the two anterior ampullae and the recessus utriculi (=ramulus anterior acustici in Retzius, 1884); the foramen for the branch of CN VIII, which innervates the

macula sacculi (=ramulus sacculi in Retzius, 1884) and a notch forming the anterior border of a foramen for the posterior branch of CN VIII (which includes the ramulus ampullae posterioris, ramulus neglectus, the additional part of ramulus sacculi, ramulus basilaris and ramulus lagenae; Retzius, 1884). The latter notch was mistakenly labelled "lymphatic foramen" in Lessner and Holliday (2020: fig. 7D); the endolymphatic foramen is located more dorsally at the Y-shaped contact of the prootic, otoccipital and supraoccipital (Figure 7c) (Iordansky, 1973; Retzius, 1884; Sedlmayr, 2002).

The prootic is deeply notched anteriorly, forming the posterior, dorsal and ventral margins of the trigeminal fossa (Figure 10c,e,f).

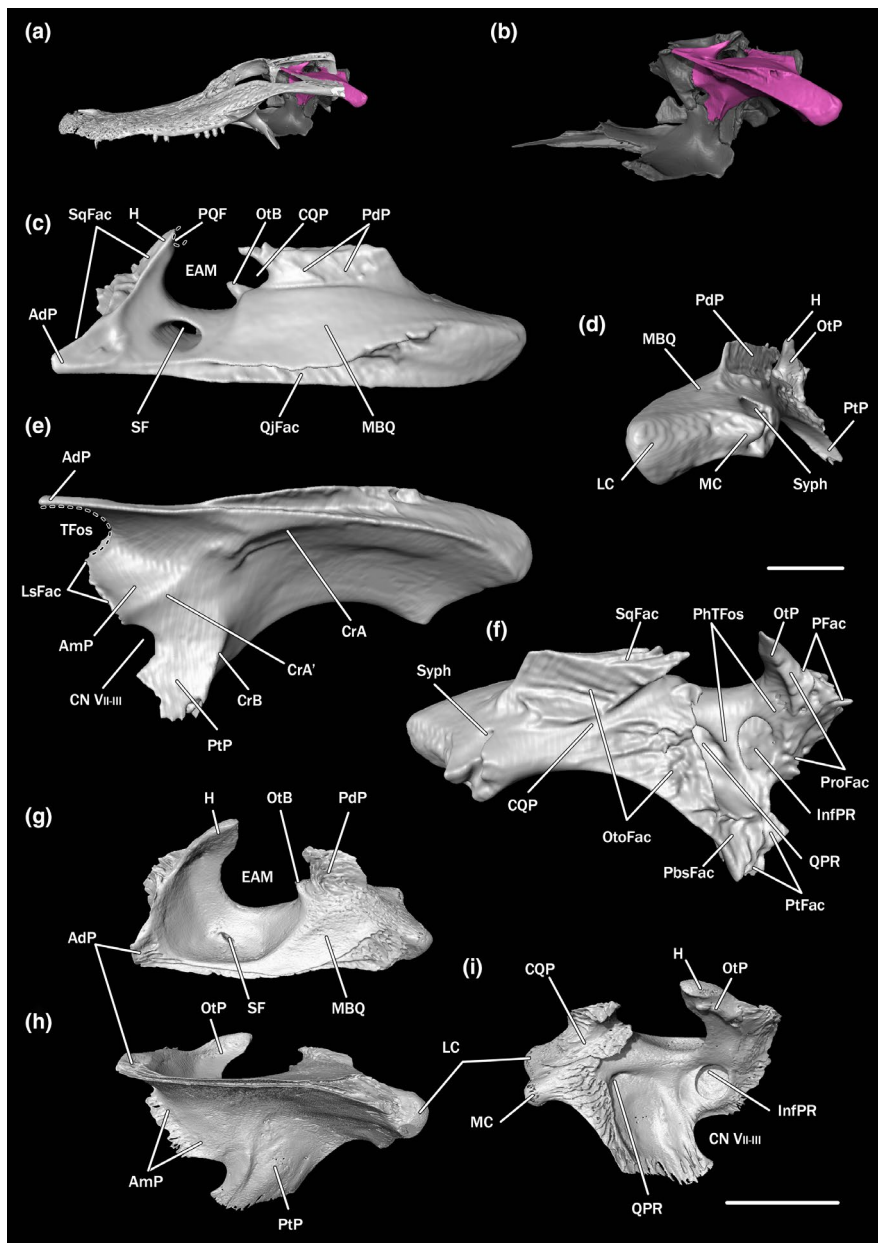


FIGURE 22 Anatomy of the quadrate of crocodylians. (a, b) Insets showing the region of interest on *Alligator mississippiensis* (DVZ M 4/13). (c–f) Quadrate of *A. mississippiensis* (DVZ M 4/13) in (c) dorsal, (d) posterior, (e) left lateral and (f) medial views. (g–i) Quadrate of hatchling *Caiman crocodilus* (PIN comparative collection, unnumbered) in (g) dorsal, (h) left lateral and (i) medial views. AdP, anterodorsal process; AmP, anteromedial process; CN VII–III, maxillomandibular foramen; CQP, cranioquadrate passage; CrA, muscular crest A; CrA', muscular crest A'; CrB, muscular crest B; EAM, external auditory meatus; H, quadrate head; InfPR, infundibular pneumatic recess; LC, lateral condyle; LsFac, laterosphenoid facet; MBQ, main body of quadrate; MC, medial condyle; OtB, otic buttress; OtoFac, otoccipital facet; OtP, otic process; PbsFac, parabasisphenoid facet; PdP, posterodorsal process; PFac, parietal facet; PhTFos, pharyngotympanic pneumatic fossa; PQF, postquadrate foramen; ProFac, prootic facet; PtFac, pterygoid facet; PtP, pterygoid process; QJFac, quadratojugal facet; QPR, quadrate pneumatic recess; SF, subtympanic foramen; SqFac, squamosal facet; Syph, pneumatic siphonium (foramen aereum); TFos, temporal fossa. Upper scale bar (for c–f) equals 1 cm; lower scale bar (for g–i) equals 5 mm

The *anterior inferior* (anteroventral) process of the prootic forms the ventral border of the internal trigeminal foramen and the trigeminal fossa (Figure 10c). This process sutures to the laterosphenoid anteriorly and to the parabasisphenoid ventrally. It includes the base of the embryonic pila antotica, as in squamates (Evans, 1986, 2008; Gower, 2002; Gower & Weber, 1998). The dorsal border of the trigeminal fossa is formed by the *anterior superior* (anterodorsal)

process (Figure 10c). The anterior superior process sutures to the laterosphenoid anteriorly and the quadrate laterally. The canal for a small tympanic branch of the trigeminal cranial (CN V_{tym}) and sympathetic nerves pierces the prootic at the posterodorsal corner of the trigeminal fossa and leads into the middle ear cavity (Figure 11) (Bellairs & Shute, 1953; Holliday & Witmer, 2009; Hopson, 1979; Lessner & Holliday, 2020; Witmer et al., 2008). It is formed either

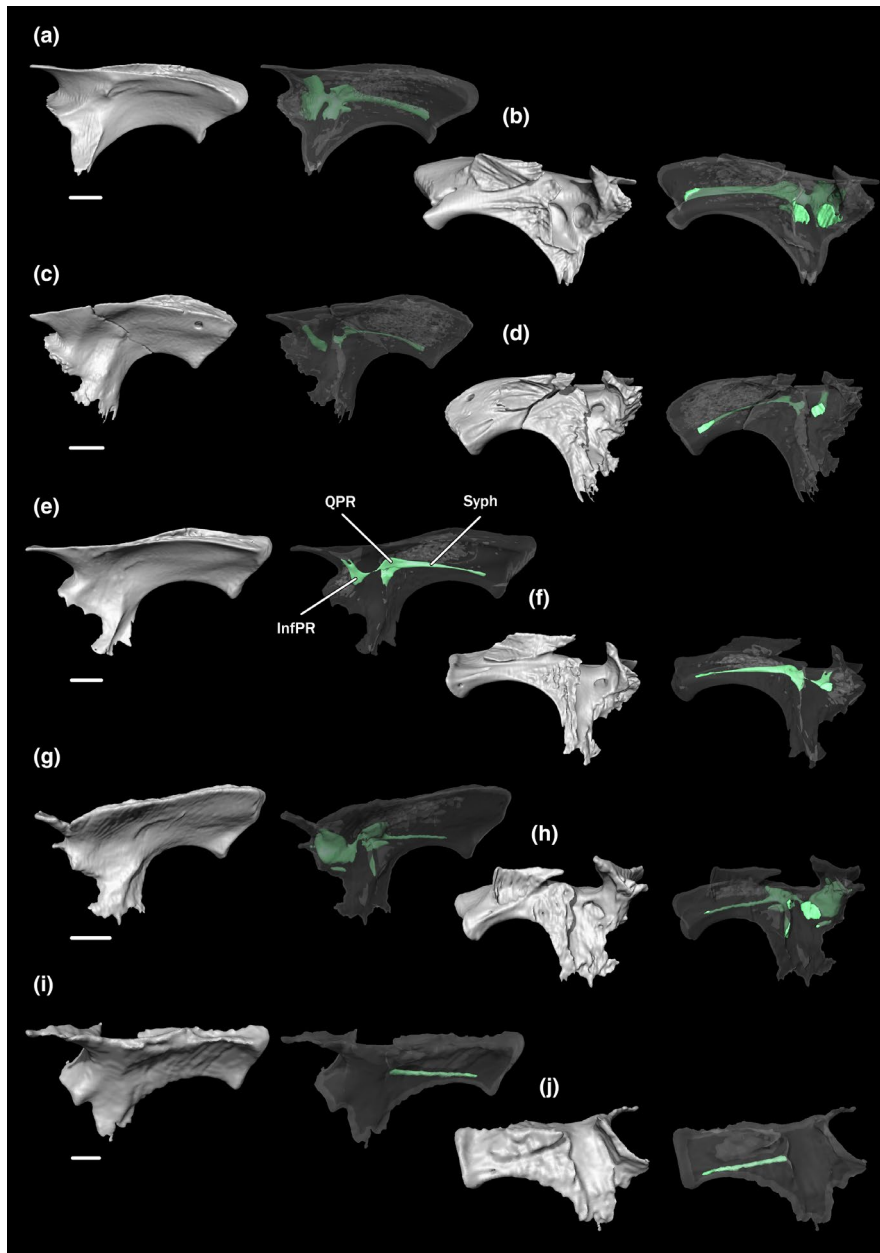


FIGURE 23 Comparison of crocodylian quadrates. (a, c, e, g, i) In left lateral view; (b, d, f, h, j) in medial view. Each pair comprises CT-based models of non-transparent skeletal element and semitransparent element with digital endocasts of relevant pneumatic structures. (a, b) *Alligator mississippiensis* (DVZ M 4/13); (c, d) *Crocodylus novaeguineae* (DVZ M 9/13); (e, f) *Mecistops cataphractus* (DVZ M 6/13); (g, h) *Osteolaemus tetraspis* (DVZ M 7/13); (i, j) *Gavialis gangeticus* (ZIN 7249). InfPR, infundibular pneumatic recess; QPR, quadrate pneumatic recess; Syph, pneumatic siphonium (extension of quadrate recess). Scale bars each equal 1 cm

entirely by the prootic (*A. mississippiensis*, *Crocodylus* spp.) or at the contact of the prootic and the quadrate (*O. tetraspis*). In the three studied specimens of *G. gangeticus* (ZIN 50, ZIN 7249 and UF11898), a short *anterior bridge* of the prootic encloses the passage for the small supraorbital nerve (branch of CN V_{II}) (Figure 11i). This process corresponds to the caudal bridge of the laterosphenoid in other taxa (see Section 4.3).

The *lateral lamina* of the prootic is a dorsoventrally extended thin process that faces anterolaterally (Figure 10c,d). It covers the capsular portion of the prootic in the lateral aspect but does

not actually contact the latter; however, the gap between these parts is very narrow in some taxa (e.g. *O. tetraspis*). The lateral lamina is incipiently developed in the studied crocodylian hatchlings (Figure 10g) but is quite prominent in the adults. The medial surface of the lateral lamina is smooth, forming the wall of the pneumatic pharyngotympanic fossa (Figure 10g). The lateral lamina has a continuous contact with the quadrate laterally. In addition, it sutures to the parabasisphenoid and the pterygoid ventrally. The presence of the externally visible contact between the prootic and pterygoid is a variable feature among crocodylians:

it was observed in all extant alligatorids, *T. schlegelii* and *G. gangeticus* but it is absent in *Crocodylus* spp., *M. cataphractus* and *O. tetraspis* (Figure 3). In the latter taxa, the prootic–pterygoid contact is present internally but is obscured by the overlying laterosphenoid–quadrate contact. Anteroventrally, the lateral lamina smoothly merges into the anterior inferior process (Figure 10c). Anterodorsally, it merges with the superior inferior process and the base of the prootic buttress.

The dorsal portion of the prootic is formed by the *prootic buttress*. The prootic buttress appears as a thin strip of bone that makes a complete loop and connects the anterior superior process with the posterior aspect of the capsular portion (Figure 10c,g). This loop surrounds the entrance of the intertympanic pneumatic recess into the prootic. The anterior part of the prootic buttress is sutured to the parietal and quadrate. It is expanded into an anterodorsally facing broad lamina in some taxa (e.g. *Alligator* spp.; Figure 10d,f). This expanded part may be termed the *dorsal lamina* of the prootic. Posteriorly, the prootic buttress forms a continuous sutural contact with the otoccipital (Figure 12). Just posterior to the head of the quadrate, the prootic buttress is notched. This notch forms the postquadrate foramen for the passage of the temporoorbital vessels (Figures 3d, 5 and 10C) (Porter et al., 2016; Walker, 1990; see Section 4.2). The dorsal surface of the prootic buttress is smooth and has a continuous contact with the supraoccipital (Figures 6 and 10e). The dorsal part of the prootic buttress participates in the floor of the temporal canal and can be observed through the supratemporal fenestra and the anterior temporal foramen (Figure 6). In present-day alligatorines (*A. mississippiensis* and *A. sinensis*), the prootic buttress is relatively robust and forms a considerable portion of the floor of the temporal canal (Figure 6b,c). The dorsal part of the prootic buttress is lateromedially thinner, compared to that of alligatorines, in *T. schlegelii*, *M. cataphractus* and caimanines (e.g. *C. crocodilus*, *C. yacare*, *M. niger*, *Paleosuchus trigonatus*). In these taxa, the prootic buttress precludes a direct supraoccipital–quadrate contact on the floor of the temporal canal; however, the supraoccipital and the quadrate closely approach each other (Figure 6f,h,i). The prootic buttress is most reduced and thin in *O. tetraspis*, *Crocodylus* spp. and *G. gangeticus* (Figures 6d,e,g and 11). In the latter taxa, it is frequently obscured on the floor of the temporal canal by the overlying suture between the supraoccipital and quadrate.

The prootic of crocodylians is heavily pneumatized (Dufeu & Witmer, 2015; Walker, 1990). A large part of the bone dorsal to the capsular portion is filled by the spacious *intertympanic recess* (Figure 11) (=intertympanic diverticulum in Dufeu & Witmer, 2015; =transverse canal in Lordansky, 1973; =mastoid antrum in Clark, 1986; Leardi et al., 2020; Walker, 1990). The latter passes through both prootics and the supraoccipital and connects the tympanic cavities of the opposite sides of the skull. If there is a communication between the prootic part of the intertympanic pneumatic recess and the parietal pneumatic recess, it extends through a foramen perforating the dorsal lamina of the prootic (Figure 10f). The anteromedial

border of the pharyngotympanic (=middle ear) cavity corresponds to a vertical fossa between the lateral lamina and the capsular portion of the prootic (Figure 10g). This pneumatic *pharyngotympanic fossa* communicates ventrally with the pneumatic recessus epitubaricus of the parabasisphenoid. The foramina for CN V_{tym} and CN VII perforate the wall of the pharyngotympanic fossa. Two grooves excavated by the hyomandibular (CN VII_{hyo}) and palatine (CN VII_{pl}) branches of the facial nerve are occasionally present and extend from the foramen for CN VII. The *prootic facial pneumatic recess* (=facial antrum in Leardi et al., 2020; Walker, 1990; =prootic diverticulum in Dufeu & Witmer, 2015) is occasionally present within the anterior superior process, just anterior to the vestibular recess of the otic capsule and the exit of CN VII (Figure 11). It is absent in some taxa (e.g. *T. schlegelii*, *M. cataphractus*, *Crocodylus* spp.). The prootic pneumatic recess communicates via corresponding foramina with both the intertympanic recess and the pharyngotympanic fossa, or with only one of these recesses (Figure 10d).

4.5 | Otoccipital

The otoccipital of crocodylians is a compound element that corresponds to the fused opisthotic and exoccipital (Bellairs & Kamal, 1981; Lordansky, 1973; Parker, 1883). The definitive otoccipital is a complex structure that incorporates several portions of different embryonic origins. Most of the bone ossifies from the cartilaginous precursors of the embryonic chondrocranium (e.g. the occipital arch, paroccipital process and otic capsule; Bellairs & Kamal, 1981; Klembara, 2005; Müller, 1967). Along with the endochondral ossifications, the otoccipital of crocodylians also incorporates two separate dermal ossifications of the embryo—the anterior and the posterior juxtaotic laminae. Klembara (2005) described these additional embryonic anlagen in *A. mississippiensis*. Later in the embryonic development, the two juxtaotic laminae fuse and enclose the otic capsule and adjacent structures (cranial nerves IX–XI, sympathetic nerve and the carotid artery) in the posterior aspect of the skull (Klembara, 2005). Consequently, the embryonic juxtaotic lamina corresponds to the ventrolateral process of the fully ossified otoccipital.

The otoccipital of crocodylians may be subdivided into the following portions: (1) the capsular portion; (2) the adjacent extracapsular structures—the extracapsular buttress and the anteroventral process; (3) the ventrolateral process; (4) the paroccipital process and (5) the occipital arch. The bone forms the posterior third of the otic capsule (Figure 12). The paired otoccipitals form large part of the posterior (occipital) surface of the cranium (Figure 4) and serve for attachment of several cervical muscles (Snively & Russell, 2007; Tsuihiji, 2010). The crocodylian otoccipital is sutured to all adjacent elements of the braincase in a complex fashion.

The *capsular portion* of the otoccipital surrounds the posterior part of the vestibular recess (Figures 12, 13e–g and 14b). Faint ridges on the floor of the vestibular recess subdivide it into cavities that correspond to particular compartments of the endolymphatic labyrinth

(the ampulla of the posterior semicircular canal, the posterior sinus of the utricle and part of the saccule; Baird, 1960; Retzius, 1884) (Figure 14b). The posterior and the lateral semicircular canals pierce the roof of the capsular portion of the otoccipital (Figure 15d). The capsular portion bulges into the endocranial cavity and forms the otic bulla together with the prootic and supraoccipital (Figure 7c).

Lateral and posterior to the capsular portion, there is an association of structures related to the metotic foramen, passages for the cranial nerves and the perilymphatic sac of the inner ear. The nomenclature of these structures is the most controversial and convoluted in published studies on the braincase anatomy of crocodylians (Gower & Weber, 1998; Klembara, 2005; Rieppel, 1985; Walker, 1990). We adopt a revised version of the terminology from Walker (1990) and Gower and Weber (1998) (see Section 3).

A brief anatomical comment on the structure of the *inner ear* in crocodylians is needed (Figure 12). The inner ear comprises the two systems of fluid-filled channels; one system surrounds the other (Baird, 1960, 1970; Retzius, 1884; Wever, 1978). The internal system includes the endolymphatic (otic or membranous) labyrinth that contains endolymph. It is surrounded by the perilymphatic (periotic) labyrinth that contains perilymph. The auditory (ventral) component of the endolymphatic labyrinth includes the saccule and the cochlear duct. The cochlear duct of crocodylians is elongated and geniculate; it bulges laterally from the level of the vestibulum (Baird, 1960, 1970; Walker, 1990). The cochlear prominence (see Section 4.4) corresponds to this unique position of the cochlear duct in crocodylians, as compared to the more medial location of the duct in other extant diapsids. The ventralmost portion of the cochlear duct of crocodylians contains the sensitive endorgan—the lagenar macula—and is termed the lagena or the lagenar compartment (Baird, 1960, 1970; Retzius, 1884; Walker, 1990). Part of the membranous wall of the cochlear duct is modified to carry the sensory hair cells, which collectively represent the endorgan known as the basilar papilla (Baird, 1960, 1970). This part of the wall of the cochlear duct is referred to as the basilar membrane. The opposite wall of the cochlear duct is termed the vestibular membrane. The vestibular and basilar membranes of crocodylians coil and shift their relationship along the length of the cochlear duct (Figure 12b) (Baird, 1960). The key perilymphatic compartments that surround the auditory component of the endolymphatic labyrinth include: (1) the large perilymphatic cistern (which abuts the saccule and receives the footplate of the columella auris); (2) the elongate cochlear extension or the scala vestibuli (abuts the vestibular membrane of the cochlear duct) and (3) the elongate posteromedial extension or the *scala tympani* (abuts the basilar membrane of the cochlear duct) (Figure 12b) (see Baird, 1960). The two latter parts are united ventrally by a short duct (helicotrema in Baird, 1960). The scala tympani terminates with a spacious *perilymphatic sac* externally and adjacent to the otic capsule, situated within a space known as the recessus scalae tympani (Figure 12a,b). The perilymphatic sac participates in the formation of the compensatory *secondary tympanic membrane* that dissipates excessive energy from the inner ear (Baird, 1960; Wever, 1978). The peculiar lateral position of the cochlear duct of crocodylians results

in the lateral, extracranial route of the entire perilymphatic system in these reptiles. This differs from the endocranial route of the perilymphatic system in most other extant diapsids (see Baird, 1960).

An obliquely oriented bony lamina arises just ventral to the foramen for the lateral semicircular canal of the otoccipital. It makes a complete loop around the perilymphatic sac and is termed the *perilymphatic loop* (Figures 12, 13e–g and 14g; Walker, 1990). The perilymphatic loop circumscribes the *perilymphatic foramen* that provides the passage for the perilymphatic sac out of the otic capsule (Figures 12 and 13g). The perilymphatic loop is a completely endochondral ossification (Klembara, 2005: figs 1, 2 and 7). It corresponds to the straight ventral ramus of the opisthotic of other diapsids (Gower, 2002; Walker, 1990).

The sharp dorsal margin of the perilymphatic loop is called the *crista interfenestralis*. The crista interfenestralis separates the more dorsally situated fenestra ovalis and the more ventrally lying fenestra pseudorotunda (Figures 12a,c and 13e–g). Anteriorly, the perilymphatic loop broadens and then turns posteromedially (Figure 13f,g). The broadened portion abuts the lateral bulge of the cochlear prominence of the prootic anteriorly. Together these bones enclose the cochlear recess and form the *cochlear prominence* of the otic capsule. Further posteriorly and medially, the perilymphatic loop becomes horizontal and thicker dorsoventrally (Figure 10g). Here, it forms the *loop-closure suture* (“the suture of the opisthotic with itself” in Walker, 1990) (Figure 13e,g). This ventral part of the perilymphatic loop forms the ventral border of the perilymphatic foramen and the anteroventral border of the metotic foramen, as evident in medial view (Figure 10h). The anterior margin of the ventral part of the perilymphatic loop is incised (Figure 10g); it receives the medial bulge of the cochlear prominence of the prootic. The ventral part of the perilymphatic loop obscures the metotic foramen in anterior, dorsal and lateral views. It attaches to the anteroventral process and the extracapsular buttress of the otoccipital but never fuses completely with them (Figure 13f). The sharp lateral margin of the ventral part of the perilymphatic loop overhangs the metotic foramen and is termed the *otoccipital ledge* (opisthotic ledge in Walker, 1990) (Figure 13e).

The *extracapsular buttress* is a bony lamina that extends from the capsular portion of the otoccipital medially to the cranioquadrate passage laterally (Figures 13f and 14b). The extracapsular buttress is a consistent feature of the crocodylian otoccipital. It is obliquely oriented, anteriorly concave, and forms a groove for numerous neurovascular structures (Figures 5d,e, 13e, 14b and 15b,d,f). The dorsal margin of the extracapsular buttress forms a continuous suture with the prootic buttress (Figure 12a). The extracapsular buttress is a compound ossification: its ventromedial portion corresponds to the embryonic cartilaginous subcapsular process and an osseous lamina extending from the latter and the dorsolateral portion of the extracapsular buttress corresponds to the ossification of the dermal juxtaotic lamina (Klembara, 2005: p. 324).

The extracapsular buttress attaches to the perilymphatic loop ventromedially and completes the anterior, lateral and posterior margins of the fenestra pseudorotunda (Figures 12b and 13e,g). The *fenestra pseudorotunda* provides the bony framework for the

secondary tympanic membrane. The space bounded by the fenestra pseudorotunda dorsally and the perilymphatic foramen medially is properly called the *recessus scalae tympani* (Figures 12 and 13f) (Rieppel, 1985). The recessus scalae tympani contains the extracapsular portion of the perilymphatic sac and is traversed by the glossopharyngeal (IX), vagus (X) and accessory (XI) cranial nerves and the sympathetic nerve (Figures 5d,e, 13e,f, 14b and 15) (Bellairs & Shute, 1953; Klembara, 2005; Lessner & Holliday, 2020; Shiino, 1914). The floor and the walls of the recessus scalae tympani are formed by the perilymphatic loop and the extracapsular buttress.

The extracapsular buttress is pierced by three separate foramina for cranial nerves and associated vasculature (e.g. the vagal vein). These are from medial to lateral: (1) the passage for CN X (=internal vagal foramen); (2) the passage for CN IX (=internal glossopharyngeal foramen) and (3) the foramen for the sympathetic nerve (Figures 13e, 14b,d and 15). Small bundles of CN XI can variably pass through the internal vagal or the internal glossopharyngeal foramina (Sedlmayr, 2002). Further posteriorly, these nerves extend in a common bony canal (e.g. Figure 15c) and exit the braincase on the posterior surface of the cranium through a common foramen (*foramen vagi* of Lordansky, 1973; Klembara, 2005; Lessner & Holliday, 2020; Müller, 1967; Shiino, 1914) (Figures 4, 13d, 14c and 15). In some specimens, a groove passes laterally from the foramen of the sympathetic nerve and marks the course of its branch (*ramus communicans*) towards the cranioquadrate passage (Figure 5e). There, the *ramus communicans* merges with the hyomandibular branch of the facial nerve (CN VII_{hyo}) and connects the fibres of CN VII_{hyo} with CN IX (Bellairs & Shute, 1953; Lordansky, 1973; Klembara, 2005; Lessner & Holliday, 2020; Shiino, 1914; Walker, 1990). Lessner and Holliday (2020 fig. 12B) figured the presence of the tympanic branches of CN IX and X that extend anteriorly into the pharyngotympanic (middle ear) cavity from their corresponding ganglia in a yearling *A. mississippiensis*. However, such branches have not been previously reported in crocodylians (Bellairs & Shute, 1953; Klembara, 2005; Müller, 1967; Shiino, 1914); neither they were figured by Lessner and Holliday (2020: fig. 12C) in an embryonic *A. mississippiensis*. It is possible that the tympanic branches of CN IX and X have been confused with the sympathetic nerve that extends in a similar direction (e.g. Bellairs & Shute, 1953; Lessner & Holliday, 2020: fig. 12C). Our interpretation of the lateralmost of the three internal foramina in question as for the passage for the sympathetic nerve is congruent with the detailed description by Bellairs and Shute (1953: text-fig. 5) and that of an embryonic specimen by Lessner and Holliday (2020: fig. 12C).

The arterial branch that connects the stapedial and cerebral carotid arteries passes just lateral to the extracapsular buttress (Figures 5e and 28c). This vessel was referred to as the true stapedial artery in Walker (1990), the stapedial artery in Klembara (2005) or the ventral vessel in Sedlmayr (2002). The bony canal of the cerebral carotid artery is fused with the ventral margin of the extracapsular buttress (Figures 13f and 14b). This canal is

formed by the juxtaotic lamina during the embryonic development (Klembara, 2005: fig. 9A).

Ventromedial, there is a process that projects anteriorly and abuts the prootic. We call it the *anteroventral process* of the otocipital (Figures 13f–h and 14d). This process was first noted in crocodylians by Walker (1990). The anteroventral process sutures to the basioccipital ventrally. It is continuous dorsolaterally with the extracapsular buttress and the bony canal of the cerebral carotid artery (Figure 14b). The anteroventral process forms the ventral margin of the metotic foramen (Figure 13h). The lateral surface of the anteroventral process makes up the medial wall of the pneumatic rhomboidal recess (Figure 13f). It appears that, in the embryonic chondrocranium, the area corresponding to the anteroventral process is formed by the cartilage and is continuous with the subcapsular process laterally and the basal plate medially (Klembara, 2005: fig. 9A).

The metotic fissure of the embryonic crocodylian chondrocranium provides the exit for CN IX–XI and associated vasculature and corresponds to the slit-like *metotic foramen* in the adult cranium (Figures 7c, 13h and 14d) (Lessner & Holliday, 2020; Müller, 1967; Shiino, 1914). The metotic foramen is seen on the endocranial surface of the otocipital posterior to the otic bulla (Figure 7c). It is obscured laterally by the overhanging perilymphatic loop and the otic capsule. Laterally, the metotic foramen leads into the ventral part of the recessus scalae tympani and to the internal vagal foramen (Figures 13h and 14d). The metotic foramen does not contain the perilymphatic sac, as it does plesiomorphically in diapsids, due to the overall rearrangement of the otic capsule and membranous inner ear of crocodylians, specifically the extracranial route of the perilymphatic sac (see a comment on the inner ear anatomy of crocodylians above and the discussion of the subdivision of the metotic foramen in File S2).

The *ventrolateral process* is a characteristic structure of the crocodylian otocipital with a distinct embryonic origin. It corresponds to the dermal ossification (juxtaotic lamina) in the developing skull of *A. mississippiensis*, which is absent in other extant diapsids (Klembara, 2005). The ventrolateral process lies ventral to the paroccipital process and has continuous contacts with the quadrate anteriorly, the parabasisphenoid anteroventrally and the basioccipital ventrally (Figures 13c,d,f and 14a). The ventrolateral process underlies the pneumatic recesses of the otocipital. It fuses with the extracapsular buttress anterodorsally and forms the floor of the cranioquadrate passage (for CN VII_{hyo} and stapedial vessels, see Section 4.2). The ventrolateral process contains the common canal for the posterior cranial nerves (CN IX, X, XI and the sympathetic nerve) and the canal for the cerebral carotid artery (Figure 15c,e). On the posterior (occipital) surface of the ventrolateral process, these canals open via separate foramina: the *foramen vagi* and the cerebral carotid foramen (Figures 13c,d and 14a,c). The ventral tip of the ventrolateral process is generally elongated in gavialids and caimanines compared to the condition in other crocodylians (Brochu, 1999) (Figures 4b,h and 15e,f). It extends ventrally to the external carotid foramen and participates in the basioccipital tuberosities. In gavialids, this process

is relatively broad anteroposteriorly and evident on the lateral surface of the braincase (Figure 3b). In caimanines, the process is thin and barely visible laterally (Figure 3h).

The *paroccipital process* is a wing-like lateral extension of the otoccipital (Figures 13c,d and 14a). It corresponds to the embryonic crista parotica of the chondrocranium (Bellairs & Kamal, 1981; Klembara, 2005) and is distinct from the ventrolateral process. Ultimately, these structures become indistinguishably fused in the fully formed otoccipital. The presumed border between the two processes is traced by the groove for the cranioquadrate passage. The paroccipital process extends laterally from the arch-like occipital arch. In hatchlings, the paroccipital and ventrolateral processes are nearly equal in the lateromedial extent (Figure 14a). Later in ontogeny, the paroccipital process becomes lateromedially wider than the ventrolateral process in extant crocodylians (Figure 13d). Internally (anteriorly) the paroccipital process houses the otoccipital pneumatic recess. Two thin bony struts generally extend through the otoccipital recess and link the capsular portion of the otoccipital with the inner surface of the paroccipital process (Figure 13e,g). The dorsally situated strut is termed the *otoccipital strut*; it contacts with the corresponding strut of the supraoccipital. In hatchlings, the capsular portion directly contacts the inner wall of the paroccipital process. The posterior surface of the paroccipital process forms most of the occiput. The paroccipital process has an oblique contact with the supraoccipital medially and a continuous contact with the squamosal dorsally. A small head (*capitulum*) lined with the compact bone is present at the contact with the squamosal. The anterior surface of the paroccipital process broadly sutures to the quadrate (Figure 13f).

The *occipital arch* corresponds to the eponymous embryonic cartilaginous arch (Bellairs & Kamal, 1981; Evans, 2008). The occipital arch forms the entire lateral margin of the foramen magnum (Figure 13c,d). It contacts the basioccipital ventrally and the occipital arch of the contralateral otoccipital dorsally. The occipital arch is generally pierced by two or three separate canals of the hypoglossal nerve (CN XII) (Lessner & Holliday, 2020). On the endocranial surface, posterior to the otic bulla, the depression houses the ventral extension of the occipital venous sinus (Porter et al., 2016; Sedlmayr, 2002; Witmer et al., 2008: fig. 6.4) (Figure 13h).

The otoccipital is invaded by the extensive *otoccipital pneumatic recess* (Dufeu & Witmer, 2015). Ventrolaterally and ventrally, this recess communicates with the pharyngotympanic cavity and with the rhomboidal recess via the two corresponding passages that surround the canals for the cranial nerves CN IX–XI and the carotid artery respectively (Figure 15a). One or both communications are absent in adult individuals of some taxa (e.g. *Crocodylus* spp., *T. schlegelii*, *G. gangeticus*, *M. cataphractus*) (Figure 15c,e). Invasion of the otoccipital by the pneumatic diverticula from the pharyngotympanic cavity and the rhomboidal recess begins rather early in the ontogeny of crocodylians (nearly at stages 6A and 7A, see Klembara, 2005). These diverticula invade the otoccipital ventrally below the extracapsular buttress and the otic capsule (Dufeu & Witmer, 2015; Klembara, 2005; Müller, 1967). Subsequently, in *A. mississippiensis*, the otoccipital recess expands dorsally and surrounds the aforementioned

neurovascular canals (Dufeu & Witmer, 2015). Dorsally, in adult individuals, the otoccipital recess communicates anteriorly and medially with the intertympanic recess in the prootic and supraoccipital. There are two corresponding pneumatic passages divided by a thin otoccipital strut in the otoccipital of extant crocodylians (Figures 13g, 14d and 15a). The anterior passage is larger and confluent with the intertympanic recess in adult crocodylians (Dufeu & Witmer, 2015). It is located lateral to the foramina of the posterior and the lateral semicircular canals and is bounded by the extracapsular buttress anteriorly and the otoccipital strut posteriorly (Figure 13g). The posterior passage is smaller and develops later in the ontogeny of *A. mississippiensis* (Dufeu & Witmer, 2015). It is situated posterior to the otoccipital strut and the foramen of the posterior semicircular canal (Figure 13g). The otoccipital and intertympanic recesses are largely confluent in the adults but are distinct pneumatic diverticula in hatchlings and juveniles (Dufeu & Witmer, 2015).

4.6 | Supraoccipital

The fully formed supraoccipital is a compound ossification that corresponds to the fused epiotics and supraoccipital (Bellairs & Kamal, 1981; Müller, 1967; Parker, 1883; Rieppel, 1993; Walker, 1990). Separate centres of ossification (endochondral epiotic and the supraoccipital) were observed in the developing skulls of *A. mississippiensis* (Rieppel, 1993) and *M. niger* (Vieira et al., 2019). They initially develop in the tectum synoticum, which is the cartilaginous roof between the embryonic otic capsules (tectum posterius in Shiino, 1914; fused tectum synoticum posterius and tectum posterius in Klembara, 2001). The trabecular bony component of the supraoccipital develops from the perichondral lining of the tectum synoticum and has the appearance of a dermal element (Klembara, 2001; Rieppel, 1993). The separate ossification posterior to the parietal of some skulls of *A. mississippiensis* (Mook, 1921) and the supraoccipital exposure on the skull table in some taxa both correspond to the perichondral trabecular component of the supraoccipital (Lordansky, 1973; Klembara, 2001; Rieppel, 1993).

The fully ossified supraoccipital of crocodylians has a trapezoidal outline (Figure 16). It surrounds the spacious intertympanic pneumatic recess and is built of several laminae connected by thin bony struts. The supraoccipital is sutured to the parietal dorsally, to the prootics and the otoccipitals ventrally, and, in caimanines, it contacts the squamosals dorsolaterally (Figures 4, 6 and 7). The supraoccipital may be subdivided into following main portions: (1) the anterior lamina; (2) the posterior lamina and (3) the dorsal lamina.

The *anterior lamina* is strongly concave anteriorly and faces anteroventrally (Figure 16d). It may be further subdivided into the two capsular portions and the central endocranial portion. The paired *capsular portions* of the supraoccipital bulge anteroventrally and complete the otic bullae dorsally (Figure 16e). Each capsular portion holds a space for the sinus superior of the utricle (which corresponds to the generally recognized *crus communis* of the anterior and posterior semicircular canals) (Retzius, 1884; Walker, 1990). The anterior

and posterior semicircular canals pierce the walls of the capsular portion and join within the recess of the common crus (Figure 12). A thin anterior process extends from each capsular portion; it sutures to the prootic and approaches but does not contact the laterosphenoid on the endocranial surface (Figure 16g). The central part of the anterior lamina forms the dorsal part of the endocranial cavity. The endocranial space formed by the concave anterior lamina of the supraoccipital contains the voluminous dorsal longitudinal venous sinus (Sedlmayr, 2002; Witmer et al., 2008; fig. 6.4). Small foramina for the dorsal branches of the longitudinal sinus (external occipital veins in Sedlmayr, 2002) are present near the contact with the parietal in some specimens (e.g. *A. sinensis* DVZ M 3/13; Figure 16g). The floccular fossa (for the flocculus cerebelli) is not evident in adult crocodylians but is more distinct in hatchlings.

Ventrally, the anterior lamina merges with the posterior lamina of the supraoccipital. The resulting ventral surface of the supraoccipital sutures to the otoccipitals dorsal to the foramen magnum (Figure 7). In addition, a thin strut extends on either side of the supraoccipital between the two laminae and forms a continuous suture with the otoccipital ventrally. Hence, we term it the *otoccipital strut* (Figure 16d). The otoccipital strut divides two pneumatic passages that invade the supraoccipital: the anterior passage corresponds to the joint intertympanic and otoccipital diverticula and the posterior passage is the second entrance of the otoccipital diverticulum (see Sections 4.5 and 4.10).

The *posterior lamina* of the supraoccipital forms the posterior (occipital) surface of the bone. The posterior exposure of the supraoccipital is triangular, with the apex pointing ventrally (Figure 16c). Two short *postoccipital processes* with rounded heads form the dorsolateral margins of the posterior surface. The vertical *sagittal nuchal crest* extends along the centre of the posterior surface. Several cervical muscles attach to the posterior surface of the supraoccipital (Snively & Russell, 2007; Tsuihiji, 2010). The narrow exposure of parietal on the occiput and restriction of some neck muscles (namely, *M. spinalis capitis* and *M. longissimus capitis*) to the posterior surface of the supraoccipital distinguish crocodylians among extant diapsids (Tsuihiji, 2010).

There are some notable differences in the structure of the posterior lamina of the supraoccipital between the studied taxa (Figure 17). The sagittal nuchal crest is blunt or absent in *A. mississippiensis* but is distinct in other taxa. In alligatorines (*A. mississippiensis*, *A. sinensis*), the postoccipital processes and the sagittal nuchal crest are separated and the postoccipital processes project further posteriorly than the sagittal crest (Figure 17a,b). In crocodylids, some caimanines (e.g. *Mourasuchus nativus*: Bona et al., 2013) and *G. gangeticus*, the postoccipital processes and the sagittal nuchal crest are closely spaced; the nuchal crest strongly projects posteriorly in these taxa (Figure 17c–j). The two conditions also differ in the dorsal aspect, resulting in undulating versus rounded posterior margins of the supraoccipital in dorsal view. The caimanines (*Caiman* spp., *M. niger*, *P. palpebrosus*) have an intermediate condition: the postoccipital processes project dorsolaterally and posteriorly and appear to be separated from the sagittal nuchal

crest (as in extant alligatorines), but the development and posterior projection of the sagittal nuchal crest are similar to those in crocodylids and *Gavialis*. This is likely due to the development of the dorsal projection of the supraoccipital in caimanines, crocodylids and *Gavialis*, as opposed to the absence of this projection in extant alligatorines. More observations and quantitative 3D morphometric analyses are needed to determine the intra- and interspecific variability of this feature.

The *dorsal lamina* of the supraoccipital forms the entire dorsal surface of the bone. Except for its lateral margins it sutures to the parietal (Figure 16f,h). The lateral margins of the dorsal lamina have complex sutural relationships with the adjacent bones and participate in the floor of the temporal canal (Figure 6; see Section 4.2). Each lateral margin of the dorsal lamina forms a continuous contact with the prootic buttress anteriorly and a short contact with the otoccipital posteriorly in most studied taxa (e.g. *Alligator* spp., *Caiman* spp., *T. schlegelii*). However, in those taxa that have a reduced prootic buttress, the quadrate contacts the supraoccipital on the floor of the temporal canal. In these taxa, the quadrate–supraoccipital contact overlies the prootic buttress in dorsal view (e.g. *O. tetraspis*, *G. gangeticus*, *Crocodylus* spp.). The supraoccipital of caimanines has lateral sutural contacts with the squamosal. In addition, the lateral margin of the dorsal lamina of the supraoccipital has a sutural contact with a small spur of the squamosal within the temporal canal in some taxa (*T. schlegelii*, *O. tetraspis*, *G. gangeticus*, *Crocodylus* spp.; Figure 17). All examined specimens of *A. mississippiensis* lack a sutural contact between the supraoccipital and squamosal. In *A. sinensis*, the two bones are closely spaced, and the lateral margin of supraoccipital touches the ventral surface of the squamosal.

The dorsal lamina of the supraoccipital is pierced by two pairs of openings that correspond to the communication of the intertympanic and parietal pneumatic recesses—the larger anterolateral and smaller posteromedial foramina (Figures 16f and 17). The supraoccipital has a variable degree of the dorsal exposure among crocodylians (Brochu, 1999). The supraoccipital generally lacks the exposure on the dorsal surface of the skull in *Alligator* (DVZ 5/13, which has this exposure, is a rare exception in the examined sample). It is slightly exposed along the posterior margin of the skull table in *Crocodylus*, *Tomistoma*, *Osteolaemus* and *Paleosuchus*. In *Caiman* and *Melanosuchus*, the supraoccipital is significantly exposed on the cranial table, excluding the parietal from the posterior margin of the skull.

4.7 | Parabasisphenoid

The definitive parabasisphenoid is a compound ossification that includes various chondral and dermal embryonic anlagen. It incorporates the endochondrally ossifying anterior portion of the basal plate, the posterior portions of the trabecles and the interorbital septum, the polar cartilages (infrapolar processes of some authors), as well as several separate dermal ossifications: the unpaired paraspheoid and the paired basitemporals and paracochlears (Bellairs

& Kamal, 1981; Klembara, 1993; Müller, 1967; Parker, 1883; see Section 5).

The parabasisphenoid of crocodylians undergoes a major transformation during post-hatchling ontogeny. This change was first described as the *cranial metamorphosis* by Tarsitano (1985). The floor of the braincase in hatchling and juvenile crocodylians is dorsoventrally flat. The parabasisphenoid and the basioccipital are plate-like and nearly equally exposed ventrally posterior to the pterygoids (Figures 18h,j and 20h,i). The pneumatic median pharyngeal foramen (=median Eustachian foramen; Brochu, 1999; Colbert, 1946; Lordansky, 1973; Owen, 1850) lies at the same level as the choanae. During the first few years of post-hatchling development, the parabasisphenoid, basioccipital and posterior portion of the pterygoids become distinctly verticalized (Tarsitano, 1985) (Figure 7). This change affects the overall anatomy of the crocodylian basicranium, including the shape and position of the parabasisphenoid and the basioccipital relative to the palate, the extent of sutural contacts, the shape of the pneumatic cavities and the alignment of the jaw adductor muscles (Dufeu & Witmer, 2015; Tarsitano, 1985). The cranial metamorphosis is less pronounced in some gavialoids such as extant *G. gangeticus*, but this is the derived condition for this group that mimics the plesiomorphic state in distantly related non-crocodylian crocodyliforms (Brochu, 2004).

The parabasisphenoid may be subdivided into the following main portions: (1) the rostrum; (2) the central part or the body; (3) the posterior descending lamina and (4) the posterolateral alar processes. The parabasisphenoid of adult crocodylians is a wedge-shaped element that constitutes the anterior part of the basicranium. It forms the anterior part of the floor of the endocranial cavity, the hypophyseal fossa, and is sutured to numerous adjacent elements of the braincase. The parabasisphenoid is almost obscured in lateral and posterior views; only the rostrum, small anterior portion of the body, the posterolateral alar processes and the descending lamina are evident externally (Figures 3 and 4).

The *parabasisphenoid rostrum (cultriform process)* of crocodylians is a lateromedially compressed process that projects anteriorly (Figure 18f,h). It has a blunt anterior margin and is overall short compared to the long and acute parabasisphenoid rostra of other diapsids (e.g. see Clark et al., 1993; Evans, 1986, 2008; Sobral et al., 2016; Walker, 1990). It does not taper anteriorly as in other diapsids but instead expands dorsoventrally at its anterior end (a feature already present in basal crocodyliforms; Clark, 1986, 1994). Here, the parabasisphenoid rostrum sutures to the descending slender processes of both laterosphenoids (Figures 3 and 7). Posterior to this contact, the dorsal margin of the rostrum is incised by the foramina for CN III and the orbital artery and vein (Figure 18f) (Lessner & Holliday, 2020; Porter et al., 2016). In both extant species of *Alligator*, a prominent depression flanked by ridges is present on either lateral surface of the parabasisphenoid rostrum, ventral to the incisure for CN III (Figure 18f). This represents the attachment site for ocular muscles (inferior rectus muscle in Underwood, 1970). The lateral surface of the rostrum anterior to the aforementioned depression

represents the attachment site for the striated depressor palpebralis inferior muscle (Underwood, 1970).

The ventral edge of the rostrum extends parallel to the dorsal margin of the pterygoids. A small foramen (two foramina in a large skull of *A. mississippiensis* DVZ 5/13) opens on either side of the parabasisphenoid rostrum, ventrolaterally at the contact with the pterygoid (Figure 18d,j). These foramina represent the external openings of the canal for the palatine branch of the facial nerve (CN VII_{pl}) and the associated small sphenopalatine arteries. Walker (1990) cited Shiino (1914) and concluded that the sphenopalatine (or simply palatine) artery is absent in extant crocodylians. However, Sedlmayr (2002) reported the presence of a small artery within the canal of CN VII_{pl} in *A. mississippiensis*. The presence of two foramina on each side of the rostrum in DVZ 5/13 supports the observations of Sedlmayr (2002). Internally, these canals lead posteriorly and dorsally into the space of the pneumatic parabasisphenoid recess and the recessus epitubaricus (Figures 19 and 27). Dorsally, CN VII_{pl} courses towards the external foramen for CN VII in the prootic along the medial wall of the recessus epitubaricus (sometimes leaving a groove) and then along the pharyngotympanic fossa on the lateral surface of the prootic (Figures 10g and 18h). The external foramina for CN VII_{pl} are located ventrally to the parabasisphenoid rostrum in *G. gangeticus* (ZIN 50, ZIN 7249, TMM M-5490, UF11898) and *M. cataphractus* (DVZ M 6/13, TMM M-3529 and ENS R-11), as opposed to other present-day crocodylians that have these foramina located ventrolaterally and divided medially by the ventral margin of the rostrum (Figure 19). According to Brochu (1999: character 164), *G. gangeticus* differs from all extant crocodylians in having the external foramina for CN VII_{pl} ventrolateral to the parabasisphenoid rostrum. Our observations do not support this; in fact, in *Gavialis*, the pterygoid contacts the ventral margin of the parabasisphenoid rostrum and forms a canal for CN VII_{pl} and associated vasculature completely ventral to the rostrum (Figures 3b and 19i,j). We suspect that Brochu (1999) mistook small vascular foramina that are located ventrolaterally to the rostrum with the exit of CN VII_{pl}. In two specimens of *C. crocodilus* (FMNH 73711 and LFAC-2013), these canals for CN VII_{pl} first penetrate the dorsolateral margins of the pterygoids and then continue into the parabasisphenoid by a directly vertical route, ventral to the parabasisphenoid rostrum. Thus, some intraspecific variability of the feature is observed in crocodylians, along with differences between species.

Posteriorly, the parabasisphenoid rostrum expands transversely and merges with the body of the parabasisphenoid. Here, the *hypophyseal fossa* is present, formed by the rostrum ventrally and the dorsum sellae of the parabasisphenoid posteriorly and dorsally (Figure 18c,g,i,k). The hypophyseal fossa extends posteroventrally and is relatively deep (Figure 7b). The cerebral carotid arteries enter the hypophyseal fossa by a pair of foramina in its posterior wall (Figures 18g,k and 19). The hypophyseal fossa of crocodylians is well vascularized: the two cerebral carotid arteries anastomose with each other and ramify into the orbital and common encephalic arteries; the orbital veins enter the cavernous sinus that is drained by the cerebral carotid veins (Porter et al., 2016). The canals for

CN VI pierce the parabasisphenoid lateral to the hypophyseal fossa and do not pass through it in crocodylians (Figures 18g,k and 19). The external CN VI foramen lies at the contact with the laterosphenoid. The internal CN VI foramen opens posteriorly on the dorsal (endocranial) surface of the parabasisphenoid (Figures 18c,i and 19). The rostrum and the area around the hypophyseal fossa are pneumatized by the *precarotid*, *postcarotid* and *rostral recesses* in some extant crocodylians (e.g. *Alligator*, *Caiman* and *Osteolaemus*) (Figures 19 and 27).

The body of the parabasisphenoid constitutes the main portion of the element (Figure 18d). It has two anteroventrally facing surfaces, a dorsal (endocranial) surface and a posterior surface (descending lamina). The two anteroventral surfaces converge anteriorly and are tightly sutured to the ascending processes of the pterygoid. The basiptyergoid processes become lost in crocodylians during embryonic development (Bellairs & Kamal, 1981; Klembara, 1993). The body of the parabasisphenoid has a small exposure on the lateral surface of the braincase, anterior to the pterygoids and ventral to the laterosphenoid, in crocodylids (e.g. *Crocodylus*, *Mecistops*, *Tomistoma*) and gavialids (*G. gangeticus*: ZIN 50, ZIN 7249, UF11898; extinct *G. bengawanicus*: MB.R. 1960) (Figure 3b,d,f,g) (Brochu, 1999: character 129). This exposure is consistently lacking in alligatorids (e.g. *Alligator* spp., *Caiman* spp., *P. trigonatus*) and variably developed in osteolaemines, being small or absent in some specimens of *O. tetraspis* (DVZ M 7/13) and the extinct *V. robustus* (MB.R. 4124) (Figure 3c,e,h). Dorsoventrally, each anteroventral surface of the parabasisphenoid body has a contact with the lateral lamina of the corresponding prootic (Figure 18f). Posteriorly, the anteroventral surfaces of the parabasisphenoid body are continuous with the descending laminae and the alar processes. The approximate border between the anteroventral surface and the alar process is at the level of the entrance of the cerebral carotid artery into the parabasisphenoid (Figure 18c,h).

The concave dorsal surface of the parabasisphenoid forms the anterior part of the floor of the endocranial cavity (Figure 18c,i). The paired canals of CN VI pierce the dorsal surface of the parabasisphenoid (Figure 19). In *G. gangeticus*, some extinct gavialoids (e.g. *Gryposuchus neogaeus*; Bona et al., 2017), and one of the three studied specimens of *T. schlegelii* (ZMMU R-13859), there is also a central canal that leads from a foramen on the dorsal surface of the parabasisphenoid into the hypophyseal cavity (Figure 19j). This canal was first noted and interpreted as containing the basilar artery by Bona et al. (2017). According to Sedlmayr (2002) and Porter et al. (2016), the basilar artery is the endocranial artery formed by the two posterior arterial branches (caudal encephalic arteries) on the floor of the endocranial cavity. Thus, the central canal in the parabasisphenoid of gavialoids and *Tomistoma* most likely transmits a vascular branch that connects the cerebral carotid and basilar arteries.

On either side of the dorsal surface of the parabasisphenoid, there are two facets—one for the laterosphenoid body anteriorly and the other for the anterior inferior process of the prootic posteriorly (Figure 18c,f). The anteroventral process of

the otoccipital approaches but does not contact the parabasisphenoid on the endocranial surface (Figure 7). The body of the parabasisphenoid has a transverse contact with the basioccipital on the floor of the endocranial cavity. Each cerebral carotid artery pierces the parabasisphenoid laterally, just ventral to the contact with the prootic (Figure 19). Posterior to this, at the junction of the parabasisphenoid body with the descending lamina and the alar process, the parabasisphenoid participates in the floor of the cochlear recess (its lagenar portion) (Figure 18c). The body of the parabasisphenoid is pneumatized by the *median pharyngeal recess* and its lateral diverticula—the *parabasisphenoid recesses* (Figure 19). The pneumatic *recessus epitubaricus* opens laterally on the anteroventral surface of the parabasisphenoid body (Figure 18f,h).

The posterior surface of the parabasisphenoid slopes ventrally and forms the anterior wall of the median pharyngeal canal (Figure 18e). This portion may be termed the *descending lamina* (Brochu, 2004). Ventral to the median pharyngeal foramen, the descending lamina is exposed on the occipital aspect of the cranium in the adults of all examined taxa except *G. gangeticus* (Figure 4). There are two continuous facets for the basioccipital on the posterior surface of the descending lamina. They are separated by the median pharyngeal canal and flanked by the pharyngotympanic canals (Figure 18e).

The dorsoventrally deep descending lamina is a feature of the parabasisphenoid of adult crocodylians. The descending lamina in adult individuals corresponds to the two distinct *posterior projections* in hatchlings (Figure 18i). The posterior projections include the paired dermal ossifications of the embryo (paracochlears in Klembara, 1993). As in the adults, the posterior projections in the hatchlings suture to the basioccipital posteriorly and are separated by the median pharyngeal recess. During the cranial metamorphosis, the posterior projections change their orientation (projecting ventrally), become substantially elongated dorsoventrally and form the descending lamina of the parabasisphenoid.

The *alar processes* project posterolaterally from the body of the parabasisphenoid (Figure 18d,e). The posterior surface of each alar process contacts the ventrolateral process of the corresponding otoccipital and forms the anterior wall of the pharyngotympanic canal (Figure 18e). The lateral surface is sutured to the quadrate dorsally and the pterygoid anteroventrally. The alar process is externally exposed posterior to these contacts (Figure 3). The lateral exposure of the alar processes varies between taxa. The exposure is largest in *G. gangeticus*; it is a notable, anteroposteriorly thick surface compared to that in other crocodylians. The latter is likely the result of the incomplete cranial metamorphosis in *Gavialis* (see also Brochu, 2004; Tarsitano, 1985). The thin lamina of the alar process is well exposed laterally in *A. mississippiensis* and slightly less so in *A. sinensis*, *T. schlegelii* and *O. tetraspis*. *Crocodylus* spp. has the least exposed surface.

The alar processes are already present in hatchlings of crocodylians (Figure 18h,i; contra Brochu, 2004), in which they are mostly horizontal and project posterolaterally. The alar processes include the dermal embryonic basitemporals (Klembara, 1993). During the

cranial metamorphosis, the alar processes project ventrally and become substantially elongated dorsoventrally.

4.8 | Basioccipital

The basioccipital corresponds to the posterior ossification of the embryonic basal plate. In hatchlings, the basioccipital is flat and plate-like (Figure 20h–j). It is broadly exposed on the ventral surface of the braincase, posterior to the parabasisphenoid. In hatchlings, the ventral surface of the basioccipital faces posteroventrally (Figure 20j,k). Along with the parabasisphenoid, the basioccipital of crocodylians undergoes a major change during the first few years of life (cranial metamorphosis sensu Tarsitano, 1985; see also Section 4.7). The basioccipital of adult crocodylians is substantially verticalized (Figure 20c–e). It is barely visible on the ventral surface of the braincase and mainly faces posteriorly. Notably, the basioccipital of *G. gangeticus* is also verticalized and faces posteriorly (Figure 7b). This suggests that the cranial metamorphosis occurs to some degree in *Gavialis* during its post-hatchling development.

The basioccipital of crocodylians forms the posterior part of the basicranium and almost the entire occipital condyle. It may be subdivided into the following portions: (1) the endocranial surface; (2) the basioccipital plate and (3) the occipital condyle itself. The basioccipital forms the posterior part of the floor of the endocranial cavity. The *endocranial surface* of the basioccipital is dorsally concave and delimited on either side by the continuous facets for the otoccipitals (Figure 20g). The anterior margins of the basioccipital contribute to the floor of the cochlear recess (its lagenar portion) along with the parabasisphenoid (Figure 20d,g). The basioccipital of crocodylians forms the ventral margin of the foramen magnum (Figure 4). The rounded *occipital condyle* is offset posteriorly on a short neck.

The *basioccipital plate* projects ventrally and forms the transversely broad but anteroposteriorly thin process (Figure 20c–e). Anteriorly, the basioccipital plate is sutured to the descending lamina of the parabasisphenoid. The posterior surface of the basioccipital forms the ventral part of the posterior (occipital) aspect of the skull. The anteroposteriorly narrow *basioccipital tuberosities* extend across the lateral and ventral margins of the basioccipital plate (Figure 20c). The basioccipital tuberosities of crocodylians correspond to the paired basal tubera of other diapsids and serve for the attachment of hypaxial cervical muscles (Iordansky, 1973; Nesbitt, 2011; Snively & Russell, 2007; Tsuihiji, 2010). A narrow *median crest* usually extends vertically and joins the basioccipital tuberosities ventrally (Figures 20c and 21). The basioccipital plate of *G. gangeticus* is robust, anteroposteriorly thick and has two pendulous basioccipital tuberosities (Figure 21i). One or two small foramina usually pierce the posterior surface of the basioccipital plate ventral to the occipital condyle (Figure 20f). These openings are for the passage for small occipital veins (Owen, 1850). The precondylar part of the

basioccipital plate is hollowed out by the *basioccipital pneumatic recess* (Figure 21). Anteriorly, the basioccipital plate forms the posterior walls of the pharyngotympanic canals and the median pharyngeal canal.

4.9 | Quadrate

The quadrate represents the principal splanchnocranial element of the crocodylian braincase. It is highly modified in crocodylians compared to those in other diapsids (see Section 4.2). The fully formed quadrate is a complex ossification. Almost the entire palatoquadrate cartilage ossifies as the quadrate in crocodylians (Klembara, 2004). A separate epipterygoid (which generally includes the anterior part of the palatoquadrate cartilage in most diapsids) in the orbitotemporal region of the braincase is absent; the corresponding portion of the palatoquadrate cartilage is included into the quadrate and the laterosphenoid in adult crocodylians (Holliday & Witmer, 2008, 2009; Klembara, 2004). In addition, a separate dermal embryonic anlage (*lamina palatoquadrati anterior*) corresponds to the anteromedial process of the fully formed quadrate of extant crocodylians (Klembara, 2004).

The quadrate of crocodylians undergoes substantial changes during post-hatchling development. In hatchlings, the main body of the quadrate is relatively short anteroposteriorly (Figure 22g–i). The mandibular condyles lie at the same level as the occipital condyle both in posterior and dorsal views. The ventrolateral surface of the quadrate is relatively smooth. In adults, the main body of the quadrate is considerably elongated (Figure 22c–f). The mandibular condyles are posteriorly displaced in adults: they lie at the same level as the occipital condyle in posterior view, but project posteriorly beyond the occipital condyle in dorsal view (Figures 4 and 6). The verticalization of the basicranium affects the conformation of the quadrate and its contacts with the parabasisphenoid and the pterygoids as well as the alignment of the jaw adductor muscles (Tarsitano, 1985). Our examination of an ontogenetic sample for *A. mississippiensis*, *C. crocodilus*, *C. niloticus* and *O. tetraspis* (see File S1 for a list of specimens) suggests that the verticalization of the basicranium in crocodylians coincides with “folding” of the pterygoid process of the quadrate. The fold corresponds to the prominent muscular crest B on the lateral surface of the quadrate in adult crocodylians, which is absent in hatchlings and weakly developed in juvenile and subadult individuals (compare Figure 22e,h).

The quadrate may be subdivided into the following main parts: (1) the head and the otic process; (2) the anterodorsal process; (3) the anteromedial process; (4) the pterygoid process; (5) the posterodorsal process and (6) the main body of the quadrate and the mandibular condyles.

A short posterodorsally arched *otic process* terminates in the rounded *quadrate head* (Figure 22c,g). These are endochondrally ossifying structures that directly correspond to the quadrate head of other diapsids (Klembara, 2004; Walker, 1990). The otic process and the quadrate head form a continuous suture with the prootic buttress medially and abut against the ventral surface of the

squamosal (Figure 22c,f). Posteriorly, they form the anterior margin of the postquadrate foramen for the passage of the temporoorbital vessels (Figures 3, 5 and 22c; see Section 4.2). The otic process is incised posteriorly (=otic incisure) and forms the rounded anterior margin of the external auditory meatus (Figure 22c,g; Montefeltro et al., 2016). The quadrate head is covered with cartilage and forms the synovial (but immobile) otic joint (Holliday & Witmer, 2008).

Anterior to the quadrate head and the otic process, the *anterodorsal process* is present (Figure 22c,e,g). This process forms a continuous straight joint with the squamosal, abutting and suturing to its ventral surface. The anterodorsal process forms the lateral margin of the supratemporal fossa. It anchors the quadrate over the skull roof, a condition developed relatively early in the evolution of Crocodylomorpha (Walker, 1990; Wu & Chatterjee, 1993).

A dorsoventrally deep and anteroposteriorly short process extends anteriorly from the otic process and the main body of the quadrate. It forms the medial and posterior walls of the temporal fossa and is here termed the *anteromedial process* (Figure 22e,h). The anteromedial process participates in the orbitotemporal region of the crocodylian braincase. It encloses the trigeminal fossa laterally and dorsally and forms the posterior margin of the *maxillomandibular foramen* (for CN V_{II}-V_{III}). It sutures to the laterosphenoid body anteriorly, the lateral lamina of the prootic medially and the parietal dorsally. The muscular crest A' extends along the lateral surface of the anteromedial process (Holliday & Witmer, 2007, 2009; Lordansky, 1964, 1973). The anteromedial process has an embryonic origin separate from that of the quadrate head, corresponding to a specific dermal ossification of the embryo (lamina palatoquadrati anterior) that is absent in other extant diapsids (Klembara, 2004).

The *pterygoid process* projects ventrally from the main body of the quadrate (Figure 22e,h). It merges with the anteromedial process anteriorly and forms the ventral margin of the maxillomandibular foramen. The pterygoid process of the quadrate sutures to the ascending process of the pterygoid and to the alar process of the parabasisphenoid ventrally. The posteromedial surface of the pterygoid process forms a continuous contact with the ventrolateral process of the otoccipital below the cranioquadrate passage. The sharp muscular crest B arches posterodorsally on the lateral surface of the pterygoid process (Holliday & Witmer, 2007, 2009; Lordansky, 1964, 1973). Posterior to this crest, there is a prominent depression.

The *main body of the quadrate* constitutes the major part of the quadrate in adult crocodylians (Figure 22c). It has a continuous facet for the quadratojugal along its anterior margin. The main body terminates distally in the quadrate condyles for the jaw joint. In crocodylians, the lateral condyle is larger than the medial (Figure 22d).

The main body of the quadrate forms the ventral border of the external auditory meatus. Here, a small process projects from the main body medially (Figure 22c,g). This process was termed the *otic buttress* by Montefeltro et al. (2016). The otic buttress sutures to the ventrolateral process of the otoccipital at the region where the ventrolateral process merges with the extracapsular buttress (see Section 4.5). The otic buttress of the quadrate forms the posteroven-tral margin of the external auditory meatus. A soft-tissue suspensory

plate attaches to the otic buttress ventrally; this plate divides the complex otic aperture of crocodylians into the anterior external auditory meatus ("true ear passage") and posterior neurovascular passages for the stapedia vessels and CN VII_{hyo} (Montefeltro et al., 2016; see Section 4.2). Thus, the otic buttress is the osteological correlate for the subdivision of the external ear of crocodylians.

The *posterodorsal process* of the quadrate projects dorsally from the main body (Figure 22c,d,g). It sutures to the descending process of the squamosal dorsally and to the distal tip of the paroccipital process posteromedially. These contacts enclose the meatal chamber of crocodylians posteriorly (Montefeltro et al., 2016; Pol et al., 2013). The cranioquadrate passage corresponds to a groove on the posteromedial surface of the quadrate that extends between the posterodorsal and the pterygoid processes (Figure 22f,i). The anterior margin of the posterodorsal process forms the incisure of the cranioquadrate passage that is visible within the meatal chamber (Figures 5 and 22c,g) (Montefeltro et al., 2016).

Several pneumatic recesses invade the quadrate of crocodylians. There are two principal pneumatic diverticula within the quadrate—the more anterior *infundibular diverticulum* and the more posterior *quadrate diverticulum* (Dufeu & Witmer, 2015; see Section 4.10). These pneumatic diverticula leave corresponding pneumatic recesses within the ossified quadrate (Figure 23). The medial surface of the quadrate has a large depression (pharyngotympanic fossa) that corresponds to the wall of the spacious pharyngotympanic (middle ear) cavity (Figure 22f,i). The internal pneumatic recesses communicate with the pharyngotympanic cavity by corresponding foramina on the medial surface of the quadrate (Figure 23). The *subtympanic foramen* lies anteroventral to the external auditory meatus in most crocodylians (Figure 22c,g) (Lordansky, 1973; Montefeltro et al., 2016). It serves for the lateral communication between the internal infundibular recess and the pharyngotympanic cavity (Figure 23). The quadrate diverticulum has a long *siphonium* that extends posteriorly over the entire length of the main body of the quadrate (Figure 23). The external opening of this siphonium lies near the medial condyle of the quadrate (Figure 22d). This foramen is dorsally displaced in alligatoroids (Brochu, 1999).

4.10 | Paratympanic pneumaticity

The braincase of extant crocodylians is invaded by a complex system of paratympanic pneumatic diverticula (Figures 24–27). These diverticula arise as evaginations of the pharyngeal epithelium during embryonic development and can be grouped into two distinct systems: (1) the pharyngotympanic sinus (=tympanic or middle ear cavity) and its outgrowth and (2) the median pharyngeal sinus (Dufeu & Witmer, 2015). Later during ontogeny, the two sinus systems tend to develop secondary diverticula and become largely confluent. This results in the complex system of pneumatic paratympanic cavities that penetrate most of the braincase elements and communicate with each other. Several studies have described aspects of the anatomy and ontogeny of the paratympanic pneumaticity in present-day

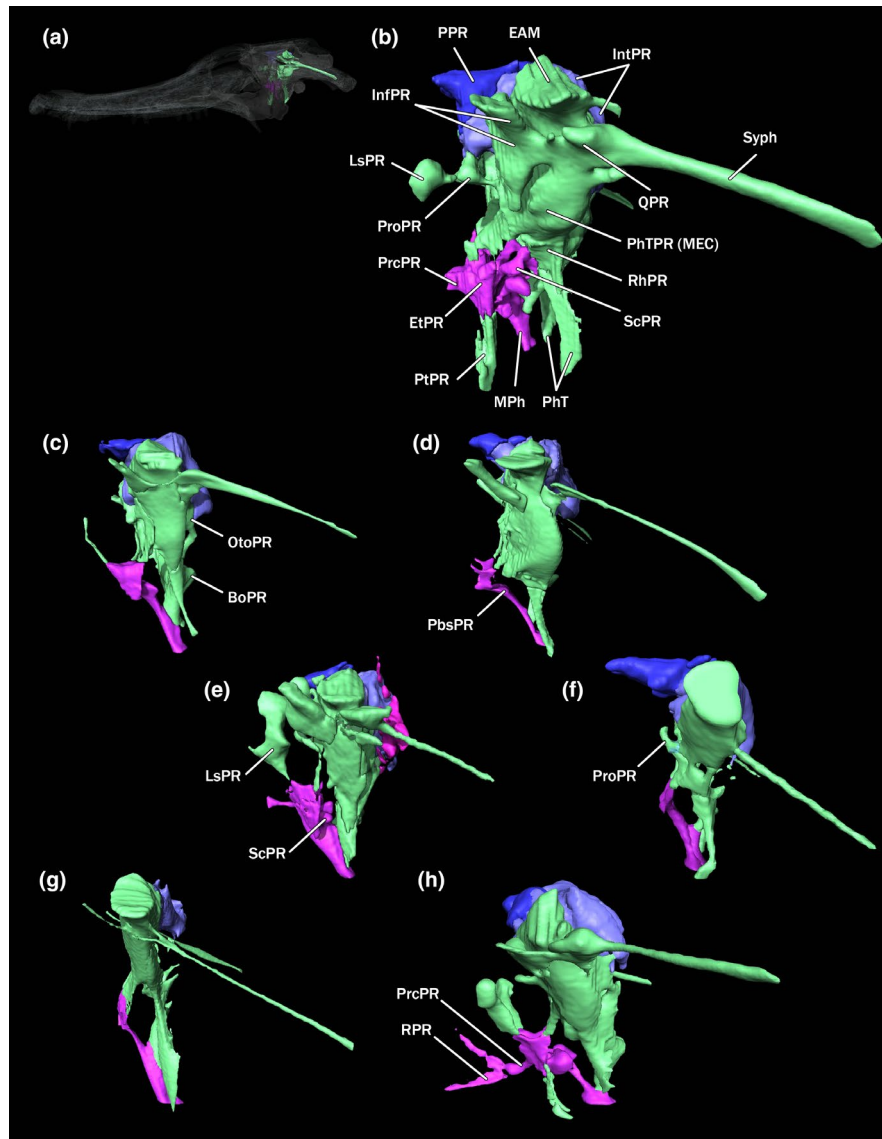


FIGURE 24 Anatomy of the paratympanic pneumatic system of crocodylians in left lateral view. (a) Inset showing the region of interest on *Alligator mississippiensis* (DVZ M 4/13, rendered semitransparent). (b) *A. mississippiensis* (DVZ M 4/13); (c) *Mestrops cataphractus* (DVZ M 6/13); (d) *Crocodylus novaeguineae* (DVZ M 9/13); (e) *Osteolaemus tetraspis* (DVZ M 7/13); (f) *Gavialis gangeticus* (ZIN 7249); (g) *Tomistoma schlegelii* (ZMMU MSU R-13859); (h) *Caiman yacare* (ZMMU MSU R-6967). BoPR, basioccipital recess; EAM, external auditory meatus; EtPR, recessus epitubaricus; InfPR, infundibular recess; IntPR, intertympanic recess; LsPR, laterosphenoid recess; MPh, median pharyngeal canal; OtoPR, otoccipital recess; PbsPR, parabasisphenoid recess; PhT, pharyngotympanic canal; PhTPR, pharyngotympanic (middle ear) cavity; PPR, parietal recess; PrcPR, precarotid pneumatic recess; ProPR, prootic facial recess; PtPR, pterygoid recess; QPR, quadrate recess; RhPR, rhomboidal recess; RPR, rostral recess; ScPR, subcarotid recess; Syph, siphonium. Not to scale

crocodylians and in extinct crocodylomorphs (e.g. Brusatte et al., 2016; Busbey & Gow, 1984; Colbert, 1946; Crompton & Smith, 1980; Dufeu & Witmer, 2015; Herrera et al., 2018; Lordansky, 1973; Leardi et al., 2020; Owen, 1850; Pierce et al., 2017; Serrano-Martínez et al., 2019; Tarsitano, 1985; Walker, 1990; Wu & Chatterjee, 1993). Here, we provide additional data from a broader sample of extant taxa. The nomenclature of various pneumatic recesses is especially complicated and controversial—see Table 2 and File S2 for the terminological approach used in this study.

The epithelial evaginations of the pharynx start to invade and hollow out the elements of the braincase in the mid-late

embryonic stages of crocodylians, in about 58- to 60-day-old embryos (Klembara, 2004, 2005; Müller, 1967; our examination of the CT scan data for embryos of *C. niloticus* from Beyrand et al., 2019). The paratympanic pneumatic system is mostly developed in perinatal and juvenile individuals of crocodylians prior to the cranial metamorphosis sensu Tarsitano (1985). The pneumatic recesses tend to decrease in size and in the number of interconnections during ontogeny (Dufeu & Witmer, 2015). The pneumatic recesses comprise a substantial volume of the braincase in all studied hatchling and juvenile specimens of crocodylids (*Crocodylus*, *Osteolaemus*) and alligatorids (*Alligator*, *Caiman*, *Paleosuchus*). Several pneumatic recesses (e.g.

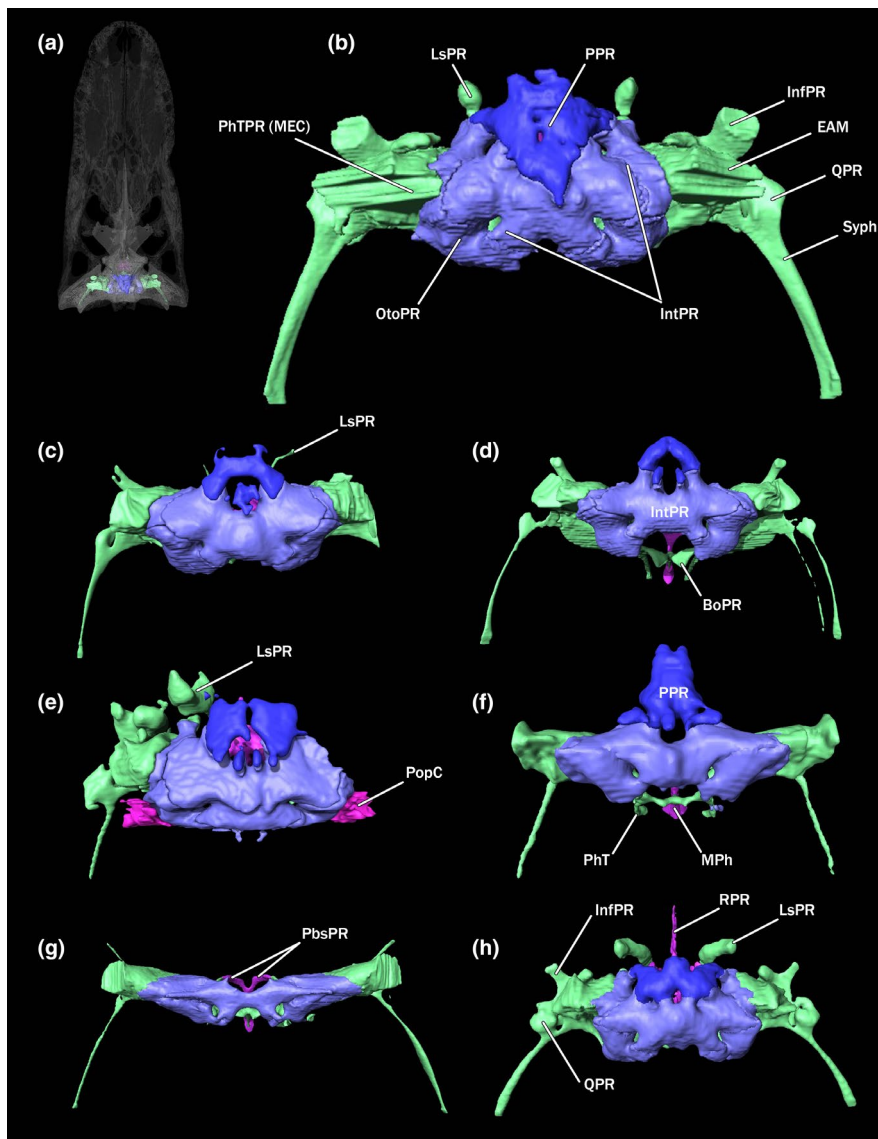


FIGURE 25 Anatomy of the paratympanic pneumatic system of crocodylians in dorsal view. (a) Inset showing the region of interest on *Alligator mississippiensis* (DVZ M 4/13; rendered semitransparent). (b) *A. mississippiensis* (DVZ M 4/13); (c) *Mecistops cataphractus* (DVZ M 6/13); (d) *Crocodylus novaeguineae* (DVZ M 9/13); (e) *Osteolaemus tetraspis* (DVZ M 7/13); (f) *Gavialis gangeticus* (ZIN 7249); (g) *Tomistoma schlegelii* (ZMMU MSU R-13859); (h) *Caiman yacare* (ZMMU MSU R-6967). BoPR, basioccipital recess; EAM, external auditory meatus; InfPR, infundibular recess; IntPR, intertympanic recess; LsPR, laterosphenoid recess; MPh, median pharyngeal canal; OtoPR, otoccipital recess; PbsPR, parabasisphenoid recess; PhT, pharyngotympanic canal; PhTPR, pharyngotympanic (middle ear) cavity; PopC, paroccipital cavity; PPR, parietal recess; QPR, quadrate recess; RPR, rostral recess; Syph, siphonium. Not to scale

the prootic facial, pterygoid, infundibular and quadrate recesses) are present and relatively voluminous in the examined hatchlings and juveniles of *C. niloticus* but are greatly reduced or absent altogether in all studied adults of the same species. In large skulls of *A. mississippiensis* (e.g. DVZ M 5/13, OUV 9761), the pneumatic recesses and communication between them tend to become obliterated, frequently in an asymmetrical manner (e.g. present on one side of the cranium but closed on the other). One large skull of *C. niloticus* (RVC-JRH-FNC7) has an almost completely obliterated paratympanic system, with only the narrow median pharyngeal canal, the intertympanic recess and the recessus epitubaricus persisting. Pneumatic recesses from both sides of this specimen communicate only via the

reduced intertympanic recess dorsally; there are no ventral connections. These observations, along with the detailed study of the ontogeny of the paratympanic sinuses in *A. mississippiensis* (Dufeu & Witmer, 2015), suggest that the pneumatic system changes continuously throughout the ontogeny in crocodylians. However, despite the ontogenetic and intraspecific variability, there are some consistently observed patterns of the pneumatic sinuses that characterize certain crocodylian taxa (see Section 5).

The *median pharyngeal recess* invades the parabasisphenoid of crocodylians (Figures 19 and 24–27); it may also contribute to the formation of the basioccipital recess (see below). It develops as the median dorsal outgrowth of the pharyngeal epithelium at

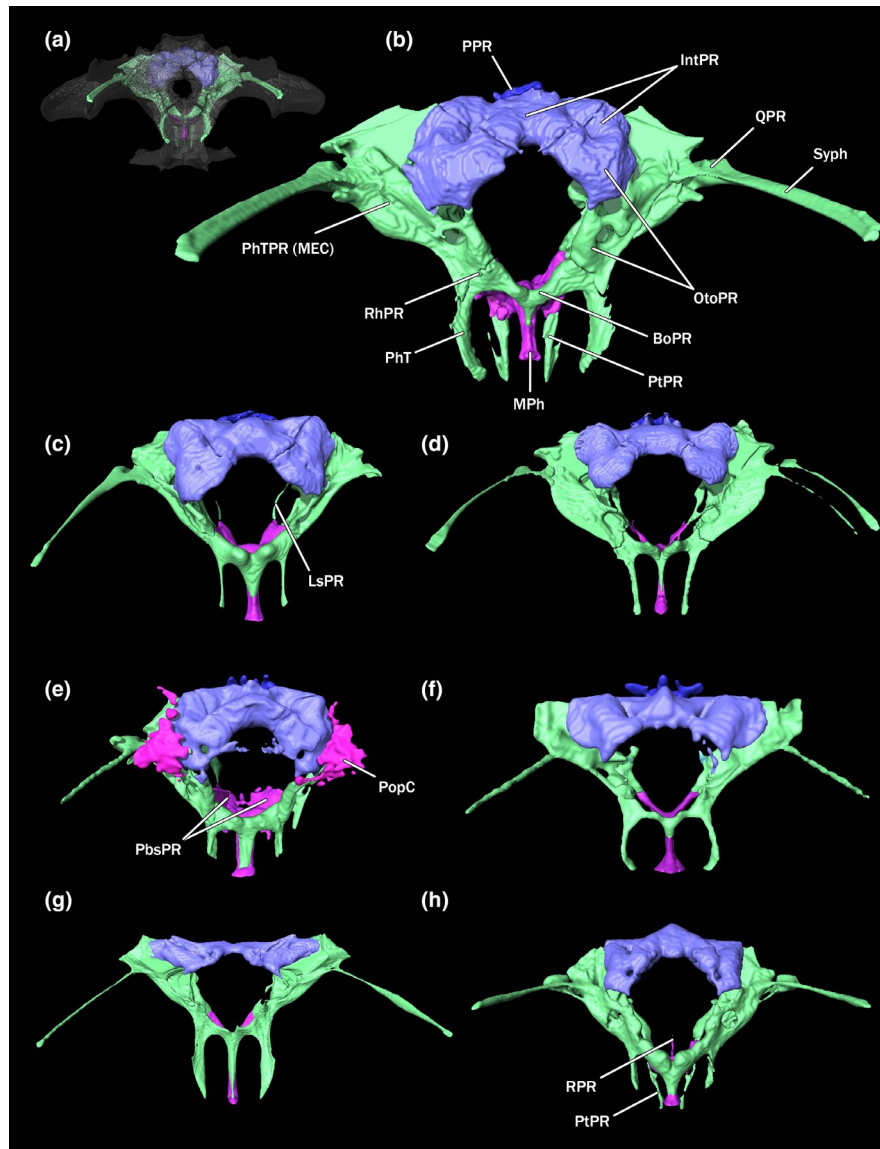


FIGURE 26 Anatomy of the paratympanic pneumatic system of crocodylians in posterior view. (a) Inset showing the region of interest on *Alligator mississippiensis* (DVZ M 4/13; rendered semitransparent). (b) *A. mississippiensis* (DVZ M 4/13); (c) *Mecistops cataphractus* (DVZ M 6/13); (d) *Crocodylus novaeguineae* (DVZ M 9/13); (e) *Osteolaemus tetraspis* (DVZ M 7/13); (f) *Gavialis gangeticus* (ZIN 7249); (g) *Tomistoma schlegelii* (ZMMU MSU R-13859); (h) *Caiman yacare* (ZMMU MSU R-6967). BoPR, basioccipital recess; IntPR, intertympanic recess; LsPR, laterosphenoid recess; MPH, median pharyngeal canal; OtoPR, otoccipital recess; PbsPR, parabasisphenoid recess; PhT, pharyngotympanic canal; PhTPR, pharyngotympanic (middle ear) cavity; PopC, paroccipital cavity; PPR, parietal recess; PtPR, pterygoid recess; QPR, quadrate recess; RhPR, rhomboidal recess; RPR, rostral recess; Syph, siphonium. Not to scale

about 60–61 days of individual development (Dufeu & Witmer, 2015; Müller, 1967; our study of CT scan dataset for embryos of *C. niloticus* from Beyrand et al., 2019). The median pharyngeal recess can be further subdivided into the median pharyngeal canal (=median Eustachian canal or tube), the paired lateral parabasisphenoid recesses (=lateral branches of the anterior communicating canal of the median Eustachian tube), and the central part formed at the junction of the aforementioned recesses (=anterior communicating canal of the median Eustachian tube) (Figure 27). The *median pharyngeal canal* opens on the ventral surface of the braincase through the *median pharyngeal foramen* between the parabasisphenoid and the basioccipital

(Figure 7b). Posterodorsally, the canal is confluent with the basioccipital recesses in adult crocodylians (Figure 24). Two separate median pharyngeal canals and external foramina (into the parabasisphenoid anteriorly and the basioccipital posteriorly) are present in some but not all examined caimanine specimens (e.g. *Caiman*, *Paleosuchus*; see also Brochu, 1999). The median pharyngeal canal becomes substantially verticalized during the cranial metamorphosis in all crocodylian taxa except for *G. gangeticus* (Dufeu & Witmer, 2015; Gold et al., 2014; Tarsitano, 1985). The *parabasisphenoid recesses* are paired pneumatic cavities that invade the body of the parabasisphenoid. They are located ventral to the canals of the cerebral carotid arteries and posterior to the

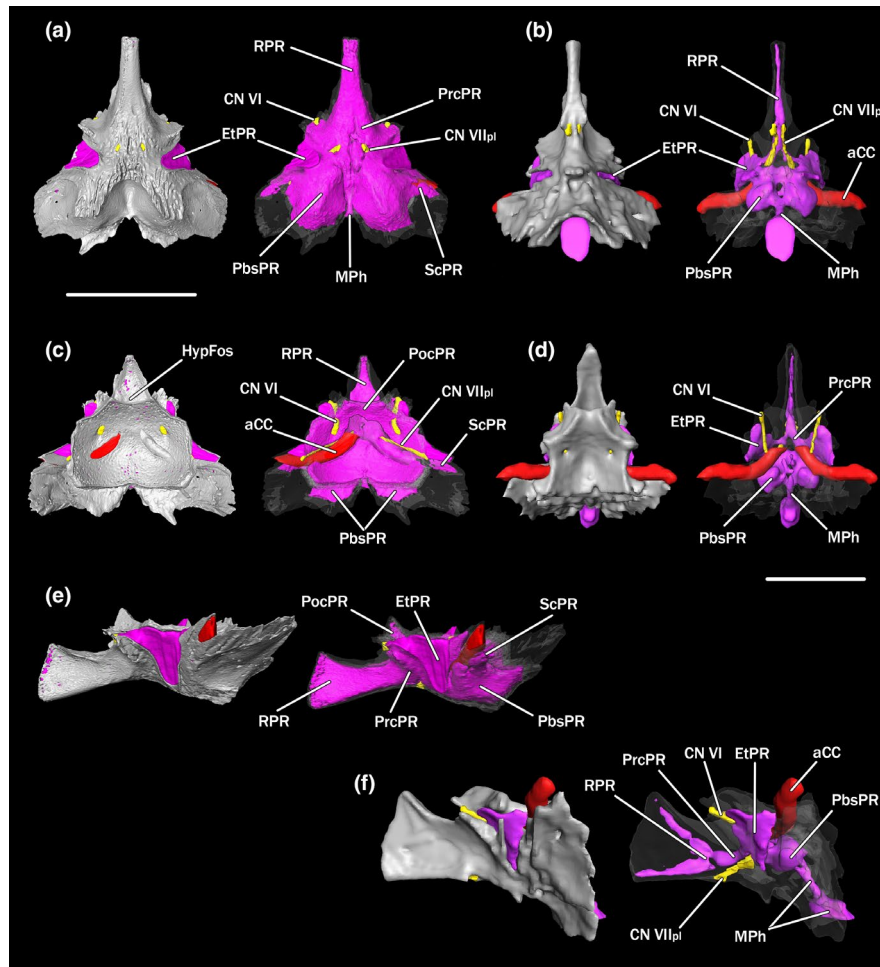


FIGURE 27 Anatomy of the median pharyngeal recess of crocodylians. (a, c, e) Parabisphenoid of hatchling *Caiman crocodilus* (PIN comparative collection, unnumbered) in (a) ventral, (c) dorsal and (e) left lateral views. (b, d, f) Parabisphenoid of adult *Caiman yacare* (ZMMU MSU R-6967) in (b) ventral, (d) dorsal and (f) left lateral views. Each pair comprises CT-based models of non-transparent skeletal element and semitransparent element with digital endocasts of relevant neurovascular and pneumatic structures. aCC, cerebral carotid artery; CN VI, abducens nerve; CN VII_{pl}, palatine branch of the facial nerve; EtPR, pneumatic recess epitubaricus; HypFos, hypophyseal fossa; MPh, median pharyngeal pneumatic canal; PbsPR, parabisphenoid pneumatic recess; PocPR, postcarotid pneumatic recess; PrcPR, precarotid pneumatic recess; RPR, rostral pneumatic recess; ScPR, subcarotid pneumatic recess. Left scale bar (for a, c, e) equals 5 mm; right scale bar (for b, d, f) equals 1 cm

course of CN VII_{pl} (Figures 19 and 27). Each parabisphenoid recess communicates medially with its counterpart and laterally with the pharyngotympanic cavity via the recessus epitubaricus (Figures 19, 24b and 27). Among studied taxa, the median pharyngeal recess appears narrow and reduced in *G. gangeticus*, *T. schlegelii* and *Crocodylus* spp. (Figure 24d,f,g).

The median pharyngeal recess of some crocodylian taxa has additional anterior and posterior continuations. The anterior continuations correspond to the rostral, precarotid and postcarotid recesses (Leardi et al., 2020; Walker, 1990). These recesses are present in the studied embryos and hatchlings (e.g. *A. mississippiensis*, *C. crocodilus*, *C. niloticus*, *P. palpebrosus* and *O. tetraspis*) but are usually greatly reduced or absent in adult individuals (Figures 24 and 27). The postcarotid recess was not found in any studied subadult or adult individual of all studied taxa. The precarotid and rostral recesses were observed in adults of only five examined taxa (*A. mississippiensis*, *C. crocodilus*, *C. yacare*, *P. palpebrosus* and *O. tetraspis*) (Figure 24b,e,h).

The *postcarotid recesses* are anterodorsal continuations of the median pharyngeal recess; they inflate the dorsum sellae of the parabisphenoid posterodorsally to the hypophyseal fossa and dorsally to the cerebral carotid arteries (Figure 27c,e). In all examined embryos and hatchlings, the postcarotid recesses are paired dorsomedial diverticula that do not connect medially. A single studied hatchling of *C. crocodilus* (PIN unnumbered) is a notable exception, in which the postcarotid recess inflates the dorsum sellae as a single continuous recess (Figure 27c,e). The *precarotid recesses* are anteroventral continuations of the median pharyngeal recess; they are located anterior to the course of CN VII_{pl} and ventral to the hypophyseal cavity and cerebral carotid arteries (Figures 24b,h and 27). The precarotid recesses are paired (not connected medially) and short in *A. mississippiensis* (in both hatchlings and adults) and in *Crocodylus niloticus* (only in embryos and hatchlings but absent in adults). In *C. crocodilus*, *C. yacare*, *P. palpebrosus* and *O. tetraspis*, the precarotid recesses are connected anteriorly, ventrally to the hypophyseal fossa, and form

the *rostral recess* that inflates the rostrum of the parabasisphenoid (Figures 19, 24e,h and 27).

In addition, the median pharyngeal recess has paired posterior continuations (*subcarotid recesses*) in some taxa (e.g. *A. mississippiensis*, *C. crocodilus*, *O. tetraspis*) (Figures 19a,b,24b,e and 27a,c,e). Each subcarotid recess extends from the corresponding parabasisphenoid recess posterodorsolaterally and inflates the dorsal part of the alar process of the parabasisphenoid. It lies ventral to the canal of the cerebral carotid artery and posterior to the recessus epitubaricus and the course of CN VII_{pt} (Figures 24b,e and 27e). The subcarotid recess has been observed in embryos and hatchlings but not in adults of *C. niloticus*; on the other hand, it is consistently found in both hatchlings and adults of *A. mississippiensis*, *C. crocodilus* and *O. tetraspis*.

Each *pharyngotympanic recess (cavity)* comprises the spacious middle ear cavity and its primary outgrowth: (1) the basioccipital recess; (2) the recessus epitubaricus; (3) the prootic facial recess; (4) the intertympanic recess; (5) the otoccipital recess and (6) the infundibular and the quadrate recesses (Figures 24–26). The pharyngotympanic recess excavates corresponding depressions on the lateral surface of the prootic and on the medial surface of the quadrate (pharyngotympanic fossae) (Figures 10g and 22f).

Each pharyngotympanic cavity is formed by the dorsal expansion of the pharyngeal epithelium (Eustachian tube in Owen, 1850; pharyngotympanic tube in Dufeu & Witmer, 2015) at about 58–60 days of individual development (Müller, 1967; our study of CT scan dataset for embryos of *C. niloticus* from Beyrand et al., 2019). In the skull of adult crocodylians, the *pharyngotympanic canals* (=“lateral Eustachian canals”) house extensions of the pharyngeal epithelium (pharyngotympanic tubes) that connect the middle ear cavity with the pharynx (Owen, 1850). The pharyngotympanic canals are enclosed by the basioccipital posteriorly and the parabasisphenoid anteriorly in crocodylians (Figures 18e and 21). They extend ventrally from the floor of each pharyngotympanic cavity (the rhomboidal recess) and open on the ventral surface of the braincase (Figures 24 and 26). The external foramina of the pharyngotympanic canals lie slightly dorsally to the median pharyngeal foramen in most crocodylians. However, the pharyngotympanic foramina are ventrally displaced and lie at the same level with the median pharyngeal foramen in several species of *Crocodylus* (Brochu, 1999: character 147).

The *basioccipital recess* inflates the basioccipital plate anterior to the occipital condyle and basioccipital tuberosities (Figure 21), as in other crocodylomorphs (Leardi et al., 2020). In adults, the recess comprises three parts: two symmetrical lateral cavities (=lateral branches of the posterior communicating canal of the median Eustachian tube) that communicate laterally with the corresponding pharyngotympanic cavities via the rhomboidal recess and the central connection between them and with the median pharyngeal recess anteriorly (Figures 21, 24 and 26). According to Dufeu and Witmer (2015), the basioccipital recesses arise as paired medial outgrowths from each pharyngotympanic cavity in hatchlings of *A. mississippiensis*; the connection with each other and with the median pharyngeal recess develops only later in ontogeny. However,

the data on the development of *M. cataphractus* from Müller (1967) and our examination of the CT scan data of embryos and hatchlings of *C. niloticus* from Beyrand et al. (2019) suggest that the median pharyngeal recess also contributes to the development of the central part of the basioccipital recess early in ontogeny, at least in these two taxa. Overall, the basioccipital pneumatic recess appears in crocodylians several days after the median pharyngeal recess, at about 63–65 days of individual development, as compared to 60–61 days for the median pharyngeal recess (Müller, 1967; CT scan dataset for embryos of *C. niloticus* from Beyrand et al., 2019). In the studied embryos of *C. niloticus*, the basioccipital recess is already connected to the pharyngotympanic cavities and to the median pharyngeal recess as early as the basioccipital recess itself could be clearly identified (at around 67 days of individual development). Moreover, the studied hatchlings of *C. crocodilus*, *P. palpebrosus* and *O. tetraspis* have developed connections of the basioccipital recess with both aforementioned recesses. In non-crocodyliform crocodylomorphs (e.g. *Almadasuchus*, *Dibothrosuchus* and *Sphenosuchus*), the paired basioccipital recesses are connected to the median pharyngeal recess (called sub-basisphenoid recess) but lack any direct communication with the pharyngotympanic cavity/rhomboidal recess (Leardi et al., 2020; Walker, 1990; Wu & Chatterjee, 1993). These data suggest that the basioccipital recess of crocodylians has a complex development and is, at least partially, derived from the median pharyngeal system. Additional data on the early development of the paratympanic pneumaticity in other crocodylian taxa are needed to establish possible intra- and interspecific variability of these features.

Laterally on both sides of the skull, the basioccipital recess merges with the pharyngotympanic cavity and the corresponding pharyngotympanic canal (Figures 21 and 26). The resulting expanded pneumatic space at the base of the pharyngotympanic cavity was termed the *rhomboidal recess* (Leardi et al., 2020; Owen, 1850; Tarsitano, 1985; Walker, 1990). It is located immediately ventral to the canal of the cerebral carotid artery, the anteroventral process and the extracapsular buttress of the otoccipital (Figures 13f and 15b). The rhomboidal recess is bounded by the basioccipital ventrally, the otoccipital dorsally and posteriorly and the alar process of the parabasisphenoid anteriorly and laterally. Iordansky (1973) confused the rhomboidal recess with the recessus epitubaricus.

The *recessus epitubaricus* is another expanded pneumatic space at the base of the pharyngotympanic cavity. It is located anterior to the rhomboidal recess; the two recesses are separated by the entrance of the cerebral carotid artery into the parabasisphenoid (Figures 19, 24 and 27). It is bounded by the parabasisphenoid medially and posteriorly and by the pterygoid and the lateral lamina of the prootic anteriorly and laterally. The recessus epitubaricus develops as the anteroventral extension of the pharyngotympanic sinus (Dufeu & Witmer, 2015). In adults, each recessus epitubaricus connects with the corresponding pharyngotympanic cavity posterodorsally and is broadly confluent with the parabasisphenoid recess medially (Figures 19, 24 and 27). In addition, it communicates with the laterosphenocephalic recess dorsally and the pterygoid recess ventrally in some

crocodylians (e.g. *A. mississippiensis*, *Caiman yacare*, *O. tetraspis* and *M. cataphractus*) (Figure 24).

The *pterygoid recess* appears as the ventral outgrowth of the recessus epitubaricus in some crocodylians (Figure 24). It excavates the ascending processes of the pterygoids and is usually separated from the paranasal pneumatic cavities. The pterygoid recess was observed in most studied hatchling crocodylians (e.g. *A. mississippiensis*, *Caiman crocodylus*, *C. niloticus*, *O. tetraspis* and *P. palpebrosus*) but is consistently greatly reduced or absent in adult *G. gangeticus* and crocodylids (e.g. *Crocodylus* spp., *M. cataphractus*, *T. schlegelii*). In these taxa, only a small remnant (a few millimetres in length) of the pterygoid recess is occasionally preserved. The pterygoid recess tends to be present in extant alligatorids (having not been found in only one of six analysed specimens of *C. crocodilus*, in two of three studied specimens of *A. sinensis*, and not observed in studied individuals of *P. palpebrosus* and *M. niger*); it is consistently present in adults of *A. mississippiensis*.

The *laterosphenoid recess* invades the body of the laterosphenoid of some crocodylians (Figures 9, 24 and 25). The laterosphenoid recess is connected either to the recessus epitubaricus ventrally or the prootic facial recess posteriorly (Figure 24). Both these recesses are likely candidates as the source of the origin of the laterosphenoid recess. The recess is present and large in most alligatorids (e.g. *Alligator* spp., *Caiman* spp., *Paleosuchus* spp.) and osteolaemines (*O. tetraspis* and the extinct *V. robustus*). The laterosphenoid recess is greatly reduced or absent in most crocodylids (e.g. *Crocodylus* spp., *M. cataphractus*, *T. schlegelii*) and in *G. gangeticus*. Large resorption cavities frequently persist in the corresponding area in the adults of these taxa.

The *prootic facial recess* excavates the anterior superior process of the prootic just anterior to the vestibular recess of the otic capsule and anterodorsal to the CN VII canal (Figures 11 and 24). It communicates via a corresponding foramen with the pharyngotympanic cavity posteriorly (Figure 10d). In some taxa (e.g. *Alligator* spp., *C. crocodilus*, *O. tetraspis*), the prootic facial recess also connects to the intertympanic recess dorsally (Figure 24b). The prootic facial recess has been observed in all studied hatchlings but it is consistently absent in adults of *Crocodylus* spp., *M. cataphractus* and *T. schlegelii*. Large resorption cavities frequently persist in the corresponding area in the adults of these taxa. Rare interspecific variability was also documented: the prootic recess was greatly reduced or absent in a single examined specimen each of *C. crocodilus*, *G. gangeticus* and *P. palpebrosus* in our sample (see File S1 for the list of specimens).

The *intertympanic recess* is a prominent feature of the crocodylian braincase. This pneumatic space invades the prootics and the supraoccipital and connects both pharyngotympanic cavities dorsally (Figures 11, 17, 24 and 25). The intertympanic recess is developed just dorsal to the otic portions of the prootic and the supraoccipital (Figures 10d,e,11 and 16d). In adult crocodylians, the intertympanic recess is largely confluent with the otoccipital recess posteriorly (Figure 25). Early in ontogeny, the intertympanic recess develops as paired medial outgrowths of each pharyngotympanic cavity that invade the corresponding prootic, then the

supraoccipital, and subsequently merge with each other (Dufeu & Witmer, 2015; Müller, 1967; our examination of the CT scan dataset for embryos of *C. niloticus* from Beyrand et al., 2019). The development of the intertympanic recess into the prootics on each side of the skull, just dorsolateral to the endolymphatic labyrinth and semicircular canals, begins in 63- to 67-day-old embryos; the midline connection between them within the supraoccipital is not yet present (Müller, 1967; CT scan dataset for *C. niloticus* embryos from Beyrand et al., 2019). In 68- to 70-day-old embryos, the midline connection within the supraoccipital is developed; the intertympanic recess is complete and continuous between both pharyngotympanic cavities (CT scan dataset for *C. niloticus* embryos from Beyrand et al., 2019).

The *parietal recess* arises from the intertympanic recess dorsally (Figures 24 and 25). It is present in all studied crocodylian taxa but is reduced in size in crocodylids. Rare individual variation was also noted: for example, a single specimen of *T. schlegelii* (ZMMU MSU R-13859) lacks the parietal recess (Figure 25g), whereas it is present in two other studied individuals of this taxon (TMM M-6342 and ZMMU MSU R-9296). The parietal pneumatic recess is consistently connected to the supraoccipital portion of the intertympanic recess via two pairs of openings (larger anterolateral and smaller postero-medial foramina; Figures 17 and 25). In alligatorids, there is an additional communication of the parietal recess with the intertympanic recess within the prootics (Figures 11a,b and 25b,h). This results in the presence of six pneumatic foramina on the ventral surface of the parietal in alligatorids versus four pneumatic foramina in crocodylids and *G. gangeticus*. This feature represents a consistent difference between these taxa and is even present in their hatchlings.

The *otoccipital recess* hollows out the otoccipital of crocodylians (Figures 15, 25 and 26). The corresponding epithelial diverticulum arises from the pharyngotympanic cavity ventrally, at the level of the rhomboidal recess (Klembara, 2005; Müller, 1967). It extends upward, envelopes the developing canals of the cerebral carotid artery and the posterior cranial nerves and underlies the extracapsular buttress. In hatchlings and juveniles, the otoccipital recess is a distinct cavity that mostly communicates with the pharyngotympanic recess (Dufeu & Witmer, 2015; our examination of the CT scan dataset for embryos of *C. niloticus* from Beyrand et al., 2019). In adults, the otoccipital recess is indistinguishably confluent with the prootic portion of the intertympanic recess anteriorly, above the extracapsular buttress (Figure 25). It also connects with the supraoccipital portion of the intertympanic recess medially through a separate passage posterior to the otoccipital strut (Figures 13g, 16d and 25). In adult individuals of *Crocodylus* spp., *M. cataphractus* and *G. gangeticus*, the ventral portion of the otoccipital recess (that envelopes the neurovascular canals in hatchlings) is largely reduced and not connected to the rhomboidal recess ventrally (Figure 26d,f,g). In *O. tetraspis*, there are additional large, and supposedly pneumatic, recesses at the bases of the paroccipital processes. However, we have been unable to trace a direct connection to the otoccipital recess so far and tentatively refer to the structure in question as the paroccipital cavity (Figures 25e and 26e).

The *infundibular* and *quadrate recesses* invade the quadrate of crocodylians (Figures 23–26). They originate as distinct lateral diverticula of the pharyngotympanic cavity and largely fuse later during ontogeny (Dufeu & Witmer, 2015). We have consistently observed this connection between the two recesses in the studied embryos, hatchlings and juveniles of all examined taxa and in most adult specimens of *Alligator* spp., *Caiman* spp., *Paleosuchus* spp., *M. niger* and *O. tetraspis* (Figure 23a,b,g,h). Although the feature is certainly age-related and subject to some intraspecific variability, the majority of studied specimens belonging to subadult/adult *Crocodylus* spp., *M. cataphractus* and *T. schlegelii* have separate infundibular and quadrate recesses. In these taxa, the recesses communicate with the pharyngotympanic cavity medially but either do not connect internally within the bone or the internal canal between them is narrow and barely traceable (Figure 23c–f). The individual infundibular and quadrate recesses themselves may be voluminous or strongly reduced; this feature is subject to both inter- and intraspecific variation. Notably, most studied specimens of *G. gangeticus* lack the infundibular recess and subtympanic foramen altogether (Figure 23i,j). The quadrate diverticulum of crocodylians has a posterior continuation that is generally referred to as the siphonium (Brochu, 1999; Dufeu & Witmer, 2015; Iordansky, 1973). The siphonium extends from the quadrate recess and connects the pneumatic recess within the articular with the quadrate diverticulum (Dufeu & Witmer, 2015) (Figures 24–26). We have observed a narrow secondary canal that parallels the siphonium in some specimens (e.g. *Crocodylus novae-guineae* DVZ M 9/13; Figures 25d and 26d).

5 | DISCUSSION

5.1 | Comparison of the braincase anatomy of extant crocodylians: inferences of new potentially phylogenetically informative characters

The braincases of various extant taxa are similar in overall structure and share the unique features that have been long recognized for Crocodylia (see Section 4.2). Iordansky (1973) provided general observations on the variability of the braincase structure within the clade. Clark (1986, 1994) and Brochu (1999, and subsequent analyses) included some characters related to the braincase in their phylogenetic analyses of crocodylomorphs and crocodylians. However, detailed patterns of variation of the braincase structure have been poorly documented to date. Discrete anatomical characters pertaining to the neurocranium, especially to its internal structure, have been insufficiently sampled in previous phylogenetic analyses of Crocodylia. For example, the braincase-related characters constitute only around 10%–12% of the dataset from Brochu (1999). Since that publication, several contributions have significantly improved taxon sampling but have not increased sampling for the braincase-related characters (e.g. Brochu & Storrs, 2012; Narváez et al., 2015). Furthermore, some of the characters (e.g. characters 161, 165 and 167 from the dataset of Brochu & Storrs, 2012) and corresponding

scorings are in need of re-evaluation based on the anatomical data provided in this study.

In the following section, we discuss several new or previously overlooked features of the braincase that have a consistent distribution among studied taxa and are potentially phylogenetically informative. In this study, we only make anatomical comparisons of these features in the studied sample of extant crocodylians; we do not propose synapomorphies for the studied taxa nor compare extant crocodylians to fossil crocodyliforms. A comprehensive phylogenetic analysis with an updated sampling of the braincase characters will be published elsewhere (I. T. Kuzmin, in prep.).

Some features pertain to the orbitotemporal region of the braincase. The prootic–pterygoid contact ventral to the trigeminal fossa is present in *Gavialis*, *Tomistoma* and most studied alligatorids (except possibly *Paleosuchus*) and is consistently absent in crocodylids such as *Crocodylus*, *Mecistops* and *Osteolaemus* (Figure 3). In addition, *Gavialis* and *Tomistoma* differ from all other extant crocodylians in having a larger prootic exposure on the lateral aspect of the braincase, posterior to the trigeminal foramen (Figure 3) (Brochu, 1999; Iordansky, 1973). The development of the laterosphenoid bridge is subject to certain variation, both among and within crocodylian species (see Section 4.3). Despite the observed variability, the contact between the laterosphenoid bridge and the pterygoid is consistently present in alligatorids (e.g. *Alligator*, *Caiman*, *Paleosuchus* and *Melanosuchus*) and in most examined specimens of *Crocodylus* spp. By contrast, *Mecistops*, *Osteolaemus*, *Tomistoma* and *Gavialis* have short lateral bridges that do not contact the pterygoid ventrally (Figures 3 and 9). In *Gavialis*, we observed certain intraspecific variation of this feature (see Section 4.3). The small sample available to the authors (four specimens) warrants additional observations for this taxon.

The sutural pattern on the floor of the temporal canal is variable among present-day crocodylians (Figure 6). Both extant species of *Alligator* have the largest exposure of the prootic buttress on the floor of the temporal canal that separates the supraoccipital and the quadrate (Figure 6b). The exposure of the prootic buttress is smaller in caimanines (e.g. *Caiman*, *Melanosuchus* and *Paleosuchus*), *Mecistops* and *Tomistoma*. In these taxa, the quadrate and the supraoccipital approach and, in some specimens, briefly contact each other. In *Crocodylus*, *Osteolaemus* and *Gavialis*, the prootic buttress is excluded from the floor of the temporal canal; the supraoccipital and the quadrate contact each other extensively (Figure 6d,e,g). The quadrate–supraoccipital contact is consistently present in *Osteolaemus* and *Gavialis* in our sample. However, this feature is variable in *Crocodylus*: the supraoccipital–quadrate contact has been observed in about half of the sampled individuals; the other specimens have the condition described above for caimanines, *Mecistops* and *Tomistoma*.

The shape of the posterior (occipital) surface of the supraoccipital is also variable (Figure 17). In *Tomistoma* and both extant species of *Alligator*, the postoccipital processes of the supraoccipital protrude further posteriorly than the sagittal nuchal crest; the

postoccipital processes and the sagittal crest are widely separated. In crocodylids (except *Tomistoma*), caimanines and *Gavialis*, these three projections merge and then together protrude posteriorly from the occipital surface of the supraoccipital. In the latter taxa, the central part of the supraoccipital that corresponds to the sagittal nuchal crest projects further posteriorly than the lateral postoccipital processes. This feature could be linked to the extensive perichondral ossification of the trabecular component of the supraoccipital (see Section 4.5) and may be correlated to the dorsal exposure of the supraoccipital on the skull table. However, the supraoccipitals of DVZ M 5/13 (*A. mississippiensis*) and ZMMU MSU R-13859 and R-9296 (*T. schlegelii*) are dorsally exposed on the skull table but their sagittal nuchal crest is incipient and barely projects posteriorly. The analysis of this trait would benefit from the application of geometric morphometric techniques to a larger sample of crocodylian supraoccipitals.

Previously, differences in the paratympanic pneumaticity between extant crocodylian taxa have been noted in several studies (Dufeu, 2011; Dufeu & Witmer, 2015; Gold et al., 2014; Serrano-Martínez et al., 2019; Tarsitano, 1985). Dufeu (2011) and Dufeu and Witmer (2015) suggested that the observed variability in the pneumatic sinuses of crocodylians stems from biomechanical constraints imposed by surrounding tissues (e.g. bones, neurovascular structures, muscles) and maintenance of the mechanical integrity of the cranium. These constraints are themselves a function of different ecological niches and varying adaptive responses. We agree with this hypothesis and consider these constraints the proximal mechanisms that shape the paratympanic systems in various crocodylian species. This is most notable in two distantly related crocodylians (the caimanine *Paleosuchus* and the crocodylid *Osteolaemus*), which share remarkably terrestrial habits (Grigg & Kirshner, 2015). Both taxa have dorsoventrally deep skulls and an expanded set of voluminous paratympanic cavities. Whereas other alligatorids share the expanded pneumaticity of the braincase with *Paleosuchus*, the proximal sister taxa of *Osteolaemus* (most crocodylids) do not (Figures 24–26). The reappearance of certain pneumatic cavities in *Osteolaemus* (e.g. laterosphenoid and prootic facial recesses, expanded median pharyngeal recess with its subsequent diverticula—the pre-, post- and subcarotid recesses) can possibly be explained by apomorphic retention of the hatchling pattern in adults. As previously noted, the skulls of hatchlings and juveniles of all crocodylians are more pneumatized than those of the adults. Thus, the definitive pattern of pneumatic cavities in crocodylians is likely the result of phylogenetic heritage, developmental mechanisms, age and biomechanical constraints imposed by ecological niches.

However, patterns of the paratympanic cavities within crocodylians skulls appear to be also phylogenetically informative. Gold et al. (2014) found that geometric morphometrics of the basicranial pneumatic recesses (the median pharyngeal recess + basioccipital recess) are unique for *Gavialis* among extant taxa and reminiscent of those of some distantly related extinct crocodyliforms (see also Brochu, 2004). Gold et al. (2014) and Serrano-Martínez et al. (2019) provided evidence that the paratympanic pneumaticity does provide

distinctions between major crocodylian clades and may prove phylogenetically informative.

Our observations of the paratympanic system show that members of Alligatoridae are characterized by an expanded set of recesses that invade almost all elements of the braincase (Figures 24–26). Alligatorids consistently have the laterosphenoid, prootic facial and pterygoid recesses throughout ontogeny. The interconnections and sizes of the recess are relatively larger in alligatorids compared to those in crocodylids and *Gavialis*. For example, alligatorids consistently have a communication of the parietal recess with the prootic portion of the intertympanic recess; this results in the presence of six pneumatic foramina on the ventral surface of the parietal in alligatorids versus only four such openings in crocodylids and *Gavialis*. The internal cavities of the quadrate (the infundibular and quadrate recesses) consistently maintain connection with each other during ontogeny in alligatorids (Figure 23).

By contrast, the paratympanic pneumatic system in subadult and adult individuals (following the cranial metamorphosis sensu Tarsitano, 1985) of the present-day crocodylids and *G. gangeticus* is reduced compared to that of alligatorids (Figures 24–26). For example, the pterygoid recess and the communication of the parietal recess with the prootic portion of the intertympanic recess are absent in all extant members of Crocodylidae and in *Gavialis*. The laterosphenoid recess and the connection between the infundibular and quadrate recess are absent in *Crocodylus*, *Gavialis*, *Mecistops* and *Tomistoma* (Figure 23). The presence of the two latter pneumatic structures appears to be characteristic of osteolaemines among crocodylids (present in *Osteolaemus* and the extinct *Voay*). The prootic facial pneumatic recess is consistently absent in individuals of *Crocodylus*, *Mecistops* and *Tomistoma* after the cranial metamorphosis, whereas adult osteolaemines and *Gavialis* have this recess (Figure 11).

Some of the characters discussed in this study may prove informative for assessing the still contentious higher level interrelationships among extant crocodylians. The phylogenetic position of *Gavialis* remains problematical (see Section 2.4). Gold et al. (2014) performed cladistic analyses with the inclusion of the geometric morphometric data from crocodylian braincases and arrived at interesting results. The braincase data alone produced the clade composed of *Gavialis* and crocodylids to the exclusion of alligatorids. Moreover, the morphometric data from braincases combined with the molecular and morphological characters supported the preferred molecular topology for Crocodylia (Gold et al., 2014).

Our comparative analysis of the braincase osteology in the present-day Crocodylia revealed several features that are present in *Gavialis* and extant members of Crocodylidae but are absent in alligatorids. These comprise: (1) the reduced pattern of paratympanic pneumatic cavities; (2) the reduced prootic buttress and the occasional presence of the supraoccipital–quadrate contact at the floor of the temporal canal and (3) the characteristic shape of the supraoccipital, with merged postoccipital processes and the sagittal nuchal crest that collectively project posteriorly. In addition, *Gavialis* and *Tomistoma* have the prootic–pterygoid contact ventral to the

trigeminal fossa, a larger lateral exposure of the prootic and a reduced lateral bridge of the laterosphenoid that does not contact the pterygoid ventrally. The inclusion of the aforementioned braincase features in phylogenetic analyses of Crocodylia could affect the position of *Gavialis* and reconcile the competing hypotheses based on morphological and molecular characters in the future.

5.2 | Evo-devo insights into the braincase anatomy of crocodylians

Extant crocodylians have a unique anatomy of the braincase among diapsids: (1) a synovial basipterygoid joint is absent and the basicranium is tightly sutured to the pterygoids; (2) the quadrate is strongly inclined anteromedially and sutured to most elements of the neurocranium and (3) the otoccipitals have distinct ventrolateral processes that conceal the posterior neurovascular structures in the bony canals and further consolidate the cranium (see Section 4.2). From a phylogenetic perspective, these anatomical features of the crocodylian braincase evolved relatively rapidly at the base of Crocodylomorpha (Busbey & Gow, 1984; Clark, 1986; Clark et al., 2004; Herrera et al., 2018; Leardi et al., 2017, 2020; Pol et al., 2013; Walker, 1990; I. T. Kuzmin, unpubl. data). The evolution of the kinetic and rigid skull is associated with the early diversification of crocodylomorphs during the Mesozoic, and it was likely linked to the development of various modes of food acquisition and oral processing and to increases in bite force, all of which can be related to the consolidated posterior region of the skull (Pol et al., 2013).

These rapid evolutionary changes of the braincase in basal crocodylomorphs must have resulted from profound developmental rearrangements in the chondrocranium. Although we cannot examine the developmental sequence in early lineages of crocodylomorphs, the embryonic development of the skull in extant crocodylians has been studied in sufficient detail (Bellairs & Kamal, 1981; Fernandez Blanco, 2019; Kesteven, 1957; Klembara, 1991, 1993, 2001, 2004, 2005; Lima et al., 2011; Müller, 1967; Parker, 1883; Rieppel, 1993; Shiino, 1914; Vieira et al., 2019). This work may provide us with important clues concerning the developmental mechanisms that underlie the evolutionary acquisition of the characteristic braincase anatomy of crocodylomorphs.

The cartilaginous basipterygoid processes are present in the early embryonic stages of *A. mississippiensis* (Klembara, 1993) and apparently also in other crocodylians (roots of infrapolar processes in Bellairs & Kamal, 1981) (Figure 28e). Consequently, they become indistinguishably fused with the ossifying polar cartilages and several dermal elements (unpaired parasphenoid, paired basitemporals and paracochlears) at late stages of the embryonic development (Klembara, 1993). The presence of the polar cartilages (=infrapolar processes of some authors) is a characteristic feature of the crocodylian chondrocranium (Bellairs & Kamal, 1981). The polar cartilages are independent elements that attach to the posterior surface of the basipterygoid processes and eventually fuse with them (Klembara, 1993) (Figure 28e). The parabasisphenoid of crocodylians also

includes separate dermal embryonic anlagen (parasphenoid, basitemporals, paracochlears) that constitute a considerable portion of the fully formed element (Figure 28c,e). Thus, the basipterygoid processes become lost during the embryonic development of crocodylians and do not persist as distinct bony elements during later developmental stages.

Some non-crocodyliform crocodylomorphs, for which the basicranial region is sufficiently known, have a dorsoventrally deep (verticalized) parabasisphenoid, with large basipterygoid processes that are located ventral to the basal tubera of the basioccipital: *Sphenosuchus acutus* (Walker, 1990) (Figure 28a), *Dibothrosuchus elaphros* (Wu & Chatterjee, 1993) and probably *Macelognathus vagans* (I. T. Kuzmin, pers. interpretation of figs 6 and 11 from Leardi et al., 2017). This highly modified condition is not directly comparable to that in adults of extant crocodylians. However, certain resemblances do exist between the basicranium of developing *A. mississippiensis* (Figure 28e) and those of basal crocodylomorphs (Figure 28a). In stage 6A of *Alligator*, the developing anterior part of the basicranium is composed of pillars, with a large gap ventral to the route of the cerebral carotid artery. This gap in *Alligator* exists prior to the extensive ossification of the basitemporals and paracochlears (compare with later stages in Klembara, 1993). Ventral to this gap, there is the anteroposteriorly elongate bar that corresponds to the fused basipterygoid process and the polar cartilage (=infrapolar process). The parabasisphenoid of the non-crocodyliform crocodylomorph *Sphenosuchus* is also composed of thin pillars and has a gap below the course of the carotid artery (pneumatic precarotid recess; Walker, 1990). The basipterygoid processes of both *Sphenosuchus* and *Dibothrosuchus* are notably elongated anteroposteriorly (Walker, 1990; Wu & Chatterjee, 1993).

We hypothesize that the parasphenoid and the elements corresponding to the polar cartilages of extant crocodylian embryos were incorporated in the fully formed parabasisphenoid of *Sphenosuchus* and *Dibothrosuchus*. The former anlage would correspond to the parabasisphenoid rostrum and the latter to the posterior parts of the elongated basipterygoid processes (compare Figure 28a,e). Walker (1990: p. 79) arrived at a similar conclusion concerning the nature of the elongated basipterygoid processes of *Sphenosuchus*; however, his usage of the terms "infrapolar process" and "basitemporals" is not consistent with the latter and a subsequent more detailed study by Klembara (1993). No parts of the parabasisphenoid of *Sphenosuchus* and *Dibothrosuchus* appear to correspond to the large plate-like basitemporals of extant crocodylian embryos (sensu Klembara, 1993).

By contrast, the parabasisphenoid of the more derived crocodylomorph *Almadasuchus figarii* lacks basipterygoid processes, is relatively flat dorsoventrally and has two plate-like processes that project posterolaterally (ventral plates in Leardi et al., 2020). This condition is strikingly similar to that in late embryos and hatchlings of extant crocodylians (Figure 18h-k). We hypothesize that the ventral plate of *Almadasuchus* corresponds to the alar processes of crocodylians. The correspondence is not complete: whereas the alar processes of extant taxa contact both the quadrate and the otoccipital and border the pharyngotympanic canals, the ventral plates of

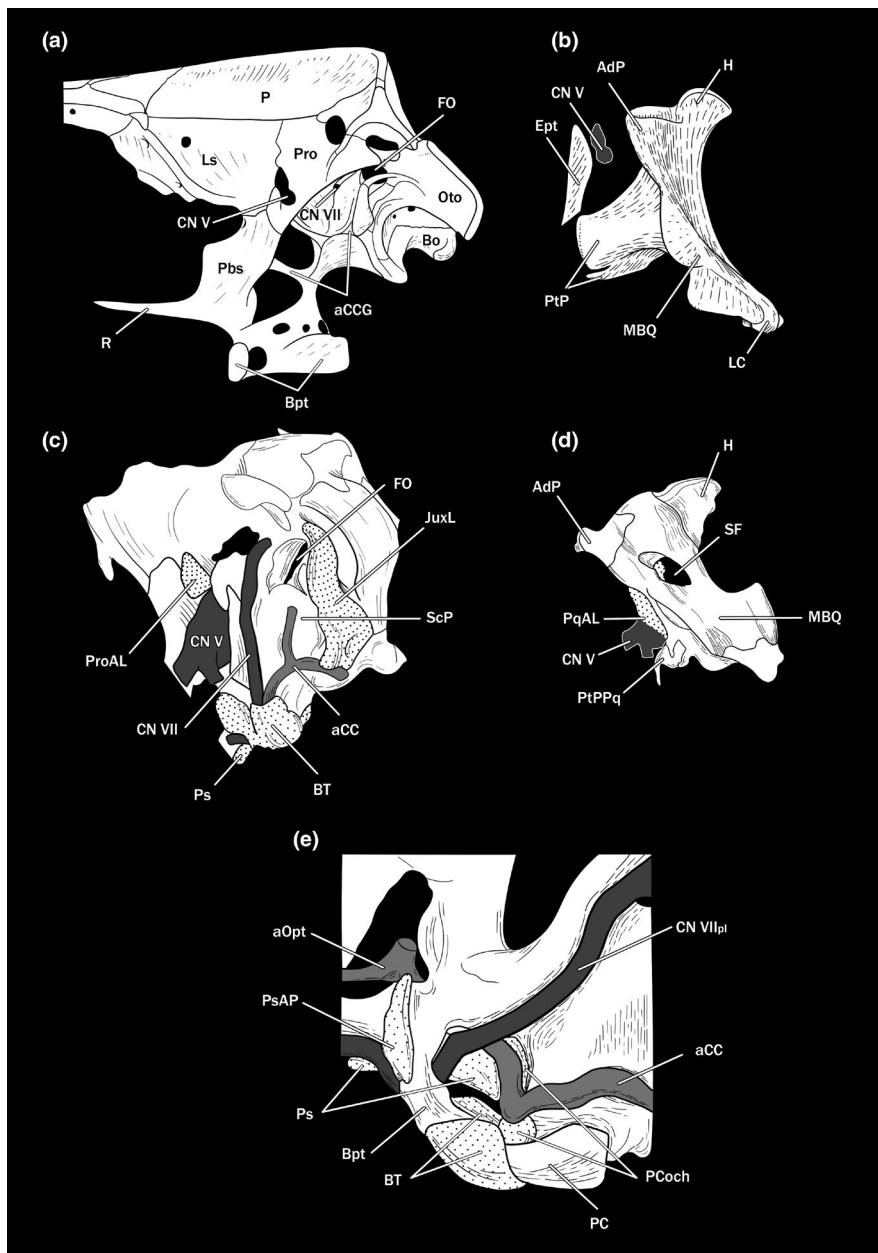


FIGURE 28 Comparison between braincase anatomy of the non-crocodyliform crocodylomorph *Sphenosuchus acutus* (a, b) and a developing embryo of *Alligator mississippiensis* (c–e). (a) *S. acutus*, neurocranium in left lateral view; (b) *S. acutus*, splanchnocranial elements in left lateral view; (c) *A. mississippiensis*, occipital region of neurocranium at Stage 8A; (d) *A. mississippiensis*, palatoquadrate at Stage 8A; (e) *A. mississippiensis*, details of developing basicranium at Stage 6A. Dermal ossifications dotted. aCC, cerebral carotid artery; aCCG, groove of cerebral carotid artery; AdP, anterodorsal process; aOpt, optic artery; Bo, basioccipital; Bpt, basipterygoid process; BT, basitemporal; CN V–CN VII, cranial nerves/corresponding foramina; Ept, epipterygoid; FO, fenestra ovalis; H, quadrate head; JuxL, juxtaotic lamina; LC, lateral condyle; Ls, laterosphenoid; MBQ, main body of quadrate; MC, medial condyle; Oto, otoccipital; P, parietal; Pbs, parabisphenoid; PC, polar cartilage; PCoch, paracochlear; PqAL, lamina palatoquadrati anterior; Pro, prootic; ProAL, lamina prootici anterior; Ps, parasphenoid; PsAP, ascending process of parasphenoid; PtP, pterygoid process; PtPPq, pterygoid process of the palatoquadrate cartilage; R, rostrum; ScP, subcapsular process; SF, subtympenic foramen. (a, b) Redrawn from Walker (1990); (b, c) Redrawn from Klembara (2004); (e) Redrawn from Klembara (1993). Not to scale

Almadasuchus contact only the quadrates (Leardi et al., 2020: fig. 1). Despite these differences, both structures are anatomically similar. Thus, the parabisphenoid of *Almadasuchus* may have incorporated dermal elements similar to the basitemporals of the late-stage crocodylian embryos.

These observations suggest that the involvement of an expanded dermal anlage into the parabisphenoid during early development might explain the characteristic anatomy of the basicranium of derived crocodylomorphs and crocodyliforms. The secondary verticalization occurred in the basicranium of crocodyliforms after the

appearance of the cranial metamorphosis sensu Tarsitano (1985); this condition is not strictly homologous to that of non-crocodyliform crocodylomorphs like *Sphenosuchus* and *Dibothrosuchus*. In the latter taxa, only the parabasisphenoid is really deep dorsoventrally (e.g. Leardi et al., 2017: fig. 6; Walker, 1990: fig. 28), whereas in adults of extant crocodylians and some fossil neosuchians (e.g. paralligatorids: Kuzmin et al., 2019), both the parabasisphenoid and the basioccipital are dorsoventrally deep. Overall, the verticalization (=dorsoventral elongation) of these basicranial elements has a complex evolutionary history among Archosauriformes (Ezcurra, 2016: character 235; Gower, 2002: character 17; Gower & Sennikov, 1996: character 7; Nesbitt, 2011: characters 97, 102; Tarsitano, 1985). Tarsitano (1985) proposed that the dorsoventral elongation of the basicranium, along with the quadrate inclination and posterior shifting of the pterygoids, affects the angle of application of the jaw adductors in crocodylians, which allows for a wider gape and a more vertical application of muscular force. This might also explain the verticalization of the basicranium in some other archosauriform clades (e.g. Erythrosuchidae, Pseudosuchia, Tyrannosauridae), which were predominantly carnivorous and required stronger bite forces. However, the hypothesis should be further tested on a wider sample of archosauriform taxa, along with the geometric morphometric data from their basicranial elements.

The palatoquadrate cartilage usually ossifies as two separate elements in diapsids: the quadrate and the epipterygoid (Bellairs & Kamal, 1981; Klembara, 2004). The epipterygoid persists in the orbitotemporal region of the braincase and covers the space around the trigeminal ganglion and associated neurovascular structures (cavum epiptericum; Holliday & Witmer, 2009; Klembara, 2004). Some amount of the residual palatoquadrate cartilage persists between the two bones and the pterygoid (Klembara, 2004; Klembara & Welman, 2009). Conversely, the quadrate of crocodylians is an extensive ossification that includes most of the palatoquadrate cartilage (Figure 28d). Only a small portion of this cartilage is incorporated into the embryonic pila antotica and ultimately ossifies as the laterosphenoid in crocodylians (columella prootica in Klembara, 2004). The quadrate of crocodylians also includes a separate dermal element (lamina palatoquadrati anterior) that is absent in other extant diapsids (Klembara, 2004). The lamina palatoquadrati anterior contacts the developing prootic and forms the trigeminal fossa posterodorsolaterally (Figure 28d).

In basal non-crocodyliform crocodylomorphs, the palatoquadrate ossifications and the arrangement of bones around the cavum epiptericum overall correspond to the general diapsid condition (e.g. Klembara & Welman, 2009) (Figure 28b). For example, in *Sphenosuchus* and *Dibothrosuchus* (Walker, 1990; Wu & Chatterjee, 1993), the quadrate is not as extensive an ossification as it is in extant crocodylians: it predominantly consists of the main body and the otic and pterygoid processes, which matches the condition in other diapsids (e.g. extant *Sphenodon*, Triassic basal archosauriform *Proterosuchus*; Klembara & Welman, 2009). The pterygoid process of the quadrate loosely overlapped the pterygoid in *Sphenosuchus* and *Dibothrosuchus* (Walker, 1990;

Wu & Chatterjee, 1993). The quadrate of the latter taxa did not participate in the orbitotemporal region and the cavum epiptericum (Figure 28b); some amount of cartilage likely persisted in the area, as in other extant and extinct diapsids (Klembara & Welman, 2009; Walker, 1990). An ossified epipterygoid was reported in *Sphenosuchus* (Walker, 1990) and some crocodyliforms (Holliday & Witmer, 2009; Klembara & Welman, 2009; Kley et al., 2010), and it has been said to participate in the cavum epiptericum. However, this element has not been reported in any other non-crocodyliform crocodylomorph to date (Clark et al., 2004; Leardi et al., 2017, 2020; Wu & Chatterjee, 1993); furthermore, its presence in *Sphenosuchus* is doubtful (J. M. Leardi, pers. commun.). Even if the epipterygoid was absent in basal crocodylomorphs, the inferred presence of the residual cartilage in the area of the cavum epiptericum and the quadrate-ptyerygoid contact (e.g. Walker, 1990: p. 30) suggests that the epipterygoid may have remained unossified in these taxa. Unossified palatoquadrate cartilage around the epipterygoid is present in extant (e.g. *Sphenodon*) and has been inferred for extinct diapsids (e.g. *Proterosuchus*) but is absent in adult crocodylians (Klembara & Welman, 2009). In either case, the anteroventral part of the palatoquadrate cartilage that corresponds to the epipterygoid ossification of other diapsids (ptyerygoid portion of palatoquadrate in Klembara, 2004; Klembara & Welman, 2009) did not ossify as part of the quadrate in *Sphenosuchus* and *Dibothrosuchus*, as is evident from its relations to surrounding elements (Figure 28b). On the other hand, the most prominent features of the quadrate of non-crocodyliform crocodylomorphs like *Sphenosuchus* and *Dibothrosuchus*, which are shared with extant crocodylians and distinguish them from other diapsids, are the anteromedial inclination of the quadrate, its contact with the lateral wall of the neurocranium (e.g. the prootic), and the presence of the anterodorsal process (Nesbitt, 2011; Pol et al., 2013; Walker, 1990; Wu & Chatterjee, 1993).

Subsequently in the evolutionary history of the clade, the quadrate attains numerous sutural contacts with the adjacent neuro- and dermatocranial elements (e.g. laterosphenoid, otoccipital, parabasisphenoid, squamosal, parietal, pterygoid) in a stepwise manner in the more derived non-crocodyliform crocodylomorphs such as *Almadasuchus*, thalattosuchians and crocodyliforms (Busbey & Gow, 1984; Clark, 1986; Clark et al., 2004; Herrera et al., 2018; Holliday & Witmer, 2009; Leardi et al., 2020; Pol et al., 2013). In crocodyliforms (e.g. *Protosuchus*: Busbey & Gow, 1984; Clark, 1986) and likely in *Almadasuchus* (I. T. Kuzmin, pers. interpretation of fig. 1 from Leardi et al., 2020), the quadrate invades the orbitotemporal region of the braincase and participates in the posterior margin of the trigeminal fossa/foramen.

We hypothesize that these profound changes result from the expanded ossification of the palatoquadrate cartilage as a single definitive quadrate, as it does during the embryonic development of extant crocodylians (Klembara, 2004; Klembara & Welman, 2009). The extensive ossification of the palatoquadrate cartilage would result in the suturing of the quadrate to the pterygoid and to the basicranium, whereas the inclusion of some neomorphic dermal anlagen similar to the lamina palatoquadrati anterior of

extant crocodylians would lead to the formation of the anteromedial process and involvement of the quadrate in the orbitotemporal region of the braincase.

Surprisingly, the most highly modified structures of the crocodylomorph braincase—the orbitotemporal portion of the quadrate (=anteromedial process), the sutural contact between the prootic and quadrate and the ventrolateral processes of the otoccipitals—initially develop as peculiar neomorphic dermal ossifications in extant crocodylians: the lamina palatoquadrati anterior, the lamina prootici anterior and the juxtaotic laminae (Figure 28c,d) (Klembara, 2004, 2005). The corresponding parts of the definitive osteocranium are absent in the non-crocodyliform crocodylomorphs *Sphenosuchus* and *Dibothrosuchus* (Figure 28a,b) but appear in a stepwise manner among derived non-crocodyliform crocodylomorphs, thalattosuchians and crocodyliforms. We hypothesize that the occurrence of corresponding neomorphic dermal embryonic anlagen in these groups modified the plesiomorphic diapsid condition and led to the peculiar braincase structure of derived crocodylomorphs and crocodyliforms. These early evolutionary modifications appear to be still reflected in the embryonic development of living crocodylians.

6 | CONCLUSION

The braincase of extant crocodylians has a distinctive anatomy that strongly diverges from that of most other diapsids. The rigid structure of this cranial region with multiple cross-suturing of bones results in a firm bony framework for adductor muscle attachment and resisting increased bite forces. This peculiar pattern appeared relatively early in the evolution of Crocodylomorpha, within the successive groups of non-crocodyliform crocodylomorphs, thalattosuchians and crocodyliforms. We conclude that three main processes likely underlie the initial steps in the evolution of the akinetic braincase of Crocodylomorpha including its living representatives: (1) the incorporation of neomorphic dermal anlagen into different portions of the developing cranium; (2) the ossification of the palatoquadrate cartilage as a single expanded quadrate and (3) the anteromedial inclination of the quadrate. These changes in development occurred rapidly at the base of Crocodylomorpha and resulted in the subsequent radiation of the clade at the end of the Triassic.

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DATA AVAILABILITY STATEMENT

3D models of the described specimens and additional figures are available online at Morphosource (Project P1193 “Braincase anatomy of extant Crocodylia, with new insights into development and evolution of the neurocranium in crocodylomorphs”). The original CT scan data are available from the corresponding author at a direct request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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