Comparative neuroanatomy of extinct horned turtles (Meiolaniidae) and extant terrestrial turtles (Testudinidae), with comments on the palaeobiological implications of selected endocranial features

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Turtles are one of the least explored clades of reptiles with respect to palaeoneuroanatomy. Few detailed descriptions of endocranial features such as the brain morphology or inner ear exist for extant and extinct forms. In this contribution, we present the first CT-based reconstructions of endocranial morphology (brain and inner ear) and the nasal cavities in the terrestrial horned meiolaniid (Meiolaniidae) turtles *Niolamia argentina* and *Gaffneylania auricularis* from the Eocene of Patagonia, as well as *Meiolania platyceps* from the Pleistocene of Lord Howe Island, Australia. In addition, these exclusively Gondwanan Cenozoic taxa are contrasted with cranial endocasts of multiple extant testudinoids, thereby providing the largest sample of digital comparative endocranial data assembled for extinct and living turtles to date. Our study thus adds much needed anatomical information on turtle palaeoneurology. Aspects of meiolaniid palaeobiology are discussed; in particular, the hypertrophied nasal cavity might not to be related to olfactory acuity, but rather perhaps adaptation to arid climatic conditions, and/or intraspecific behaviours.

ADDITIONAL KEYWORDS: Cranial endocast – *Gaffneylania auricularis* – inner ear – *Meiolania platyceps* – nasal cavity – *Niolamia argentina* – palaeoneurology – terrestrial turtles – Testudinidae – Testudinoidea.

INTRODUCTION

Few studies have been focused on the neuroanatomy of extant turtles (e.g. Bojanus, 1819; Ogushi, 1913; Edinger, 1929, 1934; Zangerl, 1960; Gaffney & Zangerl, 1968; Wyneken, 2001; Deantoni, 2015). The few taxa which have been assessed in any detail include the chelonioids *Chelonia mydas* (Linnaeus, 1758) (Zangerl, 1960), *Caretta caretta* (Linnaeus, 1758) (Zangerl, 1960), *Dermochelys coriacea* (Vandellius, 1761), *Eretmochelys imbricata* (Linnaeus, 1766), *Lepidochelys kempii* (Garman, 1880) (Wyneken, 2001), the chelydrid *Macrochelys temminckii* (Troost, 1835) (Edinger, 1934) and the pelomedusoid *Erymnochelys madagascariensis* (Grandidier, 1867) (Gaffney & Zangerl, 1968; see Paulina-Carabajal *et al.*, 2013: fig. 7A for comparisons). Furthermore, although turtles are a group whose fossil record extends from the Late Triassic to the Holocene, few descriptions of endocranial morphology (including both the empty space occupied by the brain or the cast) have been published for extinct taxa (e.g. Zangerl, 1960; Gaffney & Zangerl, 1968;

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Gaffney, 1977, 1982; Paulina-Carabajal *et al.*, 2013; Deantoni, 2015). Examples incorporate the chelonioid *Corsochelys haliniches* Zangerl, 1960, from the Late Cretaceous of Alabama, the bothremydids *Bothremys cooki* Leidy, 1865 and *B. barberi* (Schmidt, 1940) from the Late Cretaceous of North America (Gaffney & Zangerl, 1968; Gaffney, 1977), the Late Cretaceous baenid *Plesiobaena antiqua* Lambe, 1902 from Canada (Gaffney, 1982) and the pancryptodiran *Plesiochelys etalloni* (Pictet & Humbert, 1857) from the Upper Jurassic lithographic limestones of Western Europe (Joyce, 2007; Paulina-Carabajal *et al.*, 2013). Inner ear osteology has also been reconstructed three-dimensionally in the extant pleurodiran chelid *Chelus fimbriatus* (Schneider, 1783), the chelydrids *Macrochelys temminckii* and *Chelydra serpentina* (Linnaeus, 1758) and carettochelyid *Carettochelys insculpta* Ramsay, 1886 (Georgi, 2008; Thewissen & Nummela, 2008; Walsh *et al.*, 2009). Among testudinoids, the inner ear morphology of *Chelonoidis chilensis* (Gray, 1870), *C. nigra* (Quoy & Gaimard, 1824), *Terrapene carolina* (Linnaeus, 1758) and *Trachemys scripta* (Schoepff, 1792) has been studied or illustrated (e.g. Georgi, 2008; Thewissen & Nummela, 2008; Walsh *et al.*, 2009). Finally, for extinct turtles only the inner ear of the Jurassic *P. etalloni* has been documented (Paulina-Carabajal *et al.*, 2013).

Because so few studies have been conducted, our understanding of turtle palaeoneurology remains poor. In this work, we present the first CT generated digital 3D reconstructions and accompanying detailed descriptions of the nasal cavity, cranial endocast, inner ear and internal carotid passage of three meiolaniids and six extant testudinoid species assessed as comparative analogues for these extinct terrestrial turtles; these contrasting model lineages encapsulate a substantial degree of temporal and phylogenetic variation.

The clade Meiolaniidae was a peculiar group of large, fully terrestrial turtles with cranial horns, frills and armoured tails terminating in a club that lived in South America and Australasia between the Middle Eocene and Holocene (Gaffney, 1996; Sterli, de la Fuente & Krause, 2015; Poropat *et al.*, 2016). Those taxa with the best-preserved cranial remains were selected for our analysis: the Australian *Meiolania platyceps* Owen, 1886 and Patagonian *Niolamia argentina* Ameghino, 1899 and *Gaffneylania auricularis* Sterli *et al.*, 2015. *Meiolania platyceps* is the most skeletally complete meiolaniid taxon, with hundreds of specimens recovered from the Pleistocene of Lord Howe Island, Australia. Anderson (1925) and Gaffney (1983, 1985, 1996) described its osteology in detail, but only a few aspects of its endocranial morphology were mentioned or illustrated (Gaffney, 1983, 1996). The meiolaniid record from South America is restricted to the Palaeogene of Patagonia, Argentina, with two species: *N. argentina* documented by Smith Woodward (1901) and recently re-described by Sterli

& de la Fuente (2011), and *G. auricularis*, which represents the most complete meiolaniid reported from South America thus far (Sterli *et al.*, 2015).

As northern hemisphere ecological analogues, testudinids were chosen for comparison with the aforementioned meiolaniid taxa because they are also terrestrial turtles. Testudinidae today have a near-global distribution (excluding Antarctica and Australia), and a fossil record extending back to the Paleocene (Hay, 1908; Auffenberg, 1964; Crumly, 1984 and references therein; Tong *et al.*, 2016). In this work, we include five living species for examination: *Gopherus berlandieri*, *Testudo hermanni*, *Testudo graeca*, *Kinixys belliana* and *C. chilensis* (see Table 1).

Institutional Abbreviations: AM F, Australia Museum, Fossil collection, Sydney, Australia; AMNH, American Museum of Natural History, New York, USA; MPEF, Museo Egidio Feruglio, Trelew, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMF, Geological Survey of New South Wales (specimen formerly registered as a Mining Museum Fossil), Sydney, Australia; RAM, Raymond M. Alf Museum of Palaeontology, Claremont, USA; YPM, Yale Peabody Museum of Natural History, New Haven, USA.

MATERIAL AND METHODS

Our 3D reconstructions of the cranial endocast, inner ear and nasal cavities were generated using CT section data of the selected meiolaniids (Figs 1–5) and testudinids (Figs 6–9), together with the aquatic geoemydid *Rhinoclemmys funerea*, which was included for further comparisons (Figs 8G–L, 9). Different scanning facilities and parameters were used for each taxon and/or group of specimens.

1. *MEIOLANIA PLATYCEPS*

A complete cranium (and cervical vertebra) MMF 13825a was CT scanned, with a plaster endocast (AMNH 14734) also made of a second cranium AMF 43183. CT scans were undertaken at the Sydney University Veterinary Teaching Hospital on a *Phillips Brillance* 16 with 120 kV energy and 100 mA. Nine hundred and twenty-one slices were obtained at 0.63 mm increments.

2. *NIOLAMIA ARGENTINA*

The holotype MLP 26–40 was CT scanned at the IDECh (Spanish acronym for the Institute of Diagnosis from the East of Chubut, Trelew, Argentina), using a General Electric Medical Systems TAC Helicoidal at energy of 120 kV and 150 mA. Forty-eight 0.8 mm slices were produced. A latex endocast of MLP 26–40 was also made at the MEF; this revealed fine details not observable from the scans.

Table 1. Endocranial measurements of the studied specimens of Meiolaniidae, Testudinidae and Geoemydidae

Taxon	Specimen	Habit	Ecv (cm³)	Br vol (cm³)	Nc vol%	OR	ASC–PSC
Meiolaniidae†							
Gaffneylania auricularis	MPEF-PV 10556	Terrestrial	10~	10~	–	–	115°
Meiolania platyceps	MMF 13825a	Terrestrial	104.8	37.7	64	37–45	110°
Niolamia argentina	MLP 26-40	Terrestrial	156.5	64.9	58.5	22~	
Testudinidae							
Chelonoidis chilensis	MPEF-AC 25	Terrestrial	3.2	1.82	43	59.5	115°
Gopherus berlandieri	AMNH 73816	Terrestrial	1.40	0.86	38.5	36.3	101°
Kinixys belliana	AMNH 10028	Terrestrial	1.24	0.88	29	61.6	102°
Testudo graeca	YPM 14342	Terrestrial	1.03	0.73	29	45	100°
Testudo hermanni	AMNH 134518	Terrestrial	–		–	57.4	110°
Geoemydidae							
Rhinoclemmys funerea	YPM 12174	Aquatic	1.77	1.35	23.5	37.5	95°

† Extinct; ~ incomplete; Ecv, endocranial volume of complete endocranial cast (including brain and nasal cavities); Br vol, brain volume; Nc vol, volume of the nasal cavity related to the complete endocast; OR, olfactory ratio; ASC–PSC, angle formed between anterior and posterior semicircular canals.

3. *GAFFNEYLAMIA AURICULARIS*

The holotype MPEF-PV 10556 was CT scanned at Trelew Hospital (Trelew, Chubut, Argentina) using a Toshiba Alexion of 16 rows, 100 kV energy and 75 mA. Two hundred and thirteen slices were collected at 0.8 mm increments.

4. TESTUDINIDAE AND GEOEMYDIDAE

Examples of *G. berlandieri* (AMNH 73816), *T. hermanni* (AMNH 134518), *T. graeca* (YPM 14342), *K. belliana* (AMNH 10028) and *R. funerea* (YPM 12174) were CT scanned at the Stonybrook University Hospital (USA) on a General Electric Light Speed 16 tomographer with a slice increment of 0.1 mm and energy of 100 kV with 50 mA. Slice numbers ranged from 462 (AMNH 73816) to 576 (AMNH 134518; AMNH 10028) and 567 (YPM 14342; YPM 12174) (Georgi, 2008). The CT scan of *C. chilensis* (MPEF- AC 25) was made at the Trelew Hospital (Trelew, Argentina) on a Toshiba Alexion of 16 rows yielding 88 slices at 0.8 mm with energy of 120 kV and 150 mA.

All scan data were exported in either *.tif or DICOM format, and then imported into Materialise Mimics (18.0) to facilitate digital extraction. Two-dimensional illustrations were assembled in Photoshop (CS3) and Illustrator.

Volume calculations (Table 1) were made using software tools in Mimics. Olfactory ratios (ORs) were measured from the maximum diameter of the olfactory bulb versus maximum diameter of the cerebral hemisphere regardless of orientation and multiplied by 100 (see Methods in Zelenitsky, Therrien & Kobayashi, 2009 and references therein).

ENDOCRANIAL MORPHOLOGY

Cranial endocasts of reptiles usually include not only the mould of the brain and cranial nerves (CNs), but also other soft tissues and blood vessels (e.g. Edinger, 1929; Hopson, 1979). Consequently, only the most outstanding encephalic features are recognized. Moreover, in all extant and most extinct turtles, the anterior lateral and ventral walls of the braincase are not ossified, preventing the reconstruction of most of the anteroventral region of the forebrain, including CNs II–IV (Paulina-Carabajal *et al.*, 2013; Deantoni, 2015). However, since the anterior region of the snout is ossified, a complete turtle endocranial cast shows the endocranial cavity proper (space occupied by the encephalic structures) plus the cast of the nasal duct and the nasal cavity anteriorly. The nasal cavity in living reptiles is subdivided into three main regions (Parsons, 1959, 1970; Halpern, 1992): the vestibulum nasi anteriorly, a ventro-posterior ductus nasopharyngeus and between them a cavum nasi proprium. The cast of the nasal cavities reflects the size and shape of the respiratory and olfactory regions. The vestibule corresponds to the anterior and tubular region and forms only a small portion of the nasal cavity. The posterodorsal region of the cavum corresponds to the olfactory region of the nasal cavity (Parsons, 1959). The nasal cavity (cavum nasi proprium) and the choana are connected by a tubular structure, the ductus nasopharyngeus. The cavum nasi proprium lies between the vestibulum nasi and the ductus nasopharyngeus, and in most cases is a large cavity bearing sensory olfactory epithelium, which is absent in the vestibulum and the respiratory regions (Parsons, 1959, 1970). The olfactory chamber resides within the cavum nasi

at its caudal-most extent and is typically external to the main respiratory flow (Bourke *et al.*, 2014).

The cranial endocast proper comprises the forebrain, midbrain and hindbrain. The identifiable structures of the forebrain are the cerebral hemispheres and the olfactory bulbs (olfactory tracts are markedly short in all turtles), which are small and leave no clear impressions on the ventral surface of the frontals. The midbrain is not well-defined in the turtle cranial endocast, whereas the hindbrain exhibits several structures such as the dorsal knob or protuberance (= cartilaginous 'rider', dural peak), the medulla oblongata and CNs V–XII. The dorsal protuberance of the endocast has been interpreted in fossil turtles as the cast of the 'epiphysis' or pineal organ (e.g. Deantoni, Romano & Azevedo, 2012). However, although the position of the pineal gland is more or less level with the dorsal cavity, here we follow the interpretation of Zangerl (1960) of a cartilaginous 'rider', which in life houses the cartilaginous end of the supraoccipital. We base this interpretation on photographs of dissected extant species of sea turtles such as *Caretta caretta* (Wyneken, 2001: fig. 194b), *Eretmochelys imbricata*, *Chelonia mydas* (Wyneken, 2001: fig. 196b) and *Lepidochelys kempi* (Wyneken, 2001: fig. 197b), in which the epiphysis is located ventrally or slightly posteroventral to this 'notch' in the dorsal margin of the endocranial cavity, but does not infill it: the only exceptions to this statement are *D. coriacea* or *Eretmochelys imbricata* (Wyneken, 2001: figs, 192a, 199b). This un-ossified region of the roof of the endocranial cavity is reflected in fossilized specimens as an enlarged dorsal expansion of the endocranial cast, which was not filled by encephalic tissues proper but probably by blood dorsal longitudinal sinuses (see Witmer *et al.*, 2008) and/or cartilage.

MEIOLANIA PLATYCEPS

The complete cranial endocast of *M. platyceps* plus the nasal cavity measures 141 mm long from the external nares to the foramen magnum (Figs 1, 5A, D, G).

Nasal cavity

The nasal cavity of *M. platyceps* is strongly enlarged when compared with other turtles (Fig. 1A, B), with a volume that represents more than 60% of the complete endocast, as observed in *N. argentina* (Table 1). The vestibulum is a well-developed structure (particularly anteroposteriorly), clearly differentiated from the cavum nasi proprium by a posterior constriction. The dorsal surface of the vestibule bears a longitudinal median groove that reflects the presence of an osseous septum, which together with non-preserved cartilaginous parts completely separates the left and right

sides of the vestibule during life. This osseous septum is present in other specimens of *M. platyceps* (e.g. AM F398, AM F16860, AM F43183 and MM F13825a), but is absent in *N. argentina*. In the cranial endocasts of *M. platyceps* (AMNH 14734 and MMF 13825a) the lateral surfaces of the vestibulum each bear an elongate dorsal tongue-shaped expansion, posterolaterally projecting dorsal expansion recognized by Gaffney (1983) as the nasomaxillary sinus (Fig. 5A). Its function remains unknown; it may have housed soft tissues or vascular sinuses related to the respiratory or olfactory capabilities of this taxon. This expansion is not observed in *N. argentina* or in the studied testudinids. The ventral nasopharyngeal ducts are also clearly differentiated from the vestibule and the cavum nasi, as robust and short tubes oriented posteriorly and lateroventrally (Figs 1D, 5D, G). The cavum nasi proprium is globose and subcircular in dorsal view (Figs 1B, 5A). The dorsal margin of the cavum is mostly convex with a flat top and projects dorsally almost as far as the dorsal protuberance or knob. The posterior margin of the cavum narrows into a longitudinal nasal duct that connects posteriorly with the olfactory bulbs of the brain.

Cranial endocast proper

The forebrain, midbrain and hindbrain of *M. platyceps* are disposed forming a sigmoidal-shaped brain in lateral view. The angles formed between forebrain and midbrain and between midbrain and hindbrain are, however, less marked in the extinct taxa *C. haliniches* (Hopson, 1979) and *P. etalloni* (Paulina-Carabajal *et al.*, 2013) and in the extant *D. coriacea* (Wyneken, 2001) and testudinids, in which the hindbrain, midbrain and forebrain are more or less horizontally oriented in lateral view. Most of the CNs are identified and reconstructed except for CNs II, III and IV. The olfactory bulbs and tracts are not clearly visible in the endocast, being more or less continuous anteriorly with the nasal duct leading into the cavum nasi proprium. This duct is transversely wide and robust, unlike the narrow passages present in extant testudinids. The region comprising olfactory tract and bulbs is separated from the cerebral hemispheres by a poorly marked constriction (Fig. 5A). The cerebral hemispheres of *M. platyceps* are however clearly noticeable in the endocast, although they are not markedly expanded laterally [the lateral margin does not reach the level of the lateral semicircular canal (LSC), and the maximum width across the cerebral hemispheres is slightly larger than the medulla oblongata]. Posterior to the cerebral hemispheres, structures of the midbrain such as the optic lobes, and CNs III and IV were not observed.

The hindbrain is anteroposteriorly short, with a tall and robust medulla oblongata. The ventral surface of
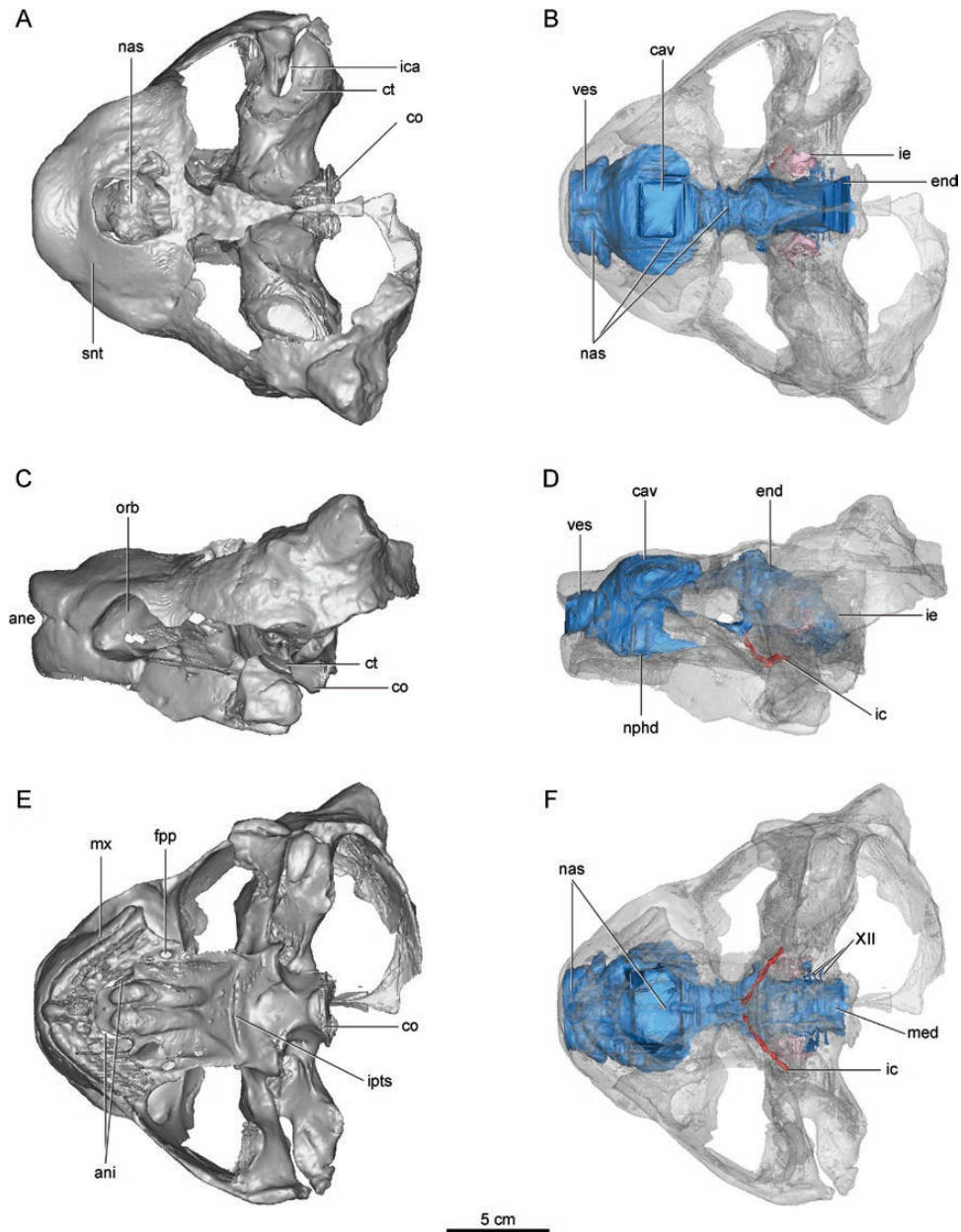
Figure 1. Digital reconstruction of the skull of *Meiolania platyceps* (MMF 13825a) in dorsal (A, B), left lateral (C, D) and ventral (E, F) views. In the images at the left the bone is rendered semitransparent to allow observation of internal structures. Abbreviations: ani, aperture narium interna; ane, apertura narium externa; cav, *cavum nasi proprium*; co, condylus occipitalis; ct, cavum tympani; end, cranial endocast; fpp, foramen palatinum posterius; ic, internal carotid; ica, incisura columellar auris; ie, inner ear; ipts, intrapterygoid slit; med, medulla; mx, maxilla; nas, nasal cavity; nphd, nasopharyngeal duct; orb, orbit; snt, snout; ves, vestibulum; XII, cranial nerve. Scale bar = 5 cm.

the medulla is flat posteriorly, but slopes anterodorsally in its anterior portion, towards the infundibulum, unlike the flat ventral surface observed in *G. auricularis* and *N. argentina* (Fig. 5D–F). In *M. platyceps*, the dorsal margin of the medulla oblongata is posteroventrally oriented from the foramen magnum threshold, as in *N. argentina* but unlike the convex dorsal margin observed in *G. auricularis*. A well-developed dorsal protuberance (= 'cartilaginous rider') is present dorsal to CN V. The vestibular eminence is ossified, separating the endocranial cavity from the endosseous inner ear, unlike the less ossified walls present in *N. argentina* and *G. auricularis*. A non-ossified vestibular eminence is also observed in *P. etalloni*, wherein the inner ear

cavity is confluent with the endocranial cavity medially (hiatus acusticus, sensu Gaffney, 1979; Paulina-Carabajal *et al.*, 2013).

CN V has the greatest diameter of all the CNs in the endocast, and all the branches of the trigeminal nerve leave the endocranial cavity through a large oval foramen. The root of this nerve is anteriorly located, slightly anterodorsal to the infundibulum (Fig. 5A, D). CN VI is small in diameter and runs anteriorly from the medulla floor. This passage is concave and runs anterolaterally, lateral to the pituitary, and exits within the canalis cavernosus (Fig. 5D, G). On the ventral surface of the endocast, just anterior to CN VI, the infundibulum – a short and slightly anteroposteriorly compressed passage – projects anteroventrally and communicates ventrally with the pituitary, which is markedly small, as in other turtles. The infundibulum is well-differentiated from the medullar section

of the endocast, to a greater degree than is observed in other turtles such as *P. etalloni* (Paulina-Carabajal *et al.*, 2013: fig. 2) and the studied testudinids here. The internal carotid arteries (cerebral branches) enter the pituitary posteroventrally and separately from each other (Figs 1F, 5G). CNs VII and VIII were not observed in the CT scans. CNs IX–XI seem to exit the endocranial cavity through a single passage of large diameter (foramen jugulare anterius), the base of which is located anterior and slightly dorsal to the level of the branches of CN XII. The exit foramen for CNs IX–XI (foramen jugulare posterius = metotic foramen) is located lateral to the occipital condyle and anterodorsal to CN XII foramina. The three branches of CN XII exit the endocranial cavity separately as illustrated by Gaffney (1983: fig. 46), although the two posterior branches merge before exiting the braincase through a single foramen; therefore, there are only two
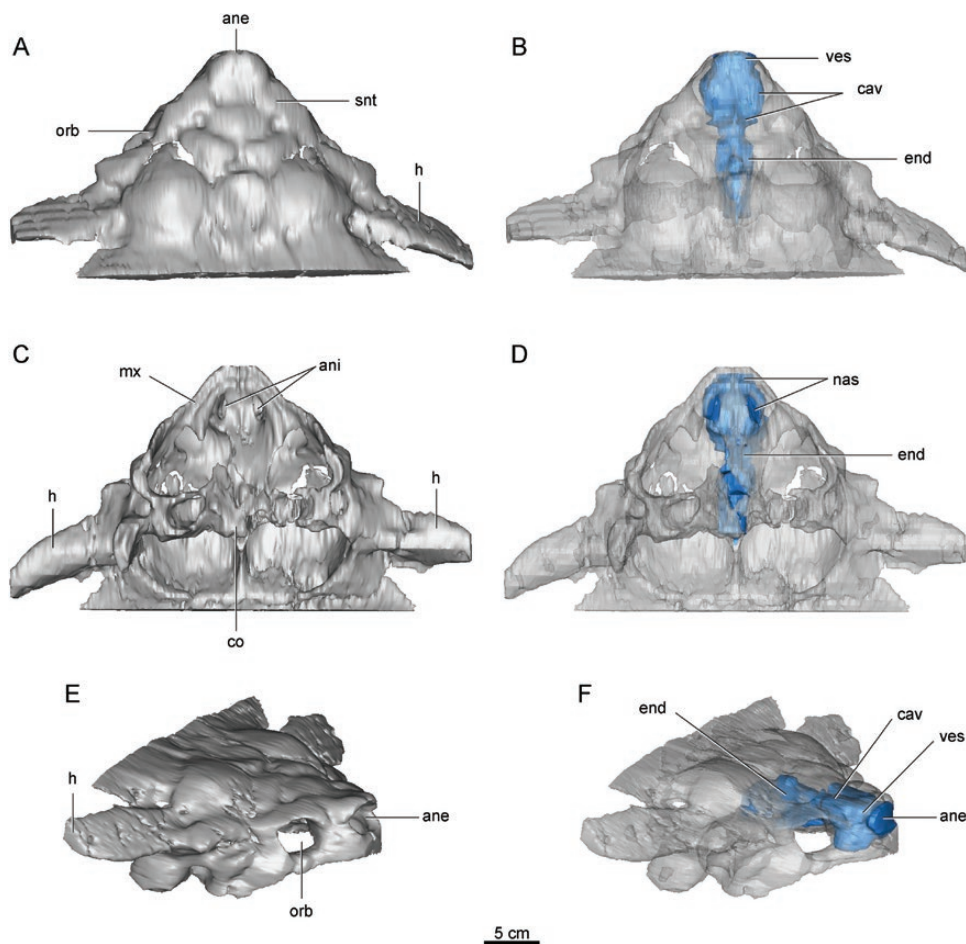
Figure 2. Digital reconstruction of the skull of *Niolamia argentina* (MLP 26–40) in dorsal (A, B), ventral (C, D) and anterolateral (E, F) views. In the images at the left the bone is rendered semitransparent to allow observation of internal structures. Abbreviations: ane, apertura narium externa; ani, aperture narium interna cav, *cavum nasi proprium*; co, condylus occipitalis; end, cranial endocast; h, skull horn; max, maxilla; nar, nare/narina; orb, orbit; snt, snout; ves, vestibulum. Scale bar = 5 cm.

external foramina for the hypoglossal nerve on the lateral side of occipital condyle (Fig. 5A, G).

Vasculature

In *M. platyceps* the foramen posterius canalis carotici interni is situated in the posterior part of the pterygoid (Gaffney, 1983). This opening has a small diameter and is located laterally on the basicranium, slightly anteroventral to the foramen jugulare posterius (Figs 1F, 5D, G). In *M. platyceps*, the CT scans do not show clear subdivisions for the cerebral and palatine branches of the internal carotid artery; however, we follow the interpretation made by Gaffney (1983) and our own observations regarding the path of the carotid artery. The internal carotid runs anteromedially and in the basisphenoid splits into cerebral and palatine branches. This bifurcation is not covered ventrally by bone, allowing us to observe that the cerebral branch pierces the basisphenoid ventrally (through the foramen posterius canalis carotici cerebralis) to run anteriorly towards the dorsum sellae. The CT scans show the internal carotid passage running into the distal end of the pituitary to exit through the foramen anterius canalis carotici cerebralis. The palatine branch leaves the skull through the fenestra caroticus (Rabi *et al.*, 2013) and re-enters the skull through the intrapterygoid slit (Gaffney, 1983).

Inner ear

In *M. platyceps* the labyrinth of the inner ear is contained in bone. Although clearly separate semicircular canals are not observed in the CT scans, the 3D shape of the complete structure was rendered, revealing that the inner ear shows a similar general morphology to that of other extinct and living turtles (Georgi, 2008; Paulina-Carabajal *et al.*, 2013 and references therein), being short with triangular semicircular canals (Figs 5A, D). The shape of the anterior semicircular canal (ASC), posterior semicircular canal (PSC) and LSC is shown in Figure 10C, D. The ASC and PSC canals are low, as in most turtles (e.g. Georgi, 2008; Paulina-Carabajal *et al.*, 2013: fig. 7 and references therein). They are slightly expanded over the common crus (heart-shaped in lateral view), forming an angle of approximately 95° in dorsal view (Fig. 10D). The PSC is slightly more expanded laterally than the ASC. The lagena is conical and markedly short. Its diameter corresponds to the diameter of the columellar foot, as observed in the extinct turtle *P. etalloni* (Paulina-Carabajal *et al.*, 2013). On the left side of the endocast, the reconstructed section of the columella runs across the acoustic meatus (middle ear) to almost reach the fenestra ovalis.

Unfortunately, the columellar foot cannot be reconstructed for *M. platyceps*.

NIOLAMIA ARGENTINA

The endocranial structures of *N. argentina* are not clearly visible in the CT scans, preventing the reconstruction of detailed structures such as neurovascular elements, and also the semicircular canals of the inner ear (Fig. 2). The general morphology of the complete cranial endocast, including the nasal cavity, is shown in Figure 5C, F, I.

Nasal cavity

The nasal cavity is extremely large, occupying a volume of *c*. 64% of the total volume of the cast, as observed in *M. platyceps* (Table 1). The vestibulum of the nasal cavity is well developed and clearly differentiated from the olfactory region by a constriction (Fig. 5C). Unlike *M. platyceps* (Fig. 5A) there is no median subdivision of the vestibule, suggesting that the median nasal septum remained cartilaginous during life. The ductus nasopharyngealis in *N. argentina* is robust, short and posterolaterally oriented. In ventral view, the left and right ducts form an arc together with the ventral section of the vestibulum (Fig. 5I), whereas the ducts in *M. platyceps* form more or less right angles (Fig. 5G). The cavum nasi proprium is globose, but poorly expanded dorsally, in a way that the dorsal surface of the cavum is mainly flat, more or less levelled with the dorsal surface of the vestibulum in lateral view (Fig. 5F). The dorsal surface of the cavum proprium is posteriorly separate in two longitudinal oval 'tubes'. These two regions are slightly divergent posteriorly and end abruptly above the anterior section of the nasal duct. The posterodorsal region of the cavum correlates mainly to the olfactory region of the nasal cavity, but the function of its subdivision in *N. argentina* remains unknown. They may represent casts of two passages or chambers, which suggests the presence of loops in the airway flow. The nasal duct connecting the nasal cavity anteriorly and the olfactory bulbs posteriorly is wide but relatively shorter than that of *M. platyceps* (Fig. 5A, C).

Cranial endocast proper

The general morphology of the cranial endocast is similar to that of *M. platyceps*, with anteroposteriorly short forebrain, midbrain and hindbrain, probably arranged in angles more marked than in the studied testudinids (Figs 5, 9). The hindbrain in particular is tall and robust, but slightly narrower than in *M. platyceps*. As in *M. platyceps*, the olfactory bulbs and tracts

of *N. argentina* are not differentiated in the endocast. The cerebral hemispheres are discernible but not markedly expanded laterally. The dorsal protuberance is large and knob-like. The dorsal margin of the medulla oblongata is posterodorsally inclined, as in *M. platyceps* but unlike the convex margin observed in *G. auricularis* (Fig. 5).

Vasculature

Unfortunately, the vasculature cannot be observed in the CT scans of *N. argentina* because it was scanned before the specimen was re-prepared. However, after cleaning, the path of the carotid artery was observed. A detailed description can be found in Sterli & de la Fuente (2011). In summary, the morphology of the
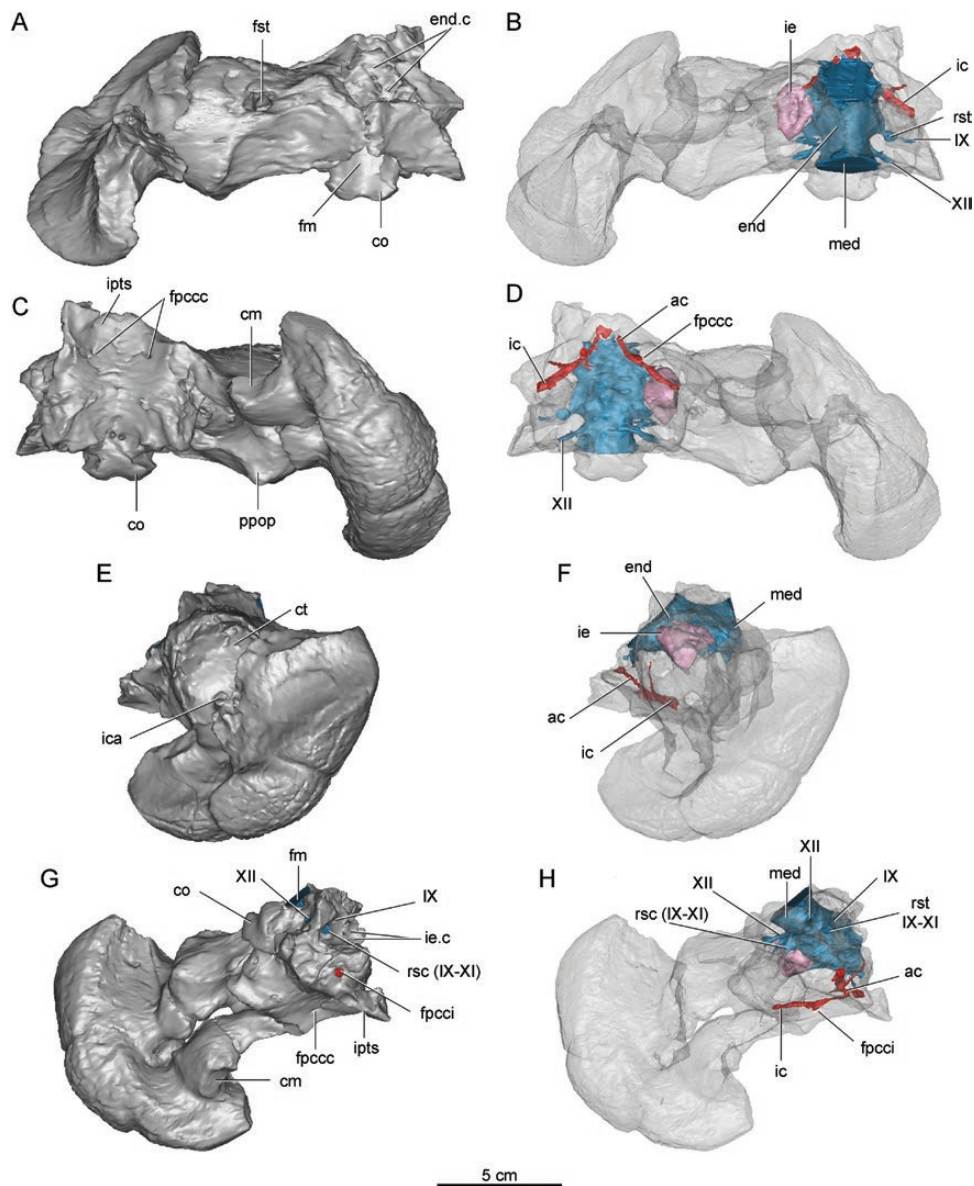
Figure 3. Digital reconstruction of the skull of *Gaffneylania auricularis* (MPEF-PV 10556) in dorsal (A, B), ventral (C, D), left lateral (E, F) and posterolateral (G, H) views. In the images at the left, the bone was rendered semitransparent to allow observation of internal structures. Abbreviations: ac, arteria cerebralis; cm, condylus mandibularis; co, condylus occipitalis; ct, cavum tympani; end, cranial endocast; end.c, endocranial cavity; ie, inner ear; ic, internal carotid artery; ica; incisura columellar auris; ipts, intrapterygoid slit; fm, foramen magnum; fpccc, foramen posterius canalis caroticus cerebralis; fpcci, foramen posterius canalis carotici interni; fst, foramen stapedio-temporale; med, medulla oblongata; ppop, procesus paraoccipitalis of opisthotic; rst, recesus scalae tympani [for cranial nerves (CNs) IX–XI]; IX–XII, CNs. Scale bar = 5 cm.

carotid circulation in *N. argentina* is similar to the one described here for *M. platyceps*.
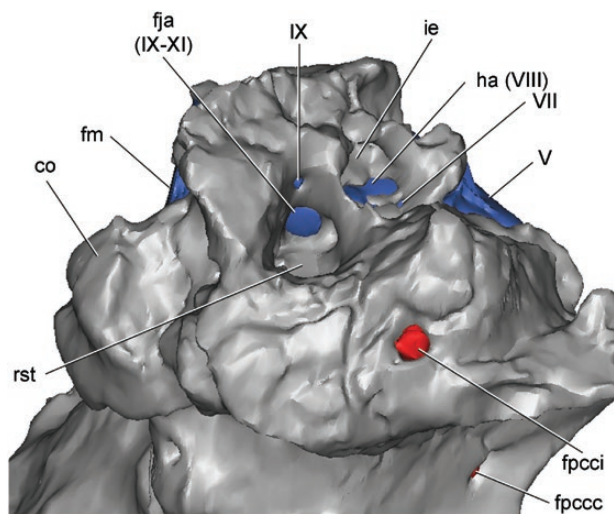
GAFFNEYLANIA AURICULARIS

Only the posterior region of the braincase of *G. auricularis* is preserved; the cranial endocast is missing the forebrain and most of the midbrain (Fig. 3). The hindbrain, however, is complete and exhibits several traits, allowing comparisons with the other two meiolaniids (Fig. 5B, E, H).

Cranial endocast proper

The medulla oblongata is a more or less horizontal tube, with a flat ventral surface and a convex dorsal margin unlike the straight and posterodorsally-oriented dorsal margin present in *M. platyceps* and *N. argentina* (Fig. 5E). The posterior-most section of the pituitary of *G. auricularis* is reconstructed, indicating it was a small structure, as in other turtles.

The posterior margins of CN V are preserved in the braincase. CN VI is reconstructed on the left side of the endocast. This passage is small in diameter, short and anteroventrally projected (Fig. 5E, H). CN VII is a small foramen posterior to CN V (Fig. 4), which enters the hiatus and is observed in lateral view because the lateral wall of the hiatus is broken. CNs IX–XI leave

Figure 4. Detail of skull of *Gaffneylania auricularis* (MPEF-PV 10556) in right lateroventral view. Lateral walls of skull are missing due to fractures allowing observation of recesus scalae tympani. Abbreviations: co, condylus occipitalis; fja, foramen jugularis anterius for cranial nerves (CNs) IX–XI; fm, foramen magnum; fpccc, foramen posterius canalis carotici cerebralis; fpcci, foramen posterius canalis carotici interni; ie, inner ear; rst, recesus scalae tympani; V, VII, IX–XII, CNs. Not to scale.

the endocranial cavity through a single opening, the foramen jugulare anterius (= metotic foramen), as in *M. platyceps* and other studied turtles. This passage runs posterolaterally and leads into the recesus scalae tympani. A markedly smaller passage diverges from the main passage dorsally before entering the recesus scalae tympani, and corresponds to CN IX (Fig. 4).

Vasculature

The vasculature of *G. auricularis* is similar to *M. platyceps* and *N. argentina*. In *G. auricularis*, both foramina posterius canalis carotici interni are preserved. The internal carotid runs inside the bone until it bifurcates in the cerebral and palatine arteries. This bifurcation is not covered ventrally by bone (see Gaffney, 1983; Sterli & de la Fuente, 2013; Sterli *et al.*, 2015). The cerebral branch of the internal carotid artery enters the basicranium through the foramen posterius canalis carotici cerebralis located in the base of the basisphenoid (Figs 4, 5E, H). The cerebral branch runs anterodorsally entering the posteroventral section of the pituitary. The palatine artery enters the skull through the intrapterygoid slit (Sterli *et al.*, 2015).

Inner ear

The left inner ear of *G. auricularis* is shown in Figures 5E and 10A, B. The inner ear is separated from the endocranial cavity by bone, as in *M. platyceps*. The general morphology of the labyrinth and the lagena of *G. auricularis* are similar to those in other studied turtles here, having low, robust and subtriangular semicircular canals, an enlarged vestibule and a short lagena. The ASC and PSC are not taller than the common crus, and they form an angle of approximately 97°–100° in dorsal view. The medial margin of the LSC cannot be differentiated from the vestibule, suggesting a cartilaginous region. The fenestra ovalis is markedly large and circular (Fig. 10A). The lagena is conical and short, suggesting hearing was not the principal sense of this taxon.

TESTUDINIDAE

Five extant testudinid species, *C. chilensis* (Fig. 6A–F), *G. berlandieri* (Fig. 6G–L), *T. graeca* (Fig. 7A–F), *T. hermanni* (Fig. 7G–L) and *K. belliana* (Fig. 8A–F) were considered in this study plus the geoemydid *R. funerea* for comparison. The general morphology of the testudinid cranial endocasts is similar to that described for other non-testudinid turtles (e.g. Paulina-Carabajal *et al.*, 2013: figs. 2, 7), in which the brain is longitudinally arranged along the midline of the skull, housed in a tubular endocranial cavity (e.g. Wyneken, 2001), although the dorsal longitudinal venous sinus plus the dura mater seem to be less developed in testudinids (Fig. 9).
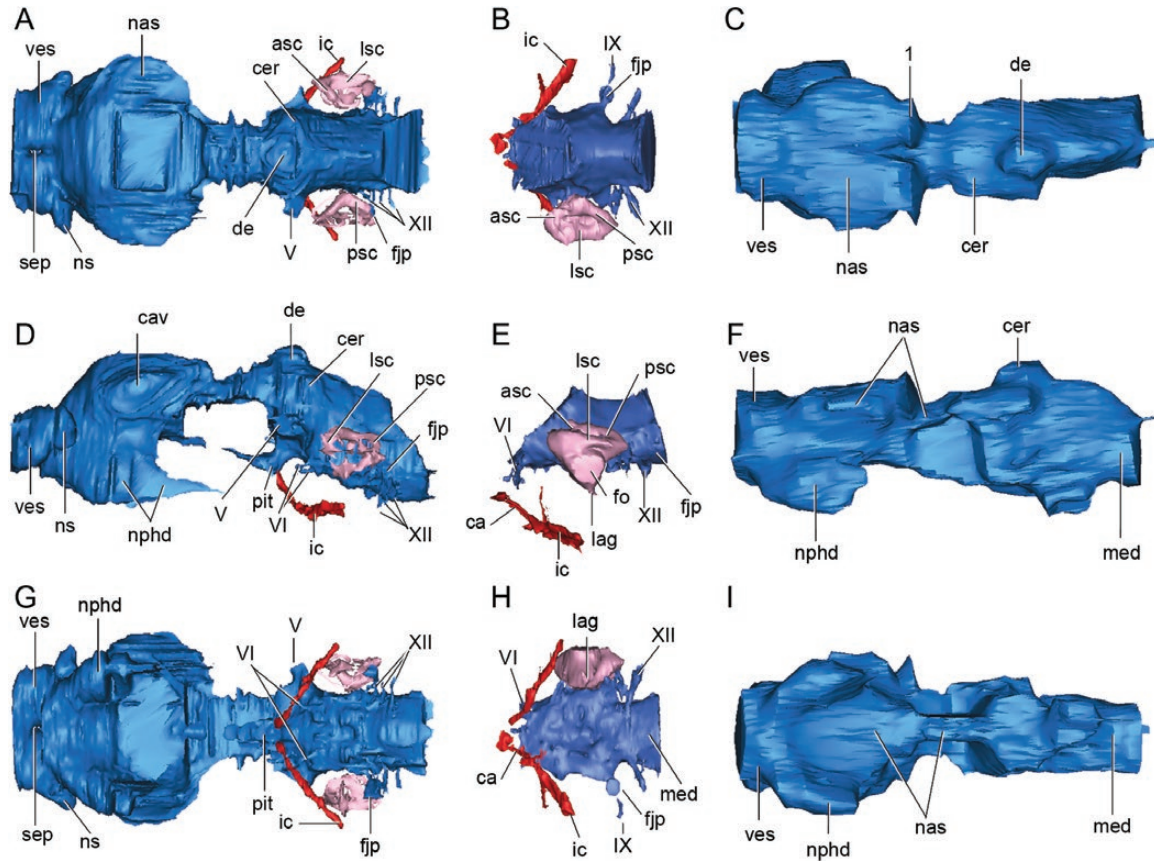
Figure 5. Cranial endocasts and nasal cavities of the meiolaniid turtles *Meiolania platyceps* (A, D, G), *Gaffneylania auricularis* (B, E, H) and *Niolamia argentina* (C, F, I), in dorsal (A–C), left lateral (D–F) and dorsal (G–I) views. Abbreviations: asc, anterior semicircular canal; ca, cerebral artery; cav, cavum nasi proprium; cer, cerebral hemisphere; de, dorsal expansion; fjp, foramen jugulare posterius; fo, fenestra ovalis; ic, internal carotid artery; ie, inner ear; lag, lagena; lsc, lateral semicircular canal; med, medulla oblongata; met, metotic passage for cranial nerves (CNs) IX–XI; nas, nasal cavity; nphd, nasopharyngeal duct; pit, pituitary; ns, nasomaxillary sinus; psc, posterior semicircular canal; sep, septum; tym, tympanic branch of glossopharyngeal nerve; ves, vestibulum; V, IX–XII, CNs; 1, partial posterior subdivision of the dorsal surface of the cavum nasi proprium of *Niolamia argentina*. Not to scale.

The complete testudinid endocranial cast, plus the nasal cavity, is characterized by relatively large nasal cavity and markedly shorter and robust olfactory duct which is markedly shorter and more robust than those of aquatic forms (Paulina-Carabajal *et al.*, 2013: fig. 7). The nasal cavities of testudinids have volumes ranging from 29% (the smallest nasal cavities are in *T. graeca* and K. belliana) to 40% (the largest nasal cavity is in *C. chilensis*) of the complete volume of the endocast (Fig. 9, Table 1). In contrast, meiolaniids have larger nasal cavities, reaching values of *c*. 60% of the total volume.

Cranial endocast proper

In general, the cranial endocast proper is sigmoidal in lateral view (Fig. 9B, E, H, K, N, Q), with poorly marked angles between forebrain, midbrain and hindbrain.

The medulla oblongata is elongate (although less elongate than in cryptodirans; see Paulina-Carabajal *et al.*, 2013: fig. 7) and low. The ventral surface of the medulla is slightly convex, whereas the dorsal margin is concave. The dorsal expansion does not project strongly dorsally, and the cartilaginous rider is a clear triangular small protuberance in most taxa, the smallest one being observed in *K. belliana*. The dorsal surfaces of the forebrain and midbrain are convex (over the level of the foramen magnum and the nasal cavity). The cerebral hemispheres are clearly discernible in the endocasts; they project laterally reaching the lateral expansion of the LSC in most forms, except in *T. graeca* and *G. berlandieri* where the cerebral hemisphere is less expanded laterally than the LSC (Fig. 9D, M). The olfactory bulbs are also clearly differentiated from the cerebral hemispheres by a shallow constriction which indicates the location of the almost non-existent
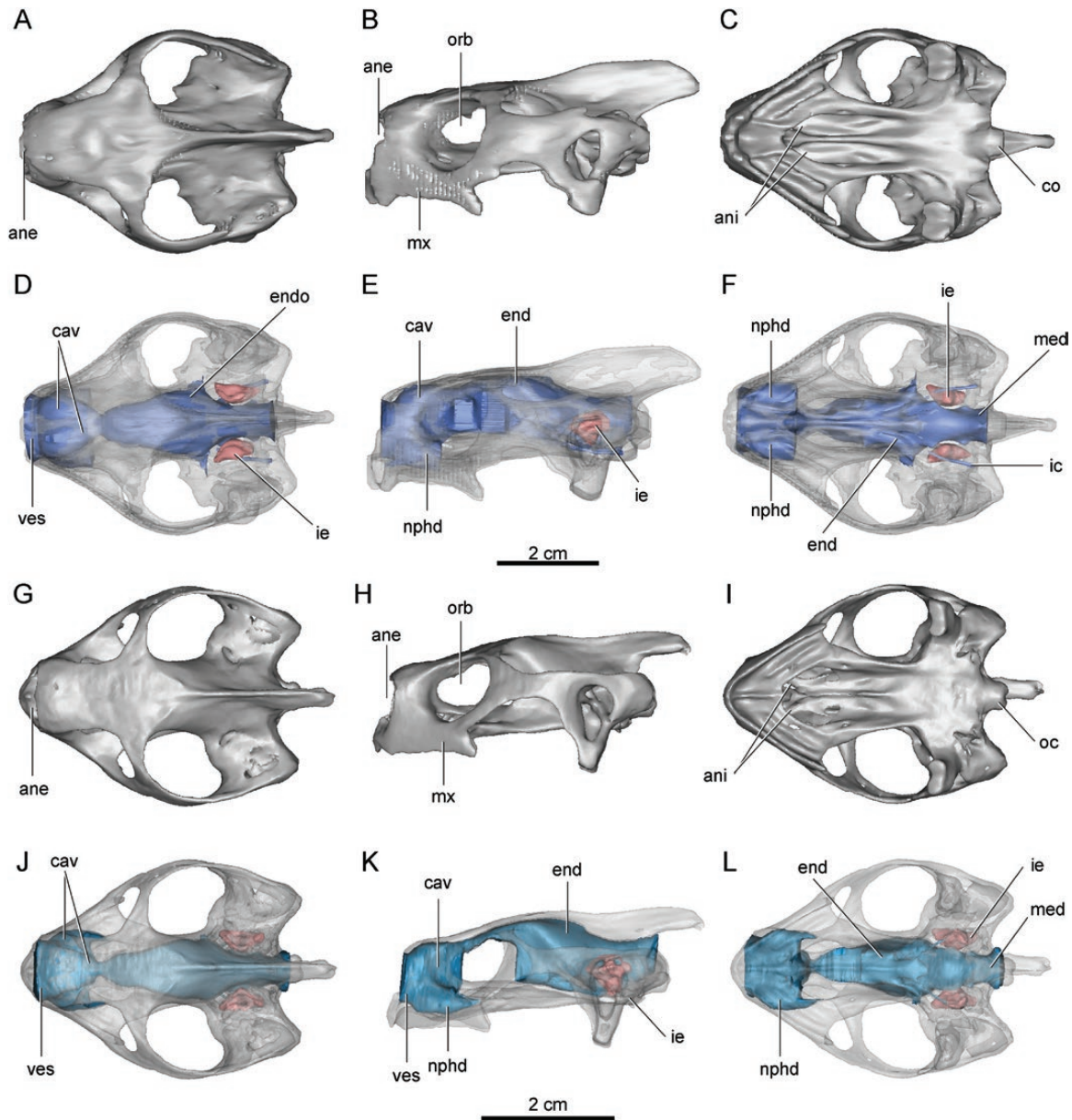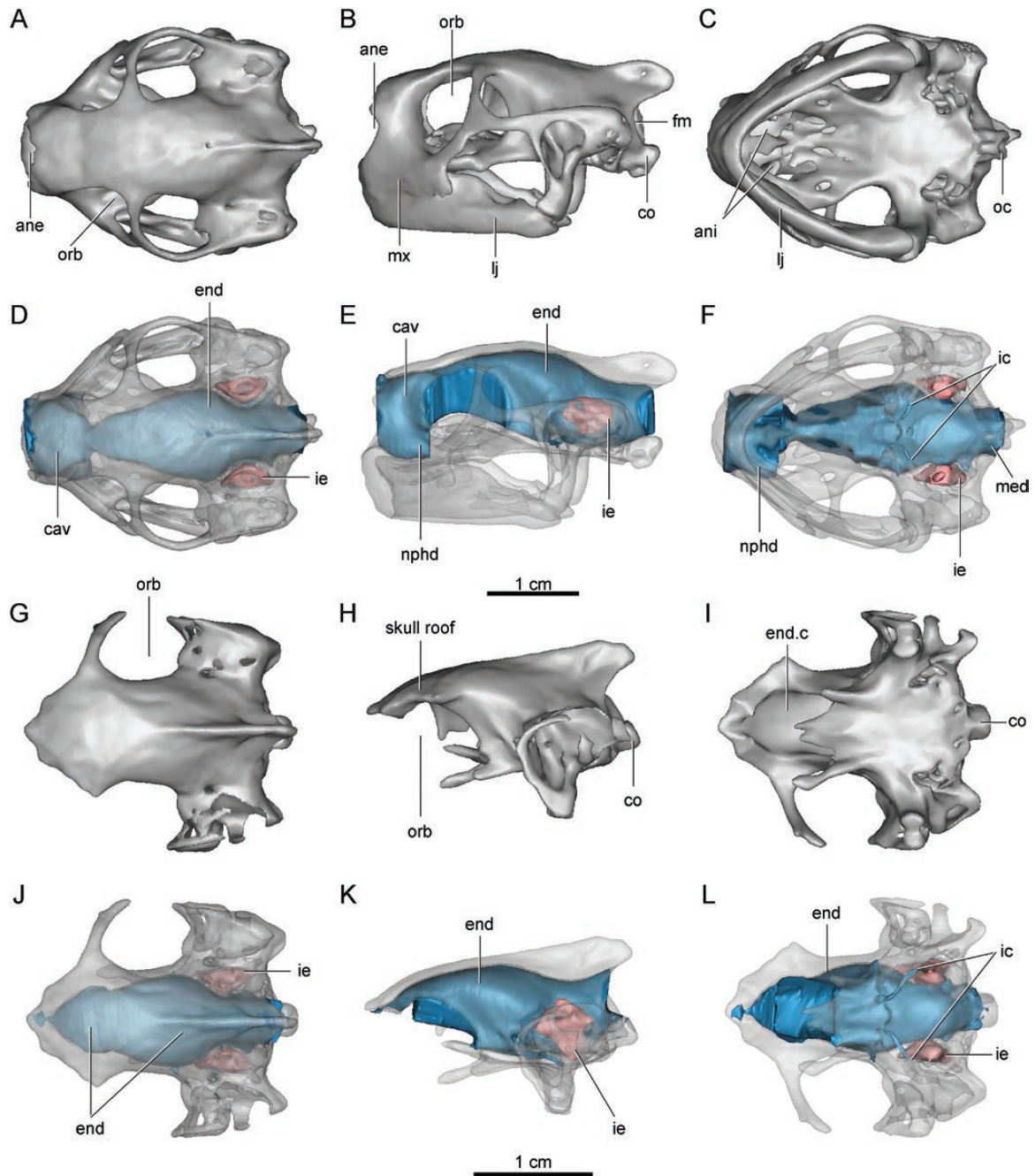
Figure 6. Digital reconstruction of the skull of *Chelonoidis chilensis* (A–F) and *Gopherus berlandieri* (G–L) in dorsal (A, G), left lateral (B, H) and ventral (C, I) views. In the ventral images the bone is rendered semitransparent to allow the observation of internal structures. Abbreviations: ane, apertura narium externa; ani, apartura narium interna; cav, cavum nasi proprium; co, condylus occipitalis; end, endocranial cast; end.c, endocranial cavity; fst. foramen stapedio-temporale; ic, internal carotid artery; ie, inner ear; mx, maxilla; med, medulla oblongata; nphd, nasopharyngeal duct; orb, orbit; ves, vestibulum. Scale bars = 20 mm.

olfactory tracts (markedly short in all turtles) (Fig. 9). In contrast, the olfactory bulbs are not clearly differentiated in the cranial endocasts of aquatic forms, suggesting that olfactory acuity of terrestrial forms is greater (Parsons, 1959). The olfactory bulbs are more or less oval in shape. The maximum transversal distance across right and left olfactory bulbs is wider than the transversal distance of the medulla oblongata between the inner ears in *G. berlandieri* and *C. chilensis*, and is markedly wider in *K. belliana* and in *T. hermanni*, whereas it is narrower/shorter in *T. graeca* (Fig. 9). The shape of the cranial endocast in dorsal view is pear-shaped and markedly anteroposteriorly elongate in *G. berlandieri*, *C. chilensis* and *K. belliana*, whereas it is
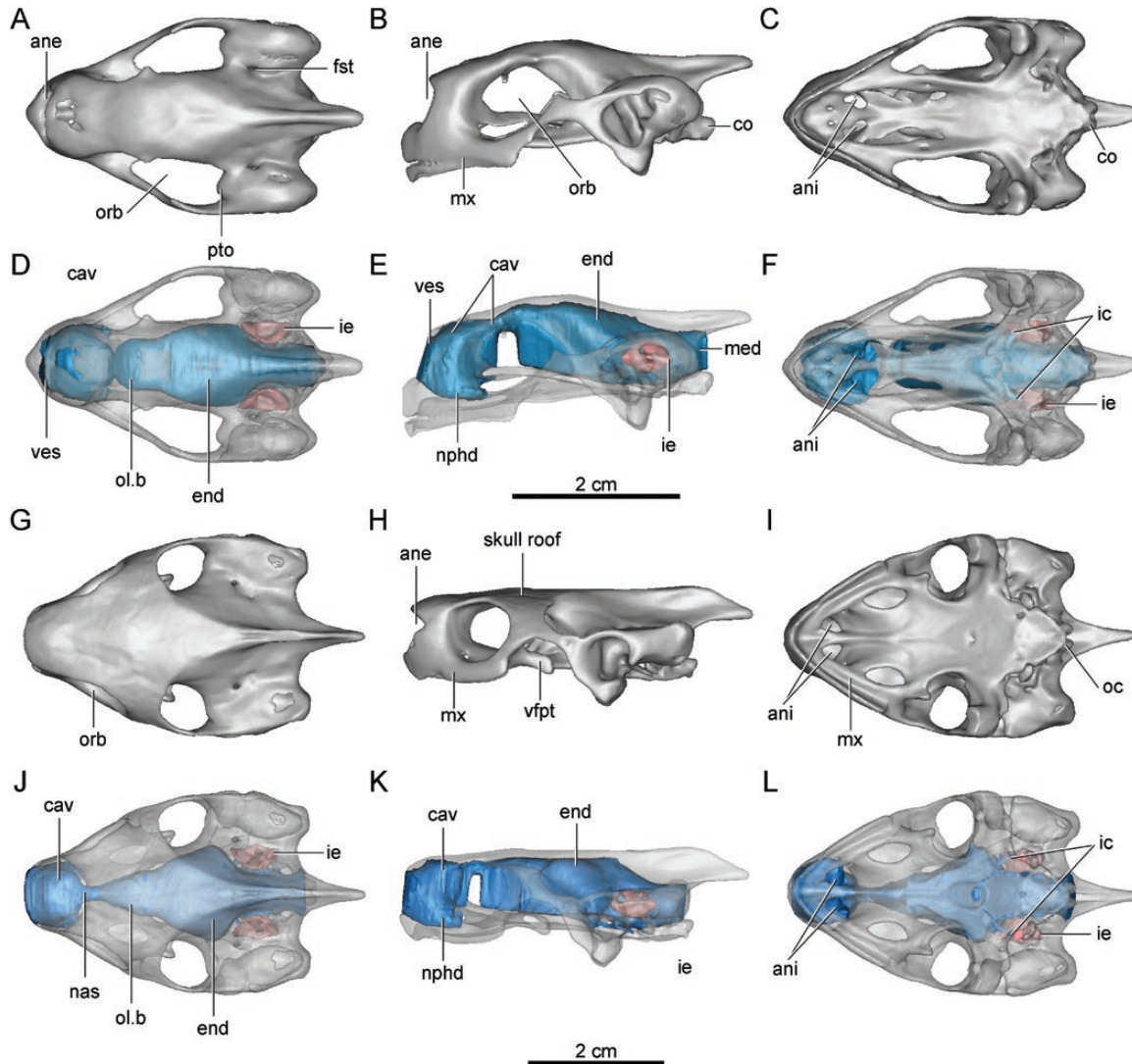
Figure 7. Digital reconstruction of the skull of *Testudo graeca* (A–F) and *Testudo hermanni* (G–L) in dorsal (A, G), left lateral (B, H) and ventral (C, L) views. In the ventral images the bone is rendered semitransparent to allow the observation of internal structures. Abbreviations: idem Fig. 6, lj, lower jaw. Scale bars = 10 mm.

less elongate in *T. graeca* and *T. hermanni*. The olfactory ducts for CN I – connecting the olfactory bulbs posteriorly and the nasal cavities anteriorly – are relatively short and more robust than those in aquatic cryptodiran forms, which have elongate olfactory ducts (Paulina-Carabajal *et al.*, 2013: fig. 7A).

Inner ear

The inner ear morphology of all the testudinids in the sample is similar, sharing short and robust common crus, low/short and robust semicircular canals (Figs 9, 10E–P). As described for *Chelonoidis* (Georgi, 2008), the vertical semicircular canals branches from the

Figure 8. Digital reconstruction of the skull of *Kinixys belliana* (A–F) and *Rhinoclemmys funerea* (G–L) in dorsal (A, G), left lateral (B, H) and ventral (C, I) views. In the ventral images the bone is rendered semitransparent to allow the observation of internal structures. Abbreviations: idem Fig. 6; pto, procesus trochlearis oticum; vfpt, vertical flange of the pterygoid. Scale bars = 20 mm.

common crus horizontally, thus not rising above the level of the top of the common crus, except (slightly) in both *Testudo* species, in which the canals project dorsally forming a curve that overpasses the level of the apex of the common crus (Fig. 10E–P). The common crus is short and markedly robust, having more than three times the width of the semicircular canals. In *T. graeca* the ASC and the PSC join the common crus so separately that in dorsal view they do not form a V-shaped angle (Fig. 10J). The angle formed between the ASC and PSC is close to 100° in most species (Table 1). The aquatic geoemydid *R. funerea* (Fig. 8G–L) has a more robust common crus than

the terrestrial testudinids, although in contrast it has more slender semicircular canals (Fig. 10O, P). In all testudinid species, the vestibule is characterized by well-developed anterior ampullae which in some cases obscure the limits of the LSC, as is the case of *T. hermanni* and *K. belliana* (Fig. 10L, N). The fenestra ovalis is circular or oval and has a large diameter, occupying more than the 50% of the vestibulum width, as described for the extinct *P. etalloni* (Paulina-Carabajal *et al.*, 2013). The fenestra ovalis is however smaller than that observed in *G. auricularis*, which occupies almost the complete width of the vestibulum (Fig. 10A).
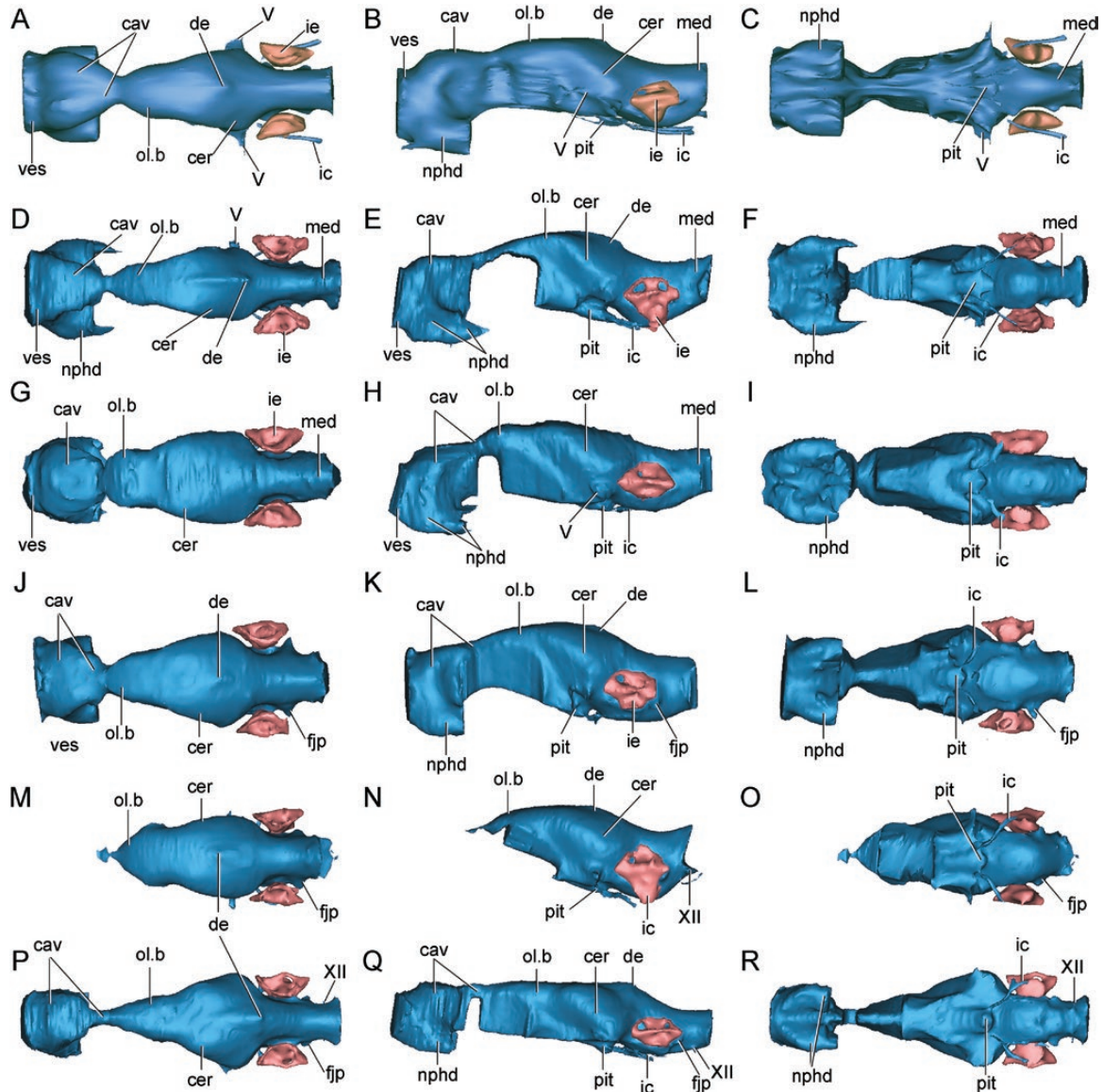
Figure 9. Testudinid and one geoemydid cranial endocasts in dorsal, left lateral and ventral views. (A–C) *Chelonoidis chilensis*; (D–F) *Gopherus berlandieri*; (G–I) *Kinixys belliana*; (J–L) *Testudo graeca*; (M–O) *Testudo hermanni*; (P–R) *Rhinoclemmys funerea*. Abbreviations: cav, cavum nasi proprium; cer, cerebral hemisphere; de, dorsal expansion; fjp, foramen jugulare posterius (for CN IX–XI); ic, internal carotid artery; ie, inner ear; med, medulla oblongata; nphd, nasopharyngeal duct; ol.b, olfactory bulb; pit, pituitary; ves, vestibulum; V, VI, XII, cranial nerves. Not to scale.

COMMENTS ON PALAEOBIOLOGICAL IMPLICATIONS

NASAL CAVITIES AND RESPIRATORY AND OLFACTORY FUNCTIONS

The nasal region of vertebrates plays a key role in sensory, thermal and respiratory physiology, but assessment of its evolutionary development has been hampered by the lack of soft-tissue preservation in fossils (Bourke *et al.*, 2014). In meiolaniids, the nasal cavity is characteristically hypertrophied (Gaffney, 1983), as reflected in the cranial endocasts of *M. platyceps* and *N. argentina* (Figs 1, 2). The volume of the nasal cavity represents approximately 60% of the complete endocranial cast, contrasting with the 29–43% observed in extant testudinids (*T. graeca* and *C. chilensis*, respectively), and approximately 20% in the geoemydid *R. funerea* (Table 1). The nasal cavity of *G. auricularis* is not preserved, but we anticipate a similar morphology to other meiolaniids.

The vestibulum nasi corresponds to the anterior tubular region and forms only a small portion of the
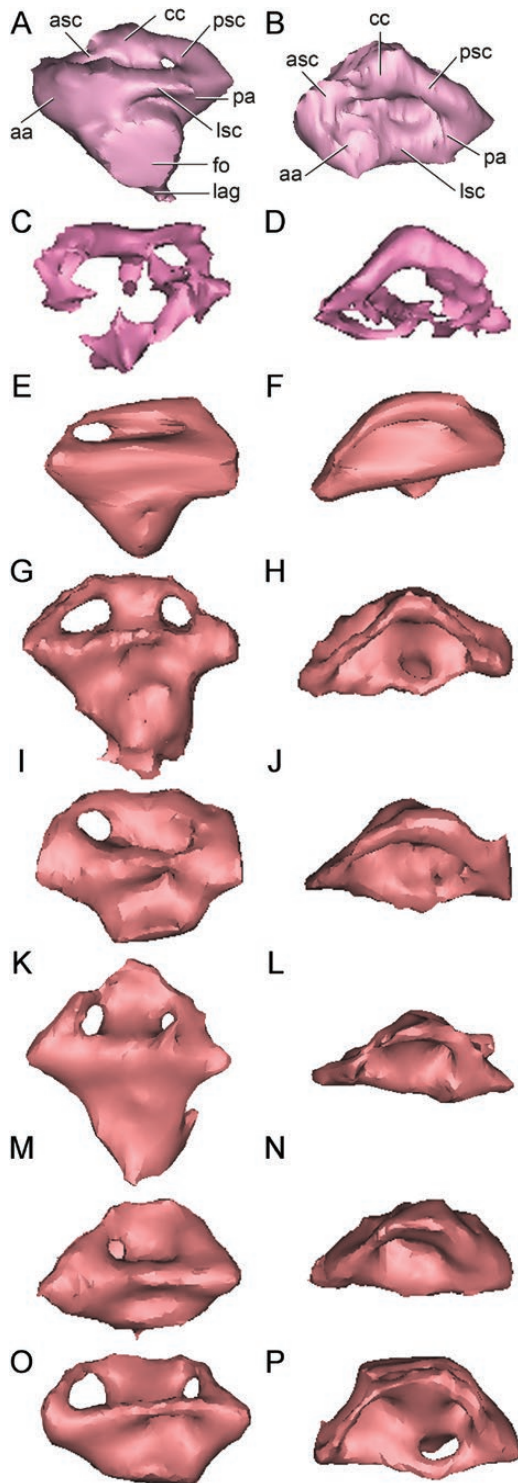
Figure 10. Digital reconstruction of the left inner ear morphologies of *Gaffneylania auricularis* (A, B), *Meiolania platyceps* (C, D), *Chelonoidis chilensis* (E, F), *Gopherus berlandieri* (G, H), *Testudo graeca* (I, J), *Testudo hermanni* (K, L), *Kinixys belliana* (M, N) and *Rhinoclemmys funerea* (O, P); in lateral (left column) and dorsal (right column) views.

nasal cavity. Testudinids have a vestibulum, which is weakly expressed in our endocasts as a short projection between the naris and the cavum nasi proprium; although the vestibulum has a bony floor, it has no osseous roof (Fig. 9), unlike meiolaniids. Meiolaniids have an enlarged vestibulum, enclosed in a tube-shaped osseous box. This morphology is reflected in the cast of the nasal cavity as an anterior projection, clearly differentiated from the cavum nasi proprium (Fig. 5). This morphology is similar only to that present in some extant aquatic turtles with snorkel-like noses and elongated vestibula such as *C. fimbriatus*, *Carettochelys insculpta* and trionychids (e.g. Schwenk, 2008). Elongation of the vestibulum of the nasal cavity in other extant terrestrial reptiles such as some lizards (e.g. iguanids) is correlated with a specialization for desert life (Parsons, 1959), since it limits the possibility of sand particles entering the nose. As mentioned by Bramble & Hutchison (2014), digging has been reported in some testudinids (e.g. *Centrochelys sulcata*) but is only fully adopted among the highly specialized gopher tortoises (*Gopherus* spp.). In meiolaniids the function of the enlarged vestibulum is unknown, and might be related to olfactory capabilities, arid-zone ecological adaptation, thermoregulation or even sound production.

The ductus nasopharyngeus is a tubular structure that connects the nasal cavity with the choana posteroventrally. It has a respiratory function in reptiles, but may also contain sensory zones in turtles (Parsons, 1959). The ductus nasopharyngeus is a convex tube projecting posteroventrally that is visible in lateral and ventral views (Figs 5, 9). All terrestrial turtles have short nasopharyngeal ducts compared to those in highly aquatic forms (e.g. Schwenk, 2008; Paulina-Carabajal *et al.*, 2013: fig. 2C). There are no marked differences in the shape and size of the nasopharyngeal duct between testudinids and meiolaniids. In both groups there are short, robust and convex posterolateral tubular projections on the ventral aspect of the nasal cavity (Figs 5G, I, 9). In testudinids, the duct is as long as the cavum nasi proprium, whereas in meiolaniids it is shorter; but slightly longer in *N. argentina* as compared with *M. platyceps* (Fig. 5G, I).

In turtles, the cavum nasi proprium is the largest region of the nasal cavity (Figs 5, 9). It can be subdivided into two sections: a posterior or posterodorsal olfactory region (= Muschelwulst) and an intermediate region, which is located between the vestibulum

Abbreviations: aa, anterior ampula; asc, anterior semicircular canal; cc, crus communis; fo, fenestra ovalis; lag, lagena; lsc, lateral semicircular canal; pa, posterior ampula; psc, posterior semicircular canal. Not to scale.

and the nasopharyngeal duct (Parsons, 1959: fig. 4B). Posteriorly, the cavum nasi proprium connects with the anterior section of the olfactory bulbs through an elongate olfactory duct. In extant reptiles, the external nasal gland is located in the posterolateral section of the cavum. It is usually the largest of the nasal glands in this group, and is located dorsolaterally within the nasal cavity, between the cartilaginous nasal capsule and the bony skull (Parsons, 1959). In testudinids this nasal gland is observed in the cast of the nasal cavity in *C. chilensis* (Figs 6D, 9A, B). The cavum nasi proprium is well developed in testudinids, but is small or absent in most other groups of extant turtles (e.g. Parsons, 1959; Beidler, 1971). Since terrestrial turtles have better olfactory capabilities than aquatic turtles (Parsons, 1959), the size of the cavum nasi proprium, together with the olfactory bulbs can probably be used as an indicator of olfactory capabilities in extinct taxa. In testudinids the dorsal surface of the cavum nasi proprium is levelled with the dorsal margin of the medulla oblongata, whereas in meiolaniids it projects dorsally over that level. The extinct meiolaniids have markedly larger cavum nasi proprium than do extant terrestrial turtles; in fact the nasal cavity in meiolaniids has a greater volume than the region of the cast occupied by the brain.

The cavum nasi proprium was observable in *M. platyceps* and *N. argentina* (Fig. 5A, G). In dorsal view, the constriction separating the cavum from the vestibulum is clearly visible, and the anteroposterior development of the cavum is similar in both species. However, the cavum is slightly more laterally and dorsally expanded in *M. platyceps* than in *N. argentina*. In lateral view, the dorsal margin of the vestibulum is situated below the dorsal margin of the cavum in *M. platyceps*. Conversely, in *N. argentina*, they are both at the same level (the naris thus opens further ventrally in *M. platyceps* than in *N. argentina*). In *M. platyceps*, the intermediate region of the cavum seems to be relatively larger than in *N. argentina*. The posterior margin of the cavum is well marked in both species. A strong constriction indicates the beginning of the olfactory duct, which has a relatively large diameter in both taxa. However, the enlarged (and subdivided in *N. argentina*) dorsal region of the cavum nasi proprium in meiolaniids might not have been limited to an olfactory function. For example, in pachycephalosaurid dinosaurs (Bourke *et al.*, 2014) the air flowing through an expanded and convoluted nasal cavity is thought to have cooled the blood before it reached to the brain. Enlarged and subdivided airway paths likewise occur in the nasal cavities of hadrosaurid ornithopods (Witmer, 2001; Evans, 2006; Witmer & Ridgely, 2008; Evans, Ridgely & Witmer, 2009) and ankylosaurs (Witmer & Ridgely, 2008; Miyashita *et al.*, 2011; Paulina-Carabajal, Lee & Jacobs, 2016), suggesting

that besides olfaction at least the dorsal region of the nasal cavity perhaps contributed to thermoregulatory and/or vocalization. Meiolaniids however, have relatively simple nasal cavities that are not septate like a putative resonating chamber. In contrast, the hypertrophied region of the nasal cavity corresponds mainly to the dorsal expansion of the cavum nasi proprium (where, presumably, the olfactory epithelium was located) inferring a primarily olfactory role. However, comparisons of the volume of the nasal cavity (relative to the volume of the cranial endocast) and the calculated ORs (Zelenitsky *et al.*, 2009) indicate that the hypertrophied nasal cavities in meiolaniids would not be directly related to olfactory acuity. For now, the primary functional morphology of the enlarged cavum nasi proprium in meiolaniids remains unknown.

Olfactory bulb morphology

Some studies have suggested that olfaction plays several roles in turtle behaviour such as foraging, feeding, aggregating, locating predators, navigating, intraspecific communication, aggression, combat, courtship and reproduction (e.g., Manton, 1979; Boiko, 1984a; Mason, 1992; Alberts, Rostal & Lance, 1994; Graham, Georges & McElhinney, 1996; Eisthen & Polese, 2007; Galeotti *et al.*, 2007). In particular, Auffenberg (1977) noticed that with respect to social and reproductive behaviours, chemical and tactile signals seem to be more important than visual and auditory signals in tortoises. A wide variety of odours can be detected by the well-developed nasal olfactory and vomeronasal systems in turtles (Halpern, 1992; Gerlach, 2005). However, the correlation of nasal chemical sense with anatomical, behavioural and physiological data is still unclear for the majority of turtle species (Halpern, 1992).

The size of the olfactory bulb has been used as an indicator of olfactory acuity or the ability to discriminate between different odours in extant archosaurs and mammals (Zelenitsky *et al.*, 2009 and references therein). Studies in extant turtles demonstrated that they have a keen sense of smell, with olfactory bulbs similar in size to those observed in pigeons (Reiner & Karten, 1985). We calculated the ORs (bulb maximum diameter vs. cerebral hemisphere maximum diameter, see Zelenitsky *et al.*, 2009) for the meiolaniids and testudinids analyzed in this study (Table 1). Amongst these turtles, the olfactory tracts and bulbs leave no clear impressions on the endocranial cavity in most specimens; however, the size and approximate shape of the olfactory bulbs are recognized as a slight widening of the anterior section of the forebrain. This enlargement is particularly clear in the extant testudinids *T. graeca* and *K. belliana*, although in the studied meiolaniids there was no clear differentiation of the olfactory

tract and bulbs in the forebrain. In this context, the ORs of meiolaniids are approximately between 20 and 45% (olfactory bulb size is particularly difficult to determine), whereas the ORs of testudinids are between 36 and 62%, the highest ORs being for *C. chilensis*, *K. belliana* and *T. hermanni*. Testudinid ORs are within the range (or even slightly higher) calculated for the living crocodile *Alligator mississippiensis* (Zelenitsky *et al.*, 2009: table 1), which is about 49.8–55%. Zelenitsky *et al.* (2009) stated that olfactory bulb's greatest diameter/cerebral hemisphere's greatest diameter ratios are influenced by body size; therefore, the ratios should not be used to directly compare olfactory acuity between the sampled turtles. Consequently, we present these calculations as a preliminary attempt to determine the palaeobiological implications of brain morphology within extinct turtles.

Chemical cues and behaviour

Mason (1992) identified Rathke's glands and the cloaca as the primary sources of chemical secretions from turtles. Rathke's glands (= musk or inframarginal glands) are located on the bridge area of the shell, or can open through pores in the skin (Weldon & Gaffney, 1998). They can also be traced in fossils where they penetrate the bony shell as musk ducts (Weldone & Gaffney, 1998), and their presence/absence has been considered a phylogenetically informative character (Shaffer, Meylan & McKnight, 1997; Joyce, 2007). Rathke's glands are present in almost all extant turtles with the exception of testudinids and the *Chrysemys* complex (Waagen, 1972). Cloacal secretions, on the other hand, have not been described in detail, and are usually mentioned anecdotally in reports on courtship behaviour in some taxa (Mason, 1992). Testudinids are also distinctive in utilizing mental glands (=chin, subdentary or submandibular glands) for secretions, in addition to the cloaca (Mason, 1992). Mental glands have been documented in 21 testudinids, as well as emydid and platysternid genera (Mason, 1992). Furthermore, responses to mental and cloacal secretions are specifically recorded in the reproductive behaviour of the testudinids *G. berlandieri* (Rose, 1970), *G. polyphemus* (Auffenberg, 1966), *Geochelone radiata* (Auffenberg, 1978), *T. graeca* (Boiko, 1984b) and *T. hermanni* (Galeotti *et al.*, 2007). Pointedly, the nasal cavity of testudinids is enlarged compared with other turtles, and Rathke's glands are absent. Unfortunately, insufficient evidence exists to draw a direct correlation between the size of the nasal cavity and the presence/absence of certain glands in extant turtles.

Chemical cues in turtles have been linked to aggression and combat behaviour (Mason, 1992). Fights between males, and occasionally males and females have been recorded in several species, particularly the testudinids *Gopherus agassizii* (Camp, 1916), *G. berlandieri* (Carr, 1952), *Geochelone elephantopus* (Carpenter, 1966), *T. hermanni* and *T. marginata* (Willemsen & Hailey, 2003). Carpenter (1978) described physical interaction during shell-shell combat as mainly comprising knocking, ramming, bumping, pushing, shell crowding, clapping shells together, tapping of shells, thrusting shell upwards and downwards, rocking shell back and forth, side to side, or twisting back and forth, pivoting or rotating the shell and so on. Similar activities might have been expressed by meiolaniids, with the characteristic horns, frills and tail armoured by bony rings playing an active role. Indeed, Jannel (2014) suggested that neck mobility coupled with horns in *M. platyceps* could have functioned in intraspecific combat. We further speculate that the hypertrophied nasal cavities could be related to social/reproductive behaviour and note that analogous structures in ceratopsian, ankylosaurian and pachycephalosaurian dinosaurs (e.g. Sues, 1978; Farke, 2004, 2014; Carpenter *et al.*, 2005; Arbour, 2009; Farke, Wolff & Tanke, 2009; Mallison, 2011; Snively & Theodor, 2011) have likewise been interpreted as combat structures (Farke, 2014). Further studies about the bone density and plausible stresses suffered by the bones in the skull and tail club (work in progress) will provide more evidence about the feasibility of certain behaviours in meiolaniids.

INNER EAR, GAZE STABILIZATION
AND HEARING CAPABILITIES

Despite the potential adaptive significance of its different regions, the up-to-date available information about the gross morphology of the inner ear is phylogenetically conservative. This is evident in the overall similarity between inner ear structure of meiolaniids and other extinct and extant turtles (e.g. Georgi, 2008; Paulina-Carabajal *et al.*, 2013 and references therein). Typical features include the robust and depressed (short) semicircular canals, robust common crus, enlarged vestibule, large fenestra ovalis and short lagena (Fig. 10). It is notable, however, that the semicircular canals appear robust in the examined meiolaniids (Fig. 10). In *Gaffneylania auricularis* in particular, the ASC and PSC branch below the apex of the common crus (Fig. 10A), a condition which is similarly expressed by some of the members of the African tortoise genus *Kinixys* (Fig. 10K). In many other testudinids the ASC and PSC usually branch from the common crus more or less horizontally, and thus do not extend above the level of the common crus (Georgi, 2008). Alternatively, the ASC and PSC in *Testudo* project dorsally forming a curve after branching from the common crus (Fig. 10); this extends the semicircular canals slightly beyond the apex of the common crus.

The angle formed between the ASC and the PSC in dorsal view is near to 100° in testudinids (Table 1). Meiolaniids have wider angles (approximately 115° in *G. auricularis*), whereas the aquatic *R. funerea*, *C. fimbriatus* (Georgi, 2008: fig. 18D) and extinct *P. etalloni* (Paulina-Carabajal *et al.*, 2013) display between 80° to 95° angles for the extant/extinct taxa, respectively. This implies that the more terrestrial turtles are characterized by a distinctly obtuse orientation between the ASC and PSC, a condition that would make the vestibular system more sensitive to rotation in the pitch plane, but less sensitive to roll inherent within an aquatic medium (Brichta, Acuña & Peterson, 1988; Davenport, Munks & Oxford, 1984). The vertical semicircular canals react to roll because their reduced angle increases the potential for head and gaze stabilization. In contrast, the typical terrestrial gait of testudinids incorporates an additional pronounced pitch-down rotation with each stride as their rigid trunk passes anterior to the base of support (Jayes & Alexander, 2009; Walker, 1971). Under these conditions a wider angle between the vertical canals would improve head and gaze stabilization; a possible exception could occur in chelonioids, whose sub-aqueous 'flight' produces significant pitch but not roll (Davenport *et al.*, 1984). The biophysics of both the acoustic and balance organs of the inner ear mean that functionally significant deviations from the basic group morphology of the inner ear can be subtle and often require large sample comparisons to detect. Although this study does not examine a broad enough sample to form any quantitative conclusions, there are some noteworthy patterns of morphological variation of potential functional significance that could warrant future investigation.

Turtles exhibit many unique features of their hearing apparatus in both the inner and middle ear regions. Although many of these features are soft tissue, notable bony features include separation of the inner from middle ear by the quadrate, a pericapsular space (fluid-filled in life) between the quadrate and fenestra ovalis, and the absence of a fenestra rotundum. In addition, meiolaniids share with extant turtles the morphological trends found in the more generic aspects of the inner ear such as the short lagena and greatly enlarged fenestra ovalis, which are common testudinatan traits. Moreover, the fenestra ovalis is large and circular, unlike that of testudinids, and occupies almost all the width of the vestibulum (the diameter of the fenestra ovalis is around 37% of the maximum width of the inner) in most species (e.g. Fig. 10A, G). Unfortunately, the columella auris has not been preserved in our specimens, but the diameter of the fenestra ovalis indicates that the columellar footplate was of comparable size to that of *P. etalloni*

(Paulina-Carabajal *et al.*, 2013: fig. 6E). The prominent fenestra ovalis and columellar footplate permit detection of lower amplification vibrations from the tympanic membrane than is possible in most other tetrapods.

Hetherington (2008) summarized the complex relationship between inner ear morphology and hearing sensitivity in turtles, and concluded that their sensitivity to low-frequency sounds (Wever, 1978) likely derived from inner ear mechanics or processing. Hetherington (2008) further stated that the hearing range of turtles is consistent with animal groups that do not rely upon vocalization to communicate. As there is no indication that meiolaniids had significantly different acoustic morphology in the inner ear region from modern turtle taxa, it is reasonable to infer that their hearing capabilities were consistent with modern turtles. This complies with the relatively high ORs (Table 1), which alternatively suggest that smell was a primary sensory mechanism.

CONCLUSIONS

Here we document the neuroanatomy of extinct meiolaniids for the first time and present comparisons with six extant testudinoids based on CT renderings and physical endocasts of the brain, inner ear and nasal cavity regions. In meiolaniids the nasal cavity is hypertrophied, and represents around 60% of the entire endocranial space; in testudinoids this proportion is only between 20 and 40%. Such nasal cavity expansion corresponds mainly to the cavum nasi proprium, whose enlargement could correlate with enhanced olfactory rather than respiratory function. Conversely, based on ORs and testudinid analogues, nasal cavity hypertrophy might also be evidence of peculiar chemosensory social behaviours during courtship or other intraspecific communication. Indeed, we further speculate that cranial horns, frills and tail armour might have contributed to such a function.

The inner ear of meiolaniids is morphologically conservative, like other turtles, and incorporates short and robust semicircular canals, robust common crus, enlarged vertibule, large fenestra ovalis and short lagena. Nevertheless, terrestrial turtles possess notably wider angles between the ASC and PSC, which renders the vestibular system less sensitive to roll, but more sensitive to rotation in the pitch plane. This condition is also evident in meiolaniids, advocating a terrestrial lifestyle and complies with a typical interpretation of the turtle ear as being orientated towards reception of low-frequency sounds (Wever, 1978). Meiolaniids were thus probably not vocal in their communication, but rather relied upon olfaction as their primary sense.

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REFERENCES

Alberts AC, Rostal DC, Lance VA. 1994. Studies on the chemistry and social significance of chin gland secretions in the Desert Tortoise, *Gopherus agassizii*. *Herpetological Monographs* **8:** 116–124.

Ameghino F. 1899. Sinopsis geológica – palaeontológica. Suplemento (adiciones y correcciones). *Censo Nacional La Plata* **4:** 1–13.

Anderson C. 1925. Notes on the extinct chelonian *Meiolania*, with record of a new occurrence. *Records of Australian Museum* **14:** 223–242.

Arbour VM. 2009. Estimating impact forces of tail club strikes by ankylosaurid dinosaurs. *PLoS One* **4:** e6738.

Auffenberg W. 1964. A redefinition of the fossil tortoise Genus *Stylemys* Leidy. *Journal of Palaeontology* **38:** 316–324

Auffenberg W. 1966. On the courtship of *Gopherus polyphemus*. *Herpetologica* **22:** 113–117.

Auffenberg W. 1977. Display behavior in tortoises. *American Zoologist* **17:** 241–250.

Auffenberg W. 1978. Courtship and breeding behavior in *Geochelone radiata* (Testudines: Testudinidae). *Herpetologica* **34:** 277–287.

Beidler LM. 1971. *Olfaction. Handbook of Sensory Physiology*. Berlin: Springer-Verlag.

Boiko VP. 1984a. The participation of chemoreception in the organization of reproductive behavior in *Emys orbicularis* (Testudines, Emydidae). *Zoologicheskii Zhurnal* **63:** 584–589.

Boiko VP. 1984b. Reproductive behavior in the Mediterranean tortoise *Testudo graeca*. *Zoologicheskii Zhurnal* **63:** 228–232.

Bojanus LH. 1819. *Anatome Testudinis Europaeae. Vilnae, Impensis Auctoris*. USA: Society for the Study of Amphibians and Reptiles, 1970.

Bourke JM, Porter WMR, Ridgely RC, Lyson TR, Schachner ER, Bell PR, Witmer LM. 2014. Breathing life into dinosaurs: tackling challenges of sort-tissue restoration and nasal airflow in extinct species. *The Anatomical Record* **297:** 2148–2186.

Bramble DM, Hutchison JH. 2014. Morphology, taxonomy, and distribution of North American Tortoises. In: Rostal DC, McCoy ED, Mushinsky HR, eds. *Biology and conservation of North American tortoises*. Baltimore: Johns Hopkins University Press.

Brichta AM, Acuña DL, Peterson EH. 1988. Planar relations of semicircular canals in awake, resting turtles, *Pseudemys scripta*. *Brain, Behavior and Evolution* **32:** 236–245.

Camp CL. 1916. *Notes on the local distribution and habits of the Amphibians and reptiles of Southeastern California in the vicinity of the Turtle mountains*. Berkeley: University of California Press.

Carr AF. 1952. *Handbook of turtles: the Turtles of the United States, Canada, and Baja California*. Ithaca: Cornell University Press.

Carpenter CC. 1966. Notes on the behavior and ecology of the Galápagos tortoise on Santa Cruz Island. *Proceedings of the Oklahoma Academy of Sciences* **46:** 28–32.

Carpenter CC. 1978. Variation and evolution of stereotyped behavior in reptiles: part I. A survey of stereotyped reptilian behavioral patterns. In: Gans C, Tinkle DW, eds. *Biology of the reptilia, Vol. 7. Ecology and Behaviour A*. London, New York, and San Francisco: Academic Press, 335–404.

Carpenter K, Sanders F, McWhinney LA, Wood L. 2005. Evidence for predator-prey relationships: examples for *Allosaurus* and *Stegosaurus*. In: Carpenter K, ed. *The Carnivorous Dinosaurs*. Bloomington: Indiana University Press, 325–350.

Crumly CR. 1984. *The evolution of land tortoises (Family Testudinidae)*. Unpublished D. Phil. thesis, Rutgers University.

Davenport J, Munks SA, Oxford PJ. 1984. A comparison of the swimming of marine and freshwater turtles. *Proceedings of the Royal Society of London B.* **220:** 447–475.

Deantoni FO. 2015. *Palaeoneurologia e morfologia intracraniana de tartarugas pleurodiras*. In *5° Congreso Latinoamericano de Palentología de Vertebrados*, Colonia, Uruguay. Abstracts: 28

Deantoni FO, Romano PSR, Azevedo SAK. 2012. Analysis of internal structure of the skull of pelomedusoides (Testudines, Pleurodira) based on three-dimensional helical tomography. In *Symposium on turtle evolution*, Tubingen, Germany. Abstracts: 17.

Edinger T. 1929. *Die fossilen Gehirne. Ergeb. Anat. und Entwicklungsgesch., Band 28*. Berlin: Julius Springer-Verlag.

Edinger T. 1934. Anton Fritsch's 'Grosshirn von Polyptychodon' ist der Steinkern eines Schildkrötenschadels. *Psychiatrische en neurologische bladen* **3–4:** 396–404.

Eisthen HL, Polese G. 2007. Evolution of vertebrate olfactory subsystems. In: Bullock TH, Kaas JH, eds. *Evolution*

of nervous systems: a comprehensive reference, *Vol.* **2.** *Non-mammalian vertebrates*. Oxford: Academic Press, 355–406.

Evans DC. 2006. Nasal cavity homologies and cranial crest function in lambeosaurine dinosaurs. *Palaeobiology* **32:** 109–125.

Evans DC, Ridgely R, Witmer LM. 2009. Endocranial anatomy of *Lambeosaurine hadrosaurids* (Dinosauria: Ornithischia): a sensorineural perspective on cranial crest function. *The Anatomical Record* **292:** 1315–1337.

Farke AA. 2004. Horn use in *Triceratops* (Dinosauria: Ceratopsidae): testing behavioral hypothesis using scale models. *Palaeontologia Electronica* **7:** 10, 3MB. Availabe at: http://palaeo-electronica.org/palaeo/2004_3/horn/issue1_04.htm

Farke AA. 2014. Evaluating combat in ornitischian dinosaurs. *Journal of Zoology* **292:** 242–249.

Farke AA, Wolff ED, Tanke DH. 2009. Evidence of combat in *Triceratops*. *PLoS One* **4:** e4252.

Gaffney ES. 1977. An endocranial cast of the side-necked turtle, *Bothremys*, with a new reconstruction of the palate. *American Museum Novitates* **2639:** 1–12.

Gaffney ES. 1979. Comparative cranial morphology of recent and fossil turtles. *Bulletin of the American Museum Natural History* **164:** 65–376.

Gaffney ES. 1982. Cranial morphology of the baenid turtles. *American Museum Novitates* **2737:** 1–22.

Gaffney ES. 1983. The cranial morphology of the extinct horned turtle, *Meiolania platyceps*, from the Pleistocene of Lord Howe Island, Australia. *Bulletin of the American Museum of Natural History* **175:** 364–479.

Gaffney ES. 1985. The cervical and caudal vertebrae of the cryptodiran turtle, *Meiolania platyceps*, from the Pleistocene of Lord Howe Island, Australia. *American Museum of Natural History* **2805:** 1–22.

Gaffney ES. 1996. The postcranial morphology of Meiolania platyceps and a review of the Meiolaniidae. *Bulletin of the American Museum of Natural History* **229:** 1–165.

Gaffney ES, Zangerl R. 1968. A revision of the chelonian genus Bothremys (Pleurodira: Pelomedusidae). *Fieldiana Geolology* **16:** 193–239.

Galeotti P, Sacchi R, Rosa DP, Fasola M. 2007. Olfactory discrimination of species, sex, and sexual maturity by the Hermann's tortoise *Testudo hermanni*. *Copeia* **2007:** 980–985.

Georgi JA. 2008. *Semicircular canal morphology as evidence of locomotor environment in amniotes*. Unpublished D. Phil. thesis, Stony Brook University.

Gerlach J. 2005. The complex vomeronasal structure of *Dipsochelys* giant tortoises and its identification as a true Jacobson's organ. *The Herpetological Journal* **15:** 15–20.

Graham T, Georges A, McElhinney N. 1996. Terrestrial orientation by the eastern long-necked turtle, *Chelodina longicollis*, from Australia. *Journal of Herpetology* **30:** 467–477.

Gray JE. 1870. *Supplement to the catalogue of shield reptiles in the collection of the British Museum. Part I: Testudinata (Tortoises) with figures of the skulls of 36 Genera*. London: British Museum (Natural History), 120 pp.

Halpern M. 1992. Nasal chemical senses in reptiles. In: Gans C, Crews D, eds. *Biology of the reptilia*, *Vol.* **18**. Chicago and London: University of Chicago Press, 423–524.

Hay OP. 1908. *The fossil turtles of North America*. Washington, DC: Carnegie Institution of Washington.

Hetherington T. 2008. Comparative anatomy and function of hearing in aquatic amphibians, reptiles, and birds. In: Thewissen JG, Nummela S, eds. *Sensory evolution on the threshold: adaptations in secondarily aquatic vertebrates*. Berkeley, Los Angeles, London: University of California Press, 183–209.

Hopson JA. 1979. Palaeoneurology. In: Gans C, ed. *Biology of the reptilia*, *Vol.* **9**. New York: Academic Press, 39–146.

Jannel A. 2014. *Neck mobility, grazing habits and intraspecific combat behaviour in the giant Pleistocene horned turtle Meiolania platyceps*. Master thesis. Montpellier University, 38 pp.

Jayes AS, Alexander RM. 2009. The gaits of chelonians: walking techniques for very low speeds. *Journal of Zoology* **191:** 353–378.

Joyce WG. 2007. Phylogenetic relationships of Mesozoic Turtles. *Bulletin of the Peabody Museum of Natural History* **48:** 3–102.

Lambe LM. 1902. On the Vertebrata of the mid-Cretaceous of the Northwest Territory. *Contributions to Canadian Palaeontology* **3:** 25–81.

Leidy J. 1865. Memoir on the extinct reptiles of the Cretaceous formations of the United States. *Smithsonian Contributions to Knowledge* **14:** 1–135.

Mallison H. 2011. Defense capabilities of *Kentrosaurus aethiopicus* Hennig, 1915. *Palaeontologia Electronica* **14:** 1–25.

Manton ML. 1979. Olfaction and behavior. In: Harless M, Morlock H, eds. *Turtles: perspectives and research*. New York: Wiley and Sons, 289–301.

Mason RT. 1992. Reptilian pheromones. In: Gans C, Crews D, eds. *Biology of the reptilia*, *18th edn*. Chicago: University of Chicago Press, 114–228.

Miyashita T, Arbour V, Witmer LM, Currie JP. 2011. The internal cranial morphology of an armoured dinosaur Euoplocephalus corroborated by X-ray computed tomographic reconstruction. *Journal of Anatomy* **219:** 661–675.

Ogushi K. 1913. Zur Anatomie der Hirnnerven und des Kopfsympathicus von *Trionyx japonicus* nebst einigen kritischen Bemerkungen. *Morphologisches Jahrbuch* **45:** 441–480.

Owen R. 1886. Description of some fossil remains of two species of a Megalanian genus (*Meiolania*) from 'Lord Howe's Island'. *Philosophical Transactions of the Royal Society, London B* **179:** 181–191.

Parsons TS. 1959. Nasal anatomy and the phylogeny of reptiles. *Evolution* **13:** 175–187.

Parsons TS. 1970. The nose and Jacobson´s organ. In: Gans C, Parsons TS, eds. *Biology of the reptilia*, *Vol.* **2**. London: Academic Press, 99–191.

Paulina-Carabajal A, Lee Y-N, Jacobs LL. 2016. Endocranial morphology of the primitive nodosaurid dinosaur *Pawpawsaurus campbelli* from the Early Cretaceous of North America. *PLoS One* **11:** e0150845.

Paulina-Carabajal A, Sterli J, Müller J, Hilger A. 2013. Neuroanatomy of the Marine Jurassic Turtle *Plesiochelys etalloni* (Testudinata, Plesiochelyidae). *PLoS One* **8:** e69264.

Pictet F-J, Humbert A. 1857. Description d'une émyde nouvelle (*Emys Etalloni*) du terrain jurassique supérieur des environs de St-Claude. In: Pictet F-J, ed. *Matériaux pour la paléontologie suisse*. Première série. Genève: J. Kessmann, 1–10.

Poropat SF, Koo L, Vickers-Rich P, Rich TH. 2016. Oldest meiolaniid turtle remains from Australia: evidence from the Eocene Kerosene Creek Member of the Rundle Formation, Queensland. *Alcheringa* **41:** 231–239.

Rabi M, Zhou CF, Wings O, Ge S, Joyce WG. 2013. A new xinjiangchelyid turtle from the Middle Jurassic of Xinjiang, China and the evolution of the basipterygoid process in Mesozoic turtles. *BMC Evolutionary Biology* **13:** 203.

Reiner A, Karten HJ. 1985. Comparison of olfactory bulb projections in pigeons and turtles. *Brain, Behavior and Evolution* **27:** 11–27.

Rose FL. 1970. Tortoise chin gland fatty acid composition: behavioral significance. *Comparative Biochemistry and Physiology* **32:** 577–580.

Schmidt KP. 1940. A new turtle of the genus *Podocnemis* from the cretaceous of Arkansas. *Field Museum of Natural History, Geology* **8:** 1–12.

Schneider JG. 1783. *Allgemeine Naturgeschichte der Schildkröten, nebst einem Systematischen Verseichnisse der einzelnen Arten und zwei Kupfern*. Müller, Leipzig.

Schwenk K. 2008. Comparative anatomy and physiology of chemical senses in nonavian aquatic reptiles. In: Thewissen JGM, Nummela S, eds. *Sensory evolution of the threshold. Adaptations in secondarily aquatic vertebrates*. Berkeley: University of California Press, 65–81.

Shaffer HB, Meylan P, McKnight ML. 1997. Tests of turtle phylogeny: molecular, morphological, and palaeontological approaches. *Systematic Biology* **46:** 235–268.

Snively E, Theodor JM. 2011. Common functional correlates of head-strike behavior in the pachycephalosaur *Stegoceras validum* (Ornithischia, Dinosauria) and combative artiodactyls. *PLoS One* **6**(6): e21422.

Sterli J, de la Fuente MS. 2011. Re-description and evolutionary remarks on the Patagonian horned turtle *Niolamia argentina* Ameghino, 1899 (Testudinata, Meiolaniidae). *Journal of Vertebrate Palaeontology* **31:** 1210–1229.

Sterli J, de la Fuente MS. 2013. New evidence from the Palaeocene of Patagonia (Argentina) on the evolution and palaeobiogeography of meiolaniform turtles (Testudinata, new taxon name). *Journal of Systematic Palaeontology* **11:** 835–852.

Sterli J, de la Fuente MS, Krause M. 2015. A new turtle from the Palaeogene of Patagonia (Argentina) shed new light on the diversity and evolution of the bizarre clade of horned turtles (Meiolaniidae, Testudinata). *Zoological Journal of the Linnean Society* **174:** 519–548.

Sues H-D. 1978. Functional morphology of the dome in pachy-cephalosaurid dinosaurs. *Neues Jahrbuch für Geologie und Paläontologie* **8:** 459–472.

Thewissen JGM, Nummela S. 2008. *Sensory evolution on the threshold: adaptations in secondarily aquatic vertebrates*. California: University of California Press.

Tong H, Li L, Li DS, Chen L-M, Li T, Yu S-H, Yu G-S, Cheng X-Q, Claude J. 2016. A revision of *Anhuichelys* Yeh 1979, the earliest known stem Testudinidae (Testudines: Cryptodyra) from the Palaeocene of China. Vertebrata *PalAsiatica* **54:** 156–179.

Waagen GN. 1972. *Musk glands in recent turtles*. Unpublished Master of Science thesis, Univeristy of Utah.

Walker WF. 1971. A structural and functional analysis of walking in the turtle, *Chrysemys picta marginata*. *Journal of Morphology* **134:** 195–213.

Walsh SA, Barrett PM, Milner AC, Manley G, Witmer LM. 2009. Inner ear anatomy is a proxy for deducing auditory capability and behavior in reptiles and birds. *Proceedings of the Royal Society of London B* **276:** 1355–1360.

Weldon PJ, Gaffney ES. 1998. An ancient integumentary gland in turtles. *Naturwissenschaften* **85:** 556–557.

Wever EG. 1978. *The reptile ear: its structure and function*. Princeton: Princeton University Press.

Willemsen RE, Hailey A. 2003. Sexual dimorphism of body size and shell shape in European tortoises. *Journal of Zoology, London* **260:** 353–365.

Witmer LM. 2001. Nostril position in dinosaur and other vertebrates and its significance for nasal function. *Science* **293:** 850–853.

Witmer LM, Ridgely R. 2008. The paranasal air sinuses of predatory and armored dinosaurs (Archosauria: Theropoda and Ankylosauria) and their contribution to cephalic structure. *The Anatomical Record* **291:** 1362–1388.

Witmer LM, Ridgely R, Dufeau DL, Semones MC. 2008. Using CT to peer into the past: 3D visualization of the brain and inner ear regions of birds, crocodiles, and nonavain dinosaurs. In: Endo H, Frey R, eds. *Anatomical imaging: towards a new morphology*. Tokyo: Springer-Verlag, 67–87.

Woodward AS. 1901. On some extinct reptiles from Patagonia of the genera *Miolania*, *Dinilysia*, and *Genyodectes*. *Proceedings of the Zoological Society of London* **1901:** 169–184.

Wyneken J. 2001. The anatomy of sea turtles. *U.S. Department of Commerce NOAA Technical Memorandum NMFS-SEFSC-470*, 1–172.

Zangerl R. 1960. The vertebrate fauna of the Selma Formation of Alabama. V. An advanced cheloniid sea turtle. *Fieldiana Geology Memoir* **3:** 281–312.

Zelenitsky DK, Therrien F, Kobayashi Y. 2009. Olfactory acuity in theropods: palaeobiological and evolutionary implications. *Proceedings of the Royal Society of London* **276:** 667–673.