



The oldest occurrence of *Crocodylus* in Madagascar and the Holocene crocodylian turnover

Jeremy E Martin, Pascale Richardin, Gwendal Perrichon, Yohan Pochat-Cottilloux, Brian Phouybanhdyt, Celine Salaviale, Jerome Adrien

► To cite this version:

Jeremy E Martin, Pascale Richardin, Gwendal Perrichon, Yohan Pochat-Cottilloux, Brian Phouybanhdyt, et al.. The oldest occurrence of *Crocodylus* in Madagascar and the Holocene crocodylian turnover. *Journal of Vertebrate Paleontology*, 2022, 41 (6), 10.1080/02724634.2021.2063058 . hal-03800414

HAL Id: hal-03800414

<https://hal.science/hal-03800414>

Submitted on 6 Oct 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

The oldest occurrence of *Crocodylus* in Madagascar and the Holocene crocodylian
turnover

JEREMY E. MARTIN,^{1,*} PASCALE RICHARDIN,^{2,3} GWENDAL PERRICHON,¹ YOHAN
POCHAT-COTTILLOUX,¹ BRIAN PHOUYBANHDYT,^{2,4} CELINE SALAVIALE,¹ and
JEROME ADRIEN⁵

¹Univ Lyon, Univ Lyon 1, ENSL, CNRS, LGL-TPE, F-69622, Villeurbanne, France,

jeremy.martin@cnrs.fr;

²Centre de Recherche et de Restauration des Musées de France (C2RMF), Palais du Louvre, Porte des
Lions, 14 quai François Mitterrand, 75001 Paris, France;

³CNRS-UMR 8068, Technologie Ethnologie des Mondes Préhistoriques (TEMPS), Université Paris
Nanterre, 21 allée de l'Université, 92023 Nanterre Cedex, France;

⁴CNRS-UMR 8212, CEA-Saclay - Orme des Merisiers - bât. 714, Université Paris-Saclay, 91191 Gif-
sur-Yvette;

⁵Univ. Lyon, INSA Lyon, MATEIS, UMR CNRS 5510, F69621 Villeurbanne, France

RH: MARTIN ET AL.—OLDEST *CROCODYLUS* FROM MADAGASCAR

* Corresponding author

ABSTRACT—The island of Madagascar is home to a distinctive fauna and flora whose biogeographic history is not fully understood. Today’s crocodylian population consists of a single species, the Nile crocodile, *Crocodylus niloticus*, whose colonization of the island may be very recent. In Madagascar, the genus *Crocodylus* has so far been described from a single subfossil specimen dated at 385 years cal BP, offering limited perspectives for discussing the timing of its arrival. On the other hand, another crocodyline, the now-extinct endemic *Voay robustus*, has been reported from several late Holocene localities throughout the island. Because of the earlier age of *Voay robustus*, it has been suggested that *Crocodylus* followed the extinction of this endemic species. Here, we report on a significantly older occurrence of the genus *Crocodylus*, between 7,670 and 7,510 years cal BP. The taxonomic identity of crocodylian subfossil specimens throughout Madagascar should be reevaluated in the context of this new occurrence, which could impact hypotheses of crocodylian turnover and the potential human impacts on the island.

INTRODUCTION

Reconstructing the colonization events that led to modern-day biodiversity of Madagascar is a work in progress. Madagascar hosts a living population of Nile crocodiles, *Crocodylus niloticus*, whose arrival on the island is assumed to be very recent, having followed the extinction of the endemic species *Voay robustus* (Brochu, 2007; Bickelmann and Klein, 2009). Current knowledge on the subfossil record of *Crocodylus* is attested by a single specimen dated at 385 years cal BP (Mathews and Samonds, 2016), limiting our understanding of the timing of its arrival. Conversely, numerous localities of late Holocene age have yielded remains of the now-extinct taxon *Voay robustus*, but direct dating is limited to a handful of diagnostic specimens with an age of about 2000 years cal BP (Hekkala et al., 2021; Godfrey et al., 2021). Among the megafauna, Holocene crocodylians have received little attention despite recent recognition that the recently extinct *Voay robustus* was a common component of

subfossil assemblages throughout the island (Grandidier and Vaillant, 1872; Brochu, 2007; Bickelmann and Klein, 2009; Samonds et al., 2019). This subfossil distribution contrasts with today's Malagasy freshwater ecosystems exclusively hosting populations of *Crocodylus niloticus*, with molecular data supporting a recent dispersal of this genus from mainland Africa (Schmitz et al., 2003; Meredith et al., 2011; Hekkala et al., 2020).

Here, we describe and provide a radiocarbon date for an overlooked specimen from the Holocene of Madagascar (MHNL QV 14) brought back by Jean-Victor Augagneur in 1909, a former mayor of Lyon (1900–1905). Augagneur resigned during his second mandate in 1905 to accept the position of Governor General of Madagascar, which he occupied until 1910. The catalogue of the Musée des Confluences in Lyon does not provide provenance information beyond Madagascar for MHNL QV 14, but indicates that Augagneur donated remains of *Hippopotamus lemerlei*, two lemur skulls from Ampasambazimba as well as *Aepyornis* bones. It is therefore likely that MHNL QV 14 originates from the Central High plateaus in the surroundings of Antsirabé as evidenced from archaeological digs that took place at Ampasambazimba before and during the time of Augagneur mandate in Madagascar, a locality known to have produced, among lemur, *Hippopotamus*, *Aepyornis* and turtle bones, crocodile remains (Jully and Standing, 1904). The specimen MHNL QV 14, despite its fragmentary nature, holds important implications for the historical biogeography of crocodylines in Madagascar.

Institutional Abbreviation—MHNL, Muséum d'Histoire Naturelle de Lyon / Musée des Confluences de Lyon; UCBL, Université Claude Bernard Lyon 1.

MATERIAL AND METHODS

Radiocarbon Dating

Bone preparation for AMS radiocarbon dating follows the Longin (1971) method and is detailed in Richardin et al. (2017). Here, a broken area from the right squamosal of MHNL QV 14 showing compact bone was selected for sampling. The sample was powdered with a diamond drill bit and slowly demineralized with hydrochloric acid in order to recover the collagen fraction. Radiocarbon measurements were performed at the Artemis AMS (Accelerator Mass Spectrometry) facility of Saclay (France) (Moreau et al., 2013). The amount of collagen prepared was sufficient to make three independent radiocarbon measurements. Calibrated dates were determined using the OxCal software v4.4 (Bronk Ramsey and Lee, 2013; Bronk Ramsey, 2017) and the most recent calibration curve data for the Southern Hemisphere SHCal20 (Hogg et al., 2020). Calibrated date ranges correspond to 95.4% probability (2σ) and are expressed in years cal BP (Table 1). Similarly, radiocarbon dates retrieved from the literature and relevant to the discussion were calibrated using the same method and are compiled in **Table S1**.

Computed Tomography

The endocranial braincase morphology of MHNL QV 14 was compared to that of *Voay robustus* (MNHN-F.1908-5) and of a modern *Crocodylus* cf. *porosus* (UCBL 2019-1-237). Both computed tomography (CT) scans of MHNL QV 14 and UCBL 2019-1-237 were performed in the winter/spring of 2021 at the Laboratoire Mateis (INSA, Lyon) with a Vtomex laboratory X-ray tomograph (GE Phoenix X-ray GmbH) under a 140 kV tube voltage, an 80 μ A current and a resolution of 80 μ m and 75 μ m, respectively. Data for MNHN-F.1908-5 were acquired before 2010 on a X8060 NDT CT scanner at Saint-Ouen-L'Aumône (Viscom France) under a 150 kV tube voltage, a 500 μ A current and a resolution of 133 μ m (David, 2011). Here, starburst effects due to diagenetic minerals blur the data slices but the contrast remains good enough to allow observations of internal structures. For repeatable comparisons, CT slices for the three crocodyline specimens (Fig. 3) were standardized for

each specimen along the sagittal plane through the supraoccipital and basioccipital, and along the transverse plane through the labyrinths and basioccipital

RESULTS

Radiocarbon Dating

Thanks to the available collagen quantity, three radiocarbon measurements could be obtained. As the three dates relate to the same specimen, the radiocarbon dates were aggregated using the R_Combine function in OxCal program (Bronk Ramsey, 2009 a, b). This procedure first combines the uncalibrated dates into a single radiocarbon date, which will be then calibrated. A χ^2 test (Ward and Wilson, 1978) is then automatically performed in the OxCal program. Radiocarbon ages and the resulting calibrated dates are collected in Table 1. As expected, the radiocarbon ages of the 3 samples are consistent (6735 ± 35 BP, 6760 ± 35 BP and 6780 ± 35 BP). After treatment with the function R_Combine, we obtain an aggregated radiocarbon age of 6758 ± 21 BP. This corresponds to a calibrated date in the range between 7670 and 7510 cal BP (Fig. 1 and Table 1) for the bone sample.

Comparative Description

MHNL QV 14 consists of the posterior region of a cranium, broken off just anterior to the supratemporal fenestrae and missing the frontal, the right postorbital and part of the right squamosal (Fig. 2). The specimen is overall well preserved with elements of the skull table, braincase and suspensorium including the laterosphenoids, most of the parietal, part of the left postorbital, the complete left squamosal, a fragment of the right squamosal, the exoccipitals, the quadrates, the supraoccipital, the basioccipital and the basisphenoid. The distance between the medial hemicondyles of the quadrates is 11.8 cm. In the genus *Crocodylus*, this corresponds to a skull length of between 30 and 40 cm, i.e. not a juvenile individual.

The preserved dorsal surface of the skull table of MHNL QV 14 is mostly flat and presents regularly spaced cupules as is typically observed in the genus *Crocodylus* but unlike in *Voay robustus*, which bears a pattern of crests ornamented by a more rugose pitting (Brochu, 2007; Bickelman and Klein, 2009). A squamosal hornlet is preserved on the left squamosal of MHNL QV 14 (Fig. 2), a feature encountered in various species of *Crocodylus* (e.g. *C. niloticus*, *C. siamensis*, *C. porosus*) and not as dramatically expressed as the squamosal horns of *Voay robustus* of comparable size, which are longitudinally more expansive, covering both the squamosal and postorbital and giving a distinctive morphology to its skull table (Brochu, 2007). Although supratemporal fenestrae undergo ontogenetic change (Cossette et al., 2021), those of MHNL QV 14 have similar proportions to those of extant species of *Crocodylus* and contrast with the small and set forward fenestrae of *Voay robustus* (Brochu, 2007). The posterior margin of the skull table formed by the parietal is convex and covers the supraoccipital in dorsal view, as in *Crocodylus* sp.. Contrary to *Voay robustus* (Brochu, 2007; Bickelmann and Klein, 2009) or *Aldabrachampsus dilophus* (Brochu, 2006), the supraoccipital of MHNL QV14 does not appear on the dorsal surface of the skull table but is completely covered by a concave posterior projection of the parietal (Fig. 2A, C, E). Additionally, MHNL QV 14 and the genus *Crocodylus* display lateral Eustachian openings nearly in line with the median opening (Fig. 2D) whereas in the African genus *Mecistops*, the lateral Eustachian openings are dorsally placed (Brochu, 2000).

As observed from CT slices, the most striking characteristic is the thickness of all internal bony walls of the skull of *Voay robustus* compared to MNHL QV 14 or *Crocodylus* cf. *porosus*, an obvious feature observed at the level of the parietal or surrounding the pharyngotympanic system (Fig. 3). A sagittal slice shows that the general morphology of the supraoccipital of MHNL QV 14 is similar to *Crocodylus* cf. *porosus* in relative height and length (Fig. 3B, E) but contrasts with the supraoccipital of *Voay robustus*, which is about twice higher and shorter (Fig. 3H). Other notable observations include the shape and extent of the intertympanic diverticulum, which is oval to round in sagittal view in

Crocodylus cf. *porosus* and MHNL QV 14 (Fig. 3B, E) and twice taller than long in *Voay robustus* (Fig. 3H). In *Voay robustus*, the intertympanic diverticulum invades the parietal far anteriorly (labelled as pd in Fig. 3B, E, H). On the other hand, the parietal diverticulum in *Crocodylus* cf. *porosus* is smaller and dorsoventrally compressed and that of MHNL QV 14 is smaller and vestigial (Fig. 3E). Although the parietal is broken off in MHNL QV 14, there is sufficient bone preserved demonstrating the significant reduction of a parietal diverticulum. In transverse view, the ventral margin of the intertympanic cavity composed by the ventral lamina of the supraoccipital (indicated by the pair of semicircular canals) is flat to concave in *Crocodylus* cf. *porosus* and MHNL QV 14 (asterisks in Fig. 3C, F) and convex in *Voay robustus* (asterisk in Fig. 3I). Finally, the median Eustachian canal ascends between the basioccipital and basisphenoid to form a large, posteriorly expanded diverticulum in *Voay robustus* (arrow in Fig. 3H) that is distinctly larger than the channelized canal of *Crocodylus* cf. *porosus* or MHNL QV 14 (Fig. 3B, E). Therefore, we observe that the braincase of *Voay robustus* is heavily pneumatized compared to that of *Crocodylus* cf. *porosus* and conclude that the morphology of MHNL QV 14 most closely resembles the latter and assign it to *Crocodylus* sp..

DISCUSSION

External and endocranial morphology help distinguish MHNL QV 14 from *Voay robustus*. Beyond the robust nature of its skull bones, CT slices highlight unique endocranial features in *Voay robustus* (Fig. 3), supporting the attribution of the newly reported specimen MHNL QV 14 to the genus *Crocodylus*. A detailed description of the endocranial anatomy of *Voay robustus* is in progress (PhD work of GP) and will be presented elsewhere.

Until this study, the subfossil record of *Crocodylus* in Madagascar was limited to a single occurrence of a juvenile individual from Anjohibe Cave dated a few centuries BP (Mathews and Samonds, 2016). Here, we document a significantly older presence of *Crocodylus* sp. based on a less

complete but larger individual. Three radiocarbon dates from a single sample of MHNL QV 14 produced radiocarbon dates between 7655 and 7580 cal BP (Table 1), which are significantly older than all unambiguous dates for *Voay robustus* (Hekkala et al., 2021). Before this study, it was assumed that *Crocodylus* arrived recently in Madagascar (Brochu, 2007), an idea then supported by a minimum date of arrival at 385 ± 75 years cal BP based on direct radiocarbon dating of a juvenile specimen (Crowley and Samonds, 2013; Mathews and Samonds, 2016; Samonds et al., 2019). The age of the *Crocodylus* specimen MHNL QV 14 significantly pushes back the temporal presence of the genus *Crocodylus* in Madagascar by several millennia, a result that clarifies our understanding of crocodylian colonization in Madagascar but also raises questions about crocodyline origins, turnover, and extinctions.

Samonds et al. (2019) inferred the chronology of the fossil record of *Voay robustus* based on radiocarbon dates measured on associated faunas. They observed that crocodylian remains are abundant at different localities of the Central High plateaus together with *Hippopotamus*. One *Hippopotamus* bone from Tsaramody is dated at 17565 cal BP (Samonds et al. 2019). In addition, Samonds *et al.* (2019) report a radiocarbon date of 1813 cal BP for a specimen attributed to *Voay* from Ankilibehandry in coastal Madagascar and Godfrey et al. (2021) report a slightly older date for another *Voay robustus* at 2253 cal BP from Soarano Cave along the southwestern coast. Indeed, there is no reason to challenge these dates, but it needs to be stressed that the taxonomic attribution to *Voay robustus* for these crocodylian specimens has yet to be demonstrated. This is important because such dates may either indicate a prolonged existence for species of *Voay* or *Crocodylus*, or both during the Holocene in Madagascar. If previous taxonomic attributions are correct, species of *Voay* and *Crocodylus* overlapped for several thousands of years in Madagascar, if not more. An alternative possibility is that a species of *Crocodylus* was present in Madagascar long before *Voay robustus* or that both species never shared the same habitats. Unambiguous data come from the direct dating of diagnostic specimens such as in this study or in a recent study based on two skulls that indicate more recent ages for *Voay robustus* at 1450 year cal BP and 1380 year cal BP (Hekkala et al., 2021).

Our findings indicate that the presence of a species of *Crocodylus* precedes the oldest unambiguous occurrence of *Voay robustus* (Hekkala et al., 2021) by several millennia, a result that contradicts the hypothesis that *Crocodylus* settled after the extinction of *Voay robustus* (Bicklemann and Klein, 2009). This also weakens another hypothesis of human-induced extirpation of *Voay robustus* leaving free habitats for *Crocodylus niloticus* or invoking a direct competition between both species (Brochu, 2007). Human presence in Madagascar may be as old as the early Holocene (i.e. ~10000 BP, Hansford et al., 2018), in which case the human impact on both crocodylian lineages could be rooted in the early Holocene. But the settlement date of humans in Madagascar is highly debated (e.g. Mitchell, 2020; Hansford et al., 2020) and a younger date for human colonization by at least 2000 cal BP (Douglass et al., 2019) would imply a much more recent human impact on crocodylian faunas, raising questions about human-hunting selectivity and the extinction of *Voay robustus* but not of *Crocodylus niloticus*. Whether *Homo sapiens* altered the composition of Malagasy crocodylian faunas can only be resolved by refining spatial and temporal occurrences of both crocodyline genera, constraining their differential occurrences and extinctions. Finally, there exists the possibility that the presently reported *Crocodylus* sp. may not be closely related to the modern-day population of *Crocodylus niloticus* inhabiting Madagascar, in which case this individual may testify for the repeated colonization of the island by some *Crocodylus* lineages from mainland Africa and/or from Australasia.

According to molecular studies, genetic divergence is small between extant NW Malagasy *Crocodylus niloticus* and eastern mainland African *Crocodylus niloticus* (Schmitz et al., 2003; Meredith et al., 2011). Mitochondrial-DNA-based phylogenetic analysis recovered *Voay* closer to Crocodylinae than to Osteolaeminae (Hekkala et al., 2021) contrary to morphology-based phylogenies (Brochu, 2007). Although this re-shuffles the taxonomic position of *Voay robustus*, the recovered divergence between *Voay robustus* and *Crocodylus niloticus* is ancient and may be as old as the Oligocene (Hekkala et al., 2021) and the presence of two distinct crocodyline lineages during the Holocene of Madagascar remains valid. Hence, the timing of arrivals of *Crocodylus niloticus* and *Voay*

robustus in Madagascar is still an open question and multiple colonization events are possible. There is emerging evidence that some components of Madagascar's modern biotas dispersed from mainland Africa multiple times during the Neogene, aided by Eastward currents across the Mozambique Channel (e.g. Hawlischek et al., 2017; Cernansky et al., 2020). The presence of crocodylians in nearby insular contexts such as Aldabra during the Late Pleistocene (Brochu, 2006; Scheyer et al., 2018) or the Seychelles up until a few centuries ago (Gerlach and Canning, 1993) is indicative of such dispersal events. Given the capacity of crocodylines to osmoregulate (Taplin, 1988; Mazzotti and Dunson, 1989), long transoceanic dispersal via Westward currents from SE Asia that aided other faunas (Warren et al., 2010), including humans (Heiske et al., 2021) to colonize Madagascar must also be considered.

CONCLUSION

The direct dating of a subfossil *Crocodylus* sp. challenges previous hypotheses surrounding crocodylian Holocene colonization of Madagascar and prompts reevaluation of the taxonomic identity of crocodylian specimens from various subfossil sites throughout Madagascar. That *Voay robustus* did not disappear before the arrival of a species of *Crocodylus* complicates the evolutionary history of Crocodylia and the human impact on faunal decline on this singular island.

ACKNOWLEDGMENTS

The authors thank D. Berthet and the Musée des Confluences de Lyon for facilitating access to MHNL QV 14 and B. Bartschi for the loan of the UCBL specimen. We thank R. Allain (MNHN) for sharing the CT data of MNHN-F.1908-5. Computed tomography data were partly supported by the Agence Nationale de la Recherche (SEBEK project N° ANR-19-CE31-0006-01 to JEM) and by INSA

de Lyon. We would like to thank the three anonymous reviewers and the editors for their constructive comments that helped improve the initial version of this work.

LITERATURE CITED

- Bickelmann, C., and N. Klein. 2009. The late Pleistocene horned crocodile *Voay robustus* (Grandidier and Vaillant, 1872) from Madagascar in the Museum für Naturkunde Berlin. *Fossil record* 12:13–21.
- Brochu, C. A. 2000. Phylogenetic relationships and divergence timing of *Crocodylus* based on morphology and the fossil record. *Copeia* 200:657–673.
- Brochu, C. A. 2006. A new miniature horned crocodile from the Quaternary of Aldabra Atoll, Western Indian Ocean. *Copeia* 2006:149–158.
- Brochu, C.A. 2007. Morphology, relationships, and biogeographical significance of an extinct horned crocodile (Crocodylia, Crocodylidae) from the Quaternary of Madagascar. *Zoological journal of the linnean society* 150:835–863.
- Bronk Ramsey, C. 2009a. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51:337–360.
- Bronk Ramsey, C. 2009b. Dealing with outliers and offsets in radiocarbon dating. *Radiocarbon* 51:1023–1045.
- Bronk Ramsey, C. 2017. Methods for summarizing radiocarbon datasets. *Radiocarbon* 59:809–1833.
- Bronk Ramsey, C, and Lee, S. 2013. Recent and planned developments of the program OxCal. *Radiocarbon* 55:720–730.
- Černansky, A., A. Herrel, J. M. Kibii, C. V. Anderson, B. Renaud, and T. Lehmann. 2020. The only complete articulated early Miocene chameleon skull (Rusinga Island, Kenya) suggests an African origin for Madagascar’s endemic chameleons. *Scientific reports* 10:1–11.

- Cossette, A. P., A. D. Grass, and T. DeGuzman. 2021. The contribution of ontogenetic growth trajectories on the divergent evolution of the crocodylian skull table. *The anatomical record*. <https://doi.org/10.1002/ar.24824>
- Crowley, B. E. and K. E. Samonds. 2013. Stable carbon isotope values confirm a recent increase in grasslands in northwestern Madagascar. *The holocene* 23:1066–1073.
- David, R. 2011. Le système des canaux semi-circulaires des archosaures: anatomie, morphométrie, morphologie fonctionnelle, évolution. PhD dissertation, Paris Muséum national d'histoire naturelle.
- Douglass, K., S. Hixon, H. T. Wright, L. R. Godfrey, B. E. Crowley, B. Manjakahery, T. Rasolondrainy, Z. Crossland, and C. Radimilahy. 2019. A critical review of radiocarbon dates clarifies the human settlement of Madagascar. *Quaternary science reviews* 221:105878.
- Gerlach, J. and K. L. Canning. 1993. On the crocodiles of the Western Indian Ocean. *Phesulma* 2:54–58.
- Godfrey, L. R., B. E. Crowley, K. M. Muldoon, S. J. Burns, N. Scroxton, Z. S. Klukkert, L. Ranivoharimanana, J. Alumbaugh, M. Borths, R. Dart, P. Faina, S. M. Goodman, I. J. Gutierrez, J. P. Hansford, E. R. Hekkala, C. W. Kinsley, P. Lehman, M. E. Lewis, D. McGee, V. R. Pérez, N. J. Rahantaharivo, M. Rakotoarijaona, H. A. M. Rasolonjatovo, K. E. Samonds, S. T. Turvey, N. Vasey, and P. Widmann. 2021. Teasing apart impacts of human activity and regional drought on Madagascar's large vertebrate fauna : insights from new excavations at Tsimanampesotse and Antsirafaly. *Frontiers in ecology and evolution* doi:10.3389/fevo.2021.742203
- Grandidier, A. and L. Vaillant. 1872. Sur le crocodile fossile d'Amboulintsatre (Madagascar). *Comptes rendus de l'académie des sciences de Paris* 75:150–151.
- Hansford, J. P., P. C. Wright, V. R. Pérez, K. M. Muldoon, S. T. Turvey, and L. R. Godfrey. 2020. Evidence for early human arrival in Madagascar is robust: A response to Mitchell. *The journal of island and coastal archaeology*, 15:596–602.

- Hansford, J., P. C. Wright, A. Rasoamiamanana, V. R. Pérez, L. R. Godfrey, D. Errickson, T. Thompson, and S. T. Turvey. 2018. Early Holocene human presence in Madagascar evidenced by exploitation of avian megafauna. *Science advances* 4:p.eaat6925.
- Hawltischek, O., S. Ramirez Garrido, and F. Glaw. 2017. How marine currents influenced the widespread natural overseas dispersal of reptiles in the Western Indian Ocean region. *Journal of biogeography* 44:1435–1440.
- Heiske, M., O. Alva, V. Pereda-Loth, M. Van Schalkwyk, C. Radimilahy, T. Letellier, J. A. Rakotarisoa, and D. Pierron. 2021. Genetic evidence and historical theories of the Asian and African origins of the present Malagasy population. *Human molecular genetics*,30:R72–R78.
- Hekkala, E. R., M. L. Aardema, A. Narechania, G. Amato, S. Ikram, M. H. Shirley, K. A. Vliet, S. W. Cunningham, M. T. P. Gilbert, and O. Smith. 2020. The secrets of Sobek—A crocodile mummy mitogenome from ancient Egypt. *Journal of archaeological science* 33:102483.
- Hekkala, E., J. Gatesy, A. Narechania, R. Meredith, M. Russello, M. L. Aardema, E. Jensen, S. Montanari, C. A. Brochu, M. Norell, and G. Amato. 2021. Paleogenomics illuminates the evolutionary history of the extinct Holocene “horned” crocodile of Madagascar, *Voay robustus*. *Communications biology* 4:1–11.
- Hogg, A., T. Heaton, Q. Hua, J. Palmer, C. Turney, J. Southon, A. Bayliss, P. Blackwell, G. Boswijk, C. Bronk Ramsey, F. Petchey, P. Reimer, R. Reimer, and L. Wacker. 2020. SHCal20 Southern Hemisphere calibration, 0–55,000 years cal BP. *Radiocarbon* 62:759–778.
- Jully, A. and H. F. Standing. 1904. Les gisements fossilifères d’Ampasambazimba. *Bulletin de l’académie Malgache* 3:87–94.
- Longin, R. 1971. New Method of Collagen Extraction for Radiocarbon Dating. *Nature* 230:241–242.
- Mathews, J. C. and K. E. Samonds. 2016. A juvenile subfossil crocodylian from Anjohibe Cave, Northwestern Madagascar. *PeerJ* 4:p.e2296.

- Mazzotti, F. J. and W. A. Dunson. 1989. Osmoregulation in crocodilians. *American zoologist* 29:903–920.
- Meredith, R. W., E. R. Hekkala, G. Amato, and J. Gatesy, J. 2011. A phylogenetic hypothesis for *Crocodylus* (Crocodylia) based on mitochondrial DNA: evidence for a trans-Atlantic voyage from Africa to the New World. *Molecular phylogenetics and evolution* 60:183–191.
- Mitchell, P. 2020. Settling Madagascar: when did people first colonize the world’s largest island? *The journal of island and coastal archaeology* 15:576–595.
- Moreau, C., I. Caffy, C. Comby, E. Delqué-Količ, J. P. Dumoulin, S. Hain, A. Quiles, V. Setti, C. Souprayan, B. Thellier, and J. Vincent. 2013. Research and development of the Artemis 14C AMS Facility: status report. *Radiocarbon* 55:331–337.
- Oaks, J. R. 2011. A time–calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles. *Evolution* 65:3285–3297.
- Richardin, P., S. Porcier, S. Ikram, G. Louarn, and D. Berthet. 2017. Cats, Crocodiles, Cattle, and More: Initial Steps Toward Establishing A Chronology of Ancient Egyptian Animal Mummies. *Radiocarbon* 59:595–607.
- Samonds, K. E., B. E. Crowley, T. R. N. Rasolofomanana, M. C. Andriambelomanana, H. T. Andrianavalona, T. N. Ramihangihajason, R. Rakotozandry, Z. B. Nomenjanahary, M. T. Irwin, N. A. Wells, and L. R. Godfrey. 2019. A new late Pleistocene subfossil site (Tsaramody, Sambaina basin, central Madagascar) with implications for the chronology of habitat and megafaunal community change on Madagascar’s Central Highlands. *Journal of Quaternary science* 34:379–392.
- Scheyer, T. M., M. Delfino, N. Klein, N. Bunbury, F. Fleischer-Dogley, and D. M. Hansen. 2018. Trophic interactions between larger crocodylians and giant tortoises on Aldabra Atoll, Western Indian Ocean, during the Late Pleistocene. *Royal society open science* 5:171800.
<http://dx.doi.org/10.1098/rsoc.171800>

Schmitz, A., P. Mansfeld, E. Hekkala, T. Shine, H. Nickel, G. Amato, and W. Böhme. 2003. Molecular evidence for species level divergence in African Nile crocodiles *Crocodylus niloticus* (Laurenti, 1786). *Comptes rendus palevol* 2:703–712.

Taplin, L. E. 1988. Osmoregulation in crocodilians. *Biological reviews* 63: 333–377.

Ward, G. K., and S. R. Wilson. 1978. Procedures for comparing and combining radiocarbon age determinations: A critique. *Archaeometry* 20:19–31.

Warren, B. H., D. Strasberg, J. H. Bruggemann, R. P., Prys-Jones, and C. Thébaud. 2010. Why does the biota of the Madagascar region have such a strong Asiatic flavour?. *Cladistics* 26:526–538.

Submitted August 2, 2021; accepted Month DD, YYYY

Figure captions

FIGURE 1. Calibrated dates (in cal BP) of the radiocarbon ages of the 3 trials and the combined date obtained for MHNL QV 14 squamosal bone using OxCal v4.4.4 (Bronk Ramsey, 2021) and atmospheric data from Hogg et al. (2020). [Intended for column width]

FIGURE 2. The specimen MHNL QV 14 attributed to *Crocodylus* sp. from the Holocene of Madagascar in **A**, dorsal; **B**, occipital and **C**, left lateral views. **D**, volume rendering of the basicranium in right ventrolateral view showing the arrangement of the Eustachian openings; not to scale.

Abbreviations: **boc**, basioccipital; **bsph**, basisphenoid; **eam**, external auditory meatus; **exo**, exoccipital; **fa**, foramen aereum; **fcp**, foramen caroticum posterius; **leu**, lateral Eustachian opening; **ltsph**, laterosphenoid; **meu**, median Eustachian opening; **p**, parietal; **po**, postorbital; **q**, quadrate; **soc**, supraoccipital; **sq**, squamosal; **stf**, supratemporal fenestra; **IX–XI**, **XII**, openings for ninth to eleventh and twelfth cranial nerves. [Intended for full page width]

FIGURE 3. Comparison of the endocranial morphology among crocodylines with inspected CT slices shown on the volume rendering (top row) and corresponding sagittal slices (middle row) and transverse slices at the level of the labyrinths (bottom row) of *Crocodylus* cf. *porosus* (UCBL 2019-1-237) (**A**, **B**, **C**), the newly reported *Crocodylus* sp. from Madagascar (MHNL QV 14) (**D**, **E**, **F**); and *Voay robustus* (MNHN-F.1908-5) (**G**, **H**, **I**). See also interpretative drawing of endocranial structures for the transverse slice of *Voay robustus* in Fig. S1 in Supplemental Data. Abbreviations: **boc**, basioccipital; **bsph**, basisphenoid; **en**, endocast cavity; **exo**, exoccipital; **ie**, inner ear; **it**, intertympanic diverticulum; **leu**, lateral Eustachian canal; **meu**, median Eustachian canal; **p**, parietal; **pd**, parietal diverticulum of the intertympanic; **pr**, prootic; **pt**, pterygoid; **soc**, supraoccipital; **sq**, squamosal; **q**, quadrate. The arrows indicate the posteriormost extension of the median Eustachian canal. The asterisks indicate the ventral margin of the supraoccipital. [Intended for full page width]

TABLE 1. Radiocarbon ages (in BP) and calibrated dates (in cal BP, round to 10) obtained for the bone samples and the calculated R_Combine result, checked for internal consistency by a Chi-squared test, which is performed automatically by the OxCal program.

Curation n°	Reference	Lab. code	Radiocarbon age (BP)	Calibrated date 2 σ (95.4 %)
MHNLQV14	1A1445	SacA 57934	6735 \pm 35	7670 – 7480 cal BP (95.4 %)
	2A1445	SacA 57935	6760 \pm 35	7670 – 7500 cal BP (95.4 %)
	3A1445	SacA 57936	6780 \pm 35	7680 – 7510 cal BP (95.4 %)
R_Combine result*			6758 \pm 21	7670 -7510 cal BP (95.4 %)

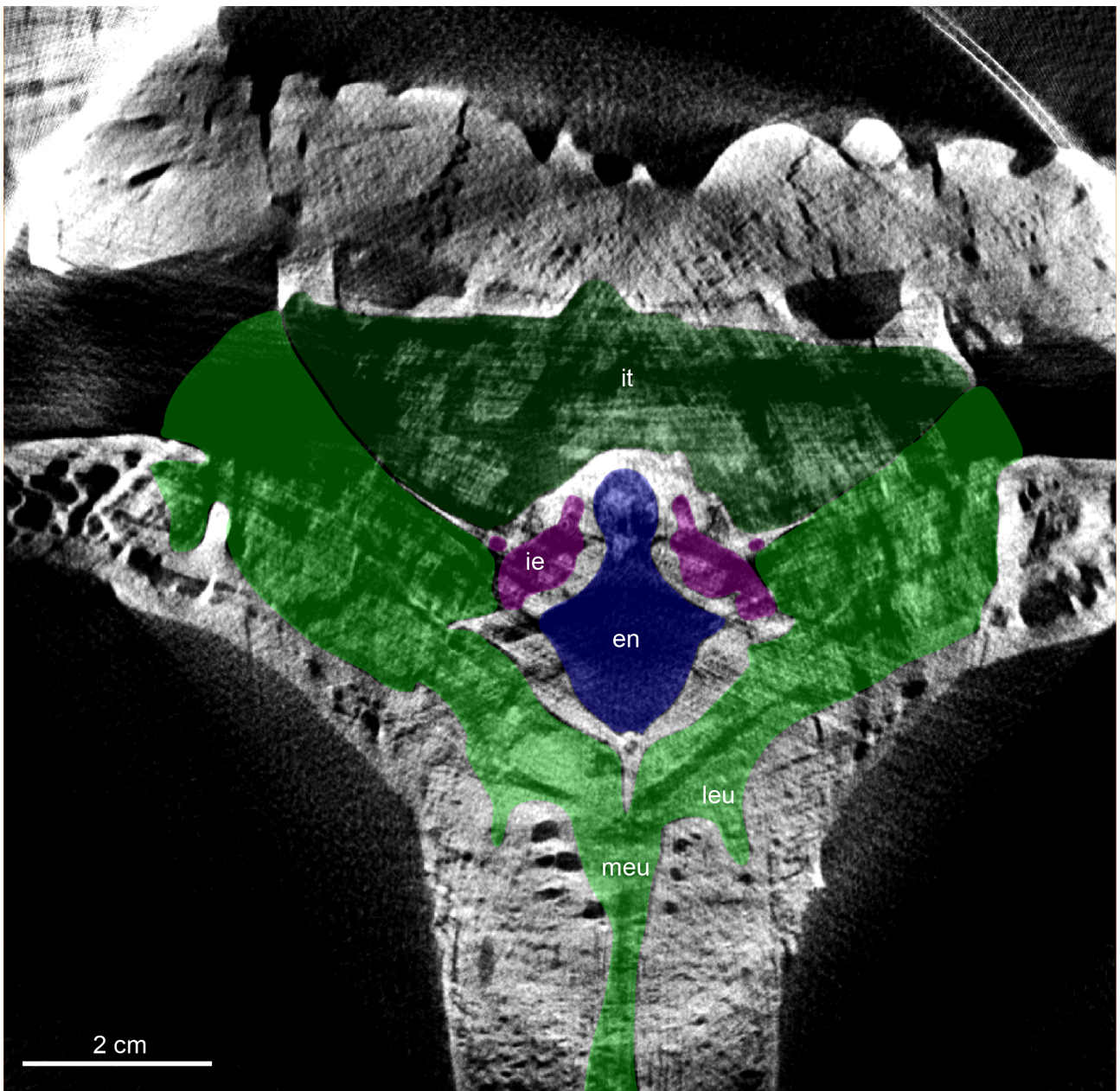
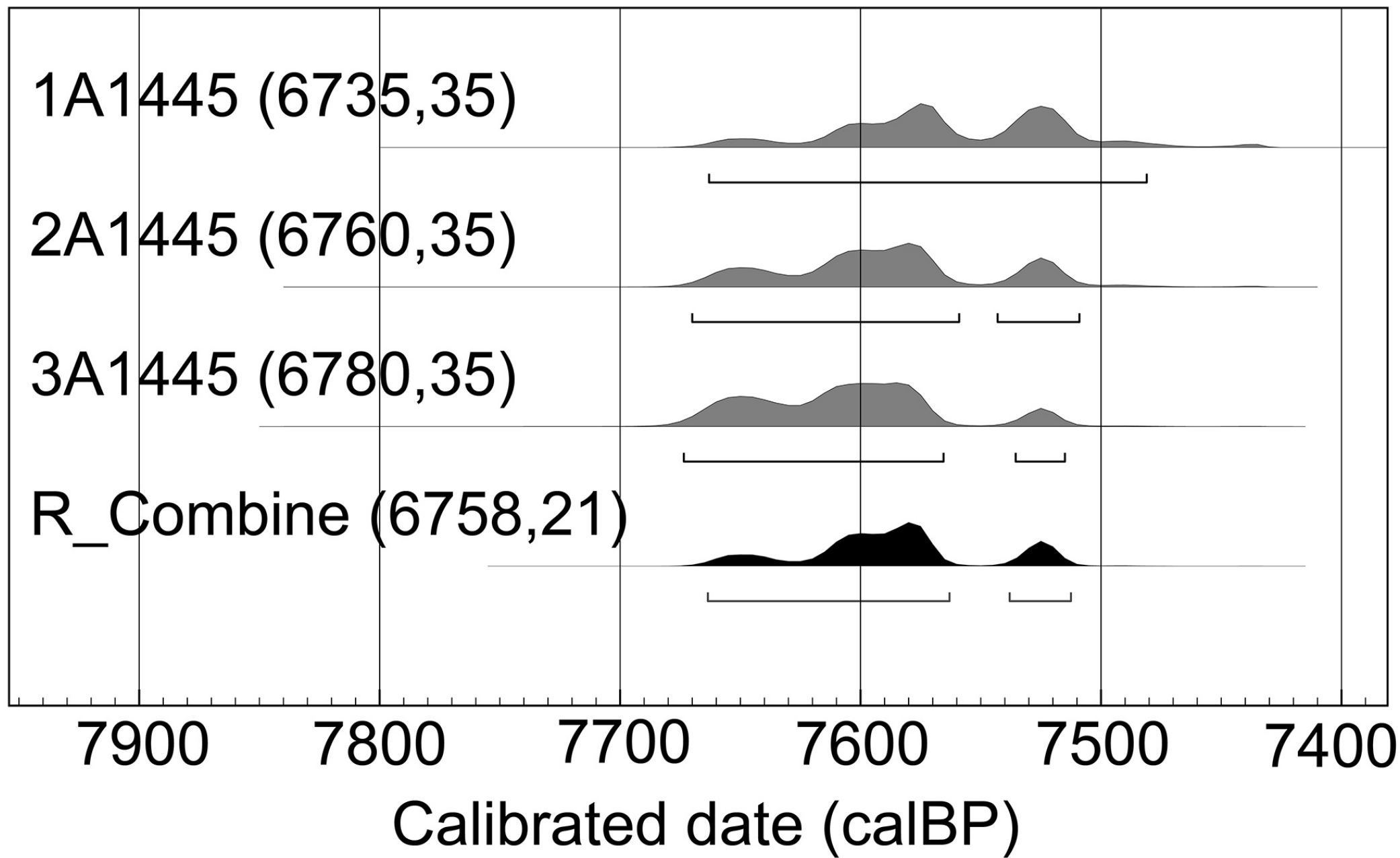
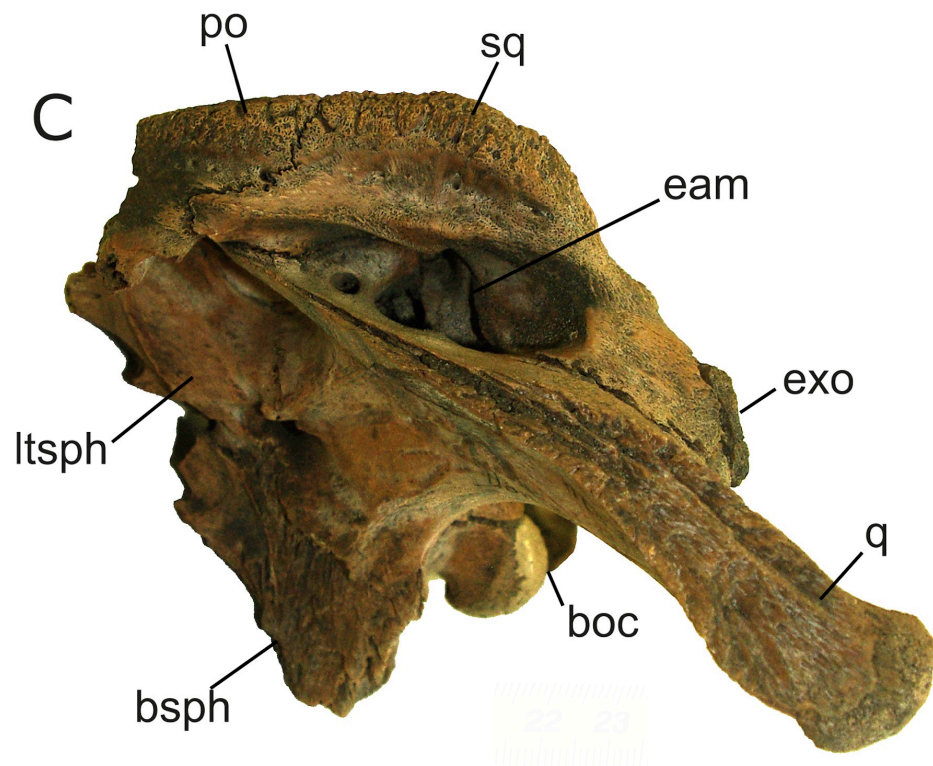
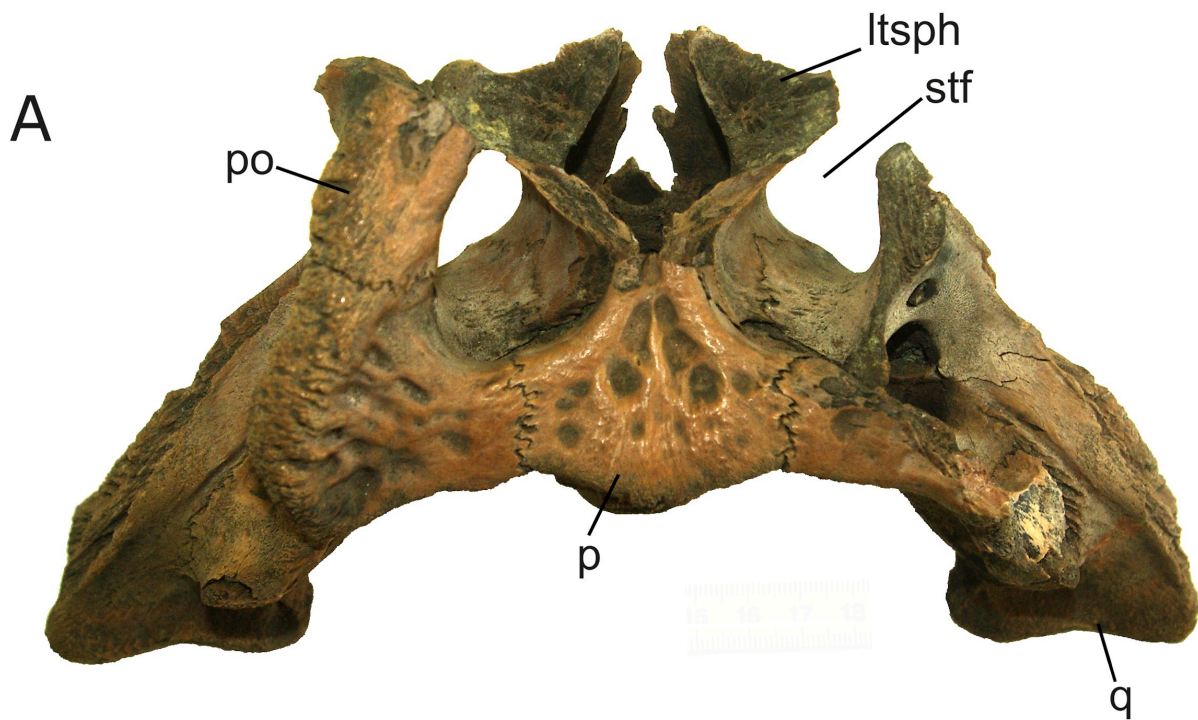


FIGURE S1. Transverse slice obtained from CT data at the level of the labyrinths in *Voay robustus* (MNHN-F-1908-5) with superimposed colored areas of endocranial structures including the intertympanic sinus (dark green), the pharyngotympanic sinus (light green), labyrinths (purple) and endocast (blue). **Abbreviations:** **en**, endocast; **ie**, Inner ear; **it**, intertympanic; **leu**, lateral Eustachian canal; **meu**, median Eustachian canal (see Figure 3 for complementary information).

TABLE S1. Direct radiocarbon dating of crocodyline specimens from this study and from the literature from the Holocene of Madagascar. For homogenous comparison, all radiocarbon dates were calibrated using the OxCal software v4.4 (Bronk Ramsey and Lee, 2013; Bronk Ramsey, 2017) and the most recent calibration curve data for the Southern Hemisphere SHCal20 (Hogg et al., 2020).

Taxonomy	Provenance	Curation number	Lab number	Radiocarbon age (BP)	Calibrated date (2 σ - cal BP)*	References
<i>Crocodylus</i> sp.	Antsirabé area	MHNL QV14	SacA 57934	6735 \pm 35	7670 - 7480	this study
<i>Crocodylus</i> sp.	Antsirabé area	MHNL QV14	SacA 57935	6760 \pm 35	7670 - 7500	this study
<i>Crocodylus</i> sp.	Antsirabé area	MHNL QV14	SacA 57936	6780 \pm 35	7680 - 7510	this study
<i>Voay robustus</i>	Soarano Cave	UABEC 1358	CAMS 183952	2340 \pm 30	2360 - 2140	Godfrey et al., 2021
<i>Voay robustus</i>	Ampoza	AMNH FR-3101	?	1450 \pm 30	1370 - 1270	Hekkala et al., 2021
<i>Voay robustus</i>	Ampoza	AMNH FR-3103	?	1380 \pm 30	1310 - 1170	Hekkala et al., 2021
<i>Voay robustus</i>	Ankilibehandry	?	CAMS 167399	1920 \pm 30	1890 - 1730	Samonds et al., 2019
<i>Crocodylus niloticus</i>	Anjohibe Cave	UAP-03.791	CAMS 150524	360 \pm 25	470 - 300	Crowley and Samonds, 2013





2 cm

