Description of the subfossil crocodylians from a new Late Pleistocene subfossil site (Tsaramody, Sambaina Basin) in central Madagascar

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Abstract

Madagascar is famous today not only for its unique biodiversity, but also for the high levels of endemism of plants and animals. Less appreciated is the fact that, in the recent past, the island had even greater biodiversity with many other endemic animals such as giant lemurs, elephant birds, pygmy hippopotami, tortoises, and crocodiles that have gone extinct within the past 2000 years. The extinction of many of these groups is thought to be the result of both human activities and environmental change. Most research has focused on the lemurs, hippopotami, and elephant birds. Other recently extinct animals, including the Malagasy horned crocodile (*Voay robustus*), are relatively poorly known. Madagascar's subfossil crocodylians include two taxa: the extinct *V. robustus* (the Malagasy horned crocodile) and the extant *Crocodylus niloticus*. The latter arrived on Madagascar relatively recently and we know little about the habitat preferences, distributions and ecological interactions (if any) of either species during the Holocene.

In order to better understand the recent history of crocodylian extinction in Madagascar, we must first identify which species were present and where they were found. We present here a description of subfossil crocodylian material collected from the newly discovered subfossil site of Tsaramody (Sambaina Basin), a high-elevation wetland environment. At 1655 m, it represents the highest-elevation subfossil site on the island. Here we describe both cranial (e.g., premaxillary, jugal, and squamosal "horns") and postcranial elements (e.g., osteoderms). Our research indicates that crocodile material from Tsaramody appears morphologically to belong to *V. robustus*, the extinct species. However, oval tuberosities on the frontal bone and a triangular extension of the squamosal bone suggest previously unrecognized variation.

Key words: extinction, Central Highlands, crocodile, *Voay robustus*

Résumé détaillé

La faune subfossile de Madagascar est d'autant plus riche et unique que sa faune et sa flore actuelles. La plupart des recherches sur cette riche faune subfossile malgache se sont concentrées sur les lémuriens géants disparus, les hippopotames pygmées et les oiseaux éléphants. Parmi ces animaux éteints sont les crocodiles qui restent encore méconnus mais ils ont eu une histoire évolutive très intéressante. Les crocodyliens subfossiles de Madagascar comprennent deux taxa : le *Voay robustus* éteint (le crocodile malgache à cornes) et le *Crocodylus niloticus* actuel. Ce dernier n'est pas endémique de Madagascar et n'est supposé arriver sur l'île que récemment. Néanmoins, les aires de répartition géographique de ces deux espèces, ainsi que les types d'environnements préférés avec leurs éventuelles interactions ne sont pas encore définis. Une description des os de crocodiles subfossiles du site de Tsaramody (bassin de Sambaina) est présentée dans cette étude. Ce site se trouve dans un milieu humide des Hautes Terres centrales à 1655 m d'altitude. Les ostéodermes des éléments crâniens tels que prémaxillaire, jugal et corne du squamosal, et postcraniens, sont décrits et comparés à ceux d'autres sites subfossilifères de Madagascar. Au cours de cette étude, il a été démontré que ces ossements de Tsaramody semblent appartenir à la forme éteinte *V. robustus*. Cependant, ils sont différents du néotype MCZ 1006 du point de vue morphologique. Ainsi, la paire de tubérosités ovales sur l'os frontal et le prolongement triangulaire du

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squamosal suggèrent une variation géographique mal connue mais qui aurait pu exister.

Mots clés : extinction, Hautes Terres Centrale, crocodile, *Voay robustus*

Introduction

The geology of Madagascar was largely formed through sedimentary processes (Besairie & Collignon, 1972). The island is famous for its Late Cretaceous fossil record (Krause *et al*., 2006) but also for younger subfossils recovered from the Late Pleistocene and Holocene (Goodman & Jungers, 2014). From the north to the south there are at least 30 subfossil sites in Madagascar (Samonds, 2007; Mittermeier *et al*., 2010, Goodman & Jungers, 2014); most of these sites have yielded crocodile bones identified as *Voay robustus* (Grandidier & Vaillant, 1872; Brochu, 2007), an extinct endemic genus known from the Late Pleistocene and Holocene. Only one other subfossil crocodile has historically been described, a 300-year-old specimen identified as the extant species *Crocodylus niloticus* (Mathews & Samonds, 2016).

Recent paleontological excavations conducted at the subfossil site of Tsaramody, within the Sambaina Basin in Madagascar's Central Highlands have yielded subfossil specimens of tortoises, elephant birds, hippopotami, and crocodiles (Samonds *et al*., 2019). This paper presents the first description, comparative analysis, and taxonomic identification of crocodile bones from Tsaramody. These specimens contribute information both about intraspecific variation within subfossil crocodiles of Madagascar and about the paleoenvironment of this recently excavated site.

There are currently two recognized species of subfossil crocodile from Madagascar. One extinct form, *V*. *robustus*, was originally described by Grandidier & Vaillant (1872) as a member of the genus *Crocodylus* (*C*. *robustus*) and later re-examined by Brochu (2007) and placed in a new genus *Voay* (neotype: Museum of Comparative Zoology, Cambridge, USA, MCZ 1006). The other species (*C*. *niloticus*) is extant and currently found throughout eastern and southern Africa, and in Madagascar (Hekkala *et al.,* 2011). A recent subfossil specimen collected from Anjohibe is possibly the oldest definitively identified *C*. *niloticus* specimen from Madagascar (Mathews & Samonds, 2016), but neither additional subfossil material, nor the Holocene distribution of this species, is known. Extant populations of *C*. *niloticus* are more abundant along the western coast of Madagascar than the eastern regions, perhaps due to availability of slow flowing and wide rivers (Glaw & Vences, 1994; Kuchling *et al*., 2003; Raxworthy, 2003).

Methods

Site description

The subfossil site of Tsaramody (~19°36',09''S, 047°10'38"E, elevation 1658 m; Figure 1, Samonds *et al.,* 2019) is located approximately 139 km south of Antananarivo following Route National 7. The oldest ^{14}C date obtained from the site is 14,580 BP (17,565 ± 1150 cal BP; Samonds *et al*., 2019) –a hippopotamus phalanx collected from the deepest excavated level (level 2) and prepared for dating at the Quaternary Paleoecology Laboratory (University of Cincinnati). The site is within the Sambaina Basin located on the Central Highlands of Madagascar, within the Commune of Mandrosohasina, Antsirabe District in the Vakinakaratra Region.

Systematics

Most subfossil sites in Madagascar are found in the southern and western portions of the island (Samonds, 2007; Mittermeier *et al*., 2010; Goodman & Jungers, 2014) and the majority of these sites have yielded crocodylian osteological elements identified as *Voay robustus.* These elements can be evaluated for the presence of diagnostic characters, such as the shape of the choanal neck and the squamosal, as described by Brochu (2007). Within the cranium, the notably larger squamosal "horns" and presence of oval bosses are frequently used to differentiate *V*. *robustus* from *Crocodylus niloticus*. These two species have also been distinguished by postcranial characters, including the shape of ilium, with *V*. *robustus* lacking a notable dorsal constriction or "wasp waisting".

Available published descriptions of catalogued material of *V*. *robustus* for comparative analysis include material from the following institutions (Table 1): The American Museum of Natural History (New York): AMNH 3101 (complete skull) and AMNH 17008 (complete right ilium); Museum of Comparative Zoology (Cambridge, Massachusetts): MCZ 1006 (complete skull); The Natural History Museum (London) and formerly known as the British Museum of Natural History: NHMUK r2197 (five osteoderms) and NHMUK uncatalogued (right femur); Museum fűr Naturkunde (Berlin): MB.R. 4097 (three osteoderms),

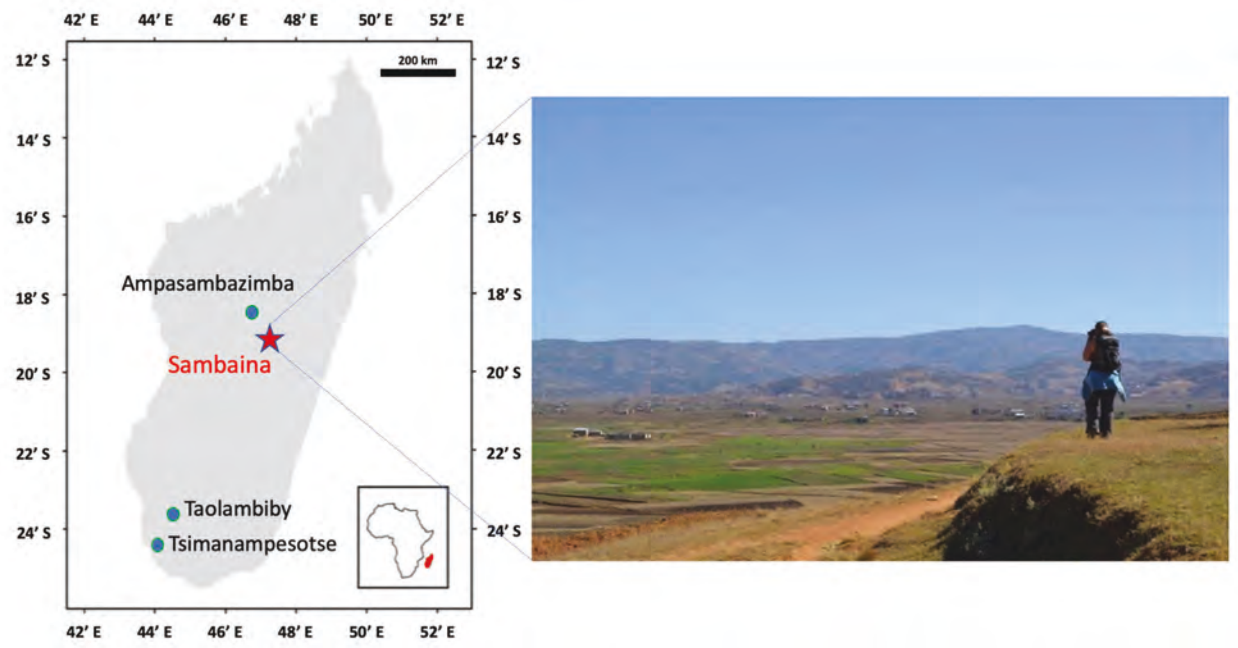

Figure 1. Map showing location of four subfossil sites: Tsaramody, Sambaina (red star), Ampasambazimba, Taolambiby, and Tsimanampesotse.

Table 1. Samples used for comparative analysis.

Institution	Catalog number	Element	Locality
***Voay robustus* specimens**			
AMNH	AMNH 3101	Complete skull	Ampoza
	AMNH 17008	Right ilium	Ampoza
MCZ	MCZ 1006	Complete skull	Near Antsirabe
NIU	NIU-AMPAS 18592	Osteoderm	Ampasambazimba
	NIU-AMPAS 18561	Left jugal	Ampasambazimba
NHMUK	Uncatalogued	Right femur	(no locality data)
	NHMUK r2197	Five osteoderms from the dorsal shield	(no locality data)
MB.R.	MB.R. 4097	Three osteoderms from the dorsal shield	(no locality data)
	MB.R. 4124	Skull elements with squamosal “horn”	(no locality data)
	MB.R. 4127.3	Skull elements with squamosal “horn”	(no locality data)
	MB.R. 4128.1	Frontal	(no locality data)
	MB.R. 4107.1,2	Right and left femur	(no locality data)
BEC (UA)	(no data)	Complete skull	(no locality data)
	UABEC 1440	Partial skull with frontal and squamosal “horn”	Antsirafaly
	UABEC 0863	Right maxilla	Tsimanampesotse
	UABEC 0369	Frontal, right jugal, right and left squamosal “horn”	Tsimanampesotse
BEC (UA)	(no data - collected from Taolambiby, 2018)	Three osteoderms from the dorsal shield	Taolambiby
ADD (UA)	(no data)	Complete skull	(no locality data)
***Crocodylus niloticus* specimens**			
BEC (UA)	(no data)	4 complete skulls	(no locality data)
NIU	UAP-03.791	Skull and some postcranial bones	Anjohibe Cave

MB.R. 4124, and MB.R. 4127.3 (skull elements), MB.R. 4124 (frontal), MB.R. 4107.1,2 (right and left femora); and Université d’Antananarivo, Bassins sédimentaires Evolution Conservation: UABEC 0863 (right maxilla), UABEC 0368 (frontal), and UABEC 0369 (right jugal, left and right squamosal). Recently, we have identified additional uncatalogued material representing *V. robustus* at UA. The neotype of *V. robustus* is MCZ 1006. It is a complete skull re-described by Brochu (2007), found near Antsirabe, Madagascar (Mook, 1921). Four uncatalogued complete skulls at UA (BEC), referred to *C. niloticus* were also used in this paper along with comparative features described in Mathews & Samonds (2016).

Abbreviations

The following abbreviations have been used in this paper.

4th: fourth trochanter of femur
ace: acetabulum
ADD: Anthropologie Biologique et Développement Durable
aip: anterior iliac process
AMPAS: Ampasambazimba
BEC: Bassins sédimentaires, Evolution, Conservation
BP: before present
ca: carinae
en: external naris
fic: foramen intermandibularis caudalis
fme: external mandibular fenestra
fpo: facet receiving the postorbital
fsmd 1: foramen for first dentary tooth
fsmd 4: foramen for fourth dentary tooth
gf: glenoid fossa of articular
inmd 4: notch for fourth dentary tooth
jc: jugal crest
m 5: maxillary alveolus 5
mg: Meckel's groove
mjf: medial jugal foramen
NIU: Northern Illinois University (DeKalb, Illinois, USA)
ob: oval boss
pip: posterior iliac process
pm 4: premaxillary alveolus 4
pob: postorbital bar
pr.r: retroarticular process
q: quadrate
sh: squamosal horn
tbm 5: swelling over the alveola of fifth maxillary tooth
TSM: Tsaramody, Sambaina

Systematic hierarchy

Crocodylia Gmelin 1789 (sensu Benton & Clark, 1988)

Crocodylidae Cuvier 1807 (sensu Brochu, 2003, context-independent)

***Voay robustus* (Grandidier & Vaillant 1872)**

Referred specimens: Partial left skull with parietal, squamosal, supraoccipital, exoccipital, basioccipital and quadrate (BEC-TSM 16223); isolated left premaxilla (BEC-TSM 14107); right maxilla (BEC-TSM 16099); two nasals (BEC-TSM 14008B; BEC-TSM 16017); frontal (NIU-TSM 15586); right postorbital (BEC-TSM 15148); left jugal (BEC-TSM16225); right squamosal (BEC-TSM16226); partial right pterygoid (BEC-TSM 15017); right ectopterygoid (BEC-TSM 16232); dentary (BEC-TSM 14002); two right articulars (BEC-TSM 14005, TSM16189); right surangular (BEC-TSM 16097); partial right angular (BEC-TSM 16008); 134 isolated teeth; right ilium (BEC-TSM 15064); left ilium (BEC-TSM15027); right radius (BEC-TSM 14087); 1 complete left femur (NIU-TSM 15044); two partial left femora (NIU-TSM 18049; NIU-TSM 18048); four osteoderms (BEC-TSM 14559; BEC-TSM 17193; BEC-TSM 18202; BEC-TSM18102).

In total, the available published material and material at hand for comparative evaluation of the Tsaramody crocodylian consists of four complete skulls with two skull elements, two maxillae, two frontal bones, two jugal bones (left and right), two squamosals (right and left), three right femora, one ilium, and nine osteoderms.

Field techniques

Subfossil bones were recovered by excavating 1 x 2 m pits approximately 1.5 - 2.5 m deep to the base of the lowest clay unit. During previous excavations, layers of travertine inhibited excavation below certain layers and continuous seepage of water into the pits sometimes obscured direct observation of in-situ fossils. As excavations proceeded, water was removed using hand pumps and buckets. All bones larger than 10 cm in length were recorded for position and orientation with respect to sedimentary context, and excavated sediment was washed through a screen to recover additional small bone fragments and isolated teeth. After recording position and orientation, specimens were washed dried, wrapped, and assigned a unique catalog number.

Specimen description and measurements

After collection, field specimens were prepared in the paleontological laboratory at the Université d'Antananarivo. Specimens were cleaned of loose debris, labeled and sorted. Specimens were typically encrusted by hard rock due to volcanic sediments at Tsaramody, Sambaina. Encrusted minerals were gently removed using an airscribe taking care not to damage surfaces. Breaks in the material were repaired using Acryloid B-72. Specimens were then photographed with a scale bar.

Analytical methods

The morphological characterization of specimens collected at Tsaramody follows character descriptions outlined in Brochu (2007). Each specimen was

Table 2. Characters for *Voay robustus* and *Crocodylus niloticus*, based on personal observations and published sources (Mook, 1921; Iordansky, 1973; Brochu, 2007).

	V. robustus	*C. niloticus*
	Skull and skull elements	
Skull	Broad	The snout is narrower more than in *V. robustus*
Premaxillae	Fsmd1 less often present, does not open into the dorsal surface (*V. robustus* has a shorter snout, more than *C. niloticus*)	Fsmd1 opens into the dorsal surface (species with longer snouts always have this character)
Frontal	Oval boss(es) present	Oval bosses absent
Jugal	Jugal crest present	Jugal crest absent
Squamosal	Prominent squamosal horn present	Prominent squamosal horn absent[1]
Quadratojugal	Spina quadratojugalis absent	Spina quadratojugalis present
Supratemporal fenestrae	Constricted	Open and larger than *V. robustus*
	Postcranial elements	
Ilium	Wasp waisting absent	Wasp waisting present
Appendicular skeleton	More robust	Less robust
Iliofibularis trochanter	More expansive	Less expansive

[1]Can be present in larger specimens of *C. niloticus* as upturned knobs on the posterolateral corners of the skull, but not prominent or sharply-demarked as seen in *Voay*.

compared with counterparts from other fossil localities for the presence, absence or variant form of a character (Table 2). Descriptions here highlight the overall resemblance of the characters to known forms of *Voay robustus* and *Crocodylus niloticus*. Intermediate or novel variants of the characters are also noted.

Fossil elements which included diagnostic characters found in the neotype of *V. robustus* (MCZ 1006) or described in Brochu (2007) were classified at *V. robustus* (Table 2). However, other specimens which shared similarity with characters found in MCZ 1006 (Brochu 2007), but which did not "match" the exact form of the character (Table 3), were ascribed to possibly novel variation in these characters within *V. robustus*.

Table 3. Taxonomic designation of elements recovered from Tsaramody. + = present; - = absent; ? = undefined.

Element	***Voay robustus***	***Crocodylus niloticus***
Premaxilla	+	?
Maxilla	+	-
Nasals	?	?
Frontal	+	-
Postorbital	+	-
Jugal	+	-
BEC-TSM 16223	+	-
Pterygoid wing	?	?
Right ectopterygoid	?	?
Dentary	?	?
Articular	+	-
Surangular	?	?
Angular	+	-
Teeth	?	?
Radius	+	-
Femur	+	-
Ilium	+	-
Osteoderms		
BEC-TSM 17493	+	-
BEC-TSM 18202	+	-
BEC-TSM 14559	+	-
BEC-TSM 18102	+	-

Results

Paleontological context

Since 2014, 845 vertebrate specimens have been collected at Tsaramody, with more than 25% of that material identified as crocodylian. Despite the abundance of material, no complete crocodylian crania have been recovered from this site. As at many Malagasy subfossil sites, the faunal assemblage is largely comprised of hippopotami, elephant birds, tortoises, and crocodiles. However, in contrast to most major subfossil localities, Tsaramody has yet to yield primate material.

Temporal distribution of the material

At Tsaramody, the sedimentary layer is divided into 10 levels from the bottom to the top. The most fossiliferous of these is level 2, and no fossils have been recovered from the top three levels (8-10; Samonds *et al.*, 2019). All crocodylian material recovered was from levels 2-4, with the most fossiliferous levels associated with travertine; both crocodiles and hippopotami dominate these levels.

Osteological data analysis

Cranial elements

BEC-TSM 16223 – This specimen preserves a few cranial elements on the left of the skull such as the parietal, squamosal, supraoccipital, exoccipital, basioccipital, and quadrate. On this specimen the parietal is nearly complete. The supratemporal fenestra border is preserved and represents a constricted supratemporal fenestra. The distance between them is approximately 1.7 cm. The diameter of the supratemporal fenestra can be seen from the left supratemporal fenestra; it is small and rounded in shape. The squamosal process or squamosal "horn" is preserved at the posterolateral corner of the squamosal and is round. The squamosal extends on the dorsal surface of the quadrate ramus away from the paroccipital process.

Premaxilla – BEC-TSM 14107 (Figures 2a & 2b) is a nearly complete left premaxilla. The dorsal surface of this specimen is rough. The notch for the fourth dentary tooth (inmd4) is present and close to the premaxilla-maxilla suture. The left part of the external nares is preserved on this specimen. The lamina, which forms the anterior part of the secondary palate, is missing. This specimen bears five almost circular alveoli close to each other; there is no diastema between them. The fourth alveolus is the largest while the second is the smallest. The first, the third and fifth alveoli are approximately the same size. There is no foramen pit for the first lower dentary tooth present on this specimen (fsnmd1).

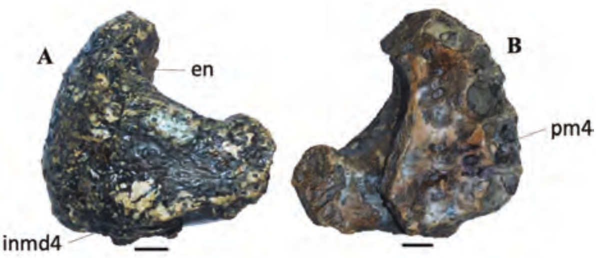

Figure 2. Left premaxilla from Tsaramody, Sambaina (BEC-TSM 14107). **A**), dorsal view; **B**), ventral view. Abbreviations: en, external naris; inmd 4, notch for fourth dentary tooth; pm 4, premaxillary alveolus 4. Scale = 1 cm.

Maxilla – BEC-TSM 16099 (Figures 3a & 3b) is a nearly complete right maxilla. Its broad palatal process is missing. The dorsal surface of this specimen is rough. There is a wide swelling over the alveoli of the fifth maxillary tooth. This maxilla bears 13 circular alveoli divided into two laterally convex series, the first to the seventh and the eighth to the 13th. All alveoli are placed close to each other; there is no diastema between them so the seventh is not isolated. The fifth is the largest and the first is placed on the premaxilla-maxilla suture.

Nasals – BEC-TSM 14008B (Figure 3d) and BEC-TSM 16017 (Figure 3c) are both nasal bones and associated fragmentary material. While the relationship between the nasal margins and external naris can be used to differentiate between *C. niloticus* and *V. robustus*, material referred here is too fragmentary to preserve this information.

Frontal – NIU-TSM 15586 (Figures 3e & 3f) is a complete frontal bone; all sutural surfaces present on this bone are still preserved. The bone has a pentagonal shaped posterior part. On the anterior surface there is one oval boss which is placed centrally. The orbital borders of the frontal are very short. The dorsal surface is less rough than other dorsal bones, however it is still rough. On the ventral side there is a trough which runs from the anterior part to the posterior part as an olfactory tract.

Postorbital – BEC-TSM 15148 (Figures 3g & 3h) is a complete right postorbital bone. Its orbital border, infratemporal fenestra and supratemporal fenestra are preserved. The postorbital bar portion is also present, and the supratemporal fenestra is constricted.

Jugal – BEC-TSM 16225 is a nearly complete left jugal bone, however it does not preserve the complete length. The jugal bone is a plate bone which extends along the sides of the dermatocranium from the anterior corners of the orbits almost to the level of the mandibular condyles. On this specimen the anterior part is widest and the posterior part is narrowest. The anterior process forms the lateral wall of the orbit while the posterior process forms the inferior temporal arcade. The dorsal surface is extremely rough, and there is a remarkable "crest" which lies alongside and below the orbital border. On the ventral surface, the medial jugal foramen is represented by three pits which are placed below the lateral wall of the orbit (on the anterior process and near the postorbital bar). The jugal-ectopterygoid suture is preserved. BEC-TSM 16105 has the same general characteristics.

Squamosal – BEC-TSM 16226 is a right partial squamosal. The horn is identical to that seen in BEC-TSM 16223. Half of the basioccipital and part of the quadrate are also preserved.

The pterygoid wing (= lateral descending flange, lateral wing; BEC-TSM 15017) is a piece of the right

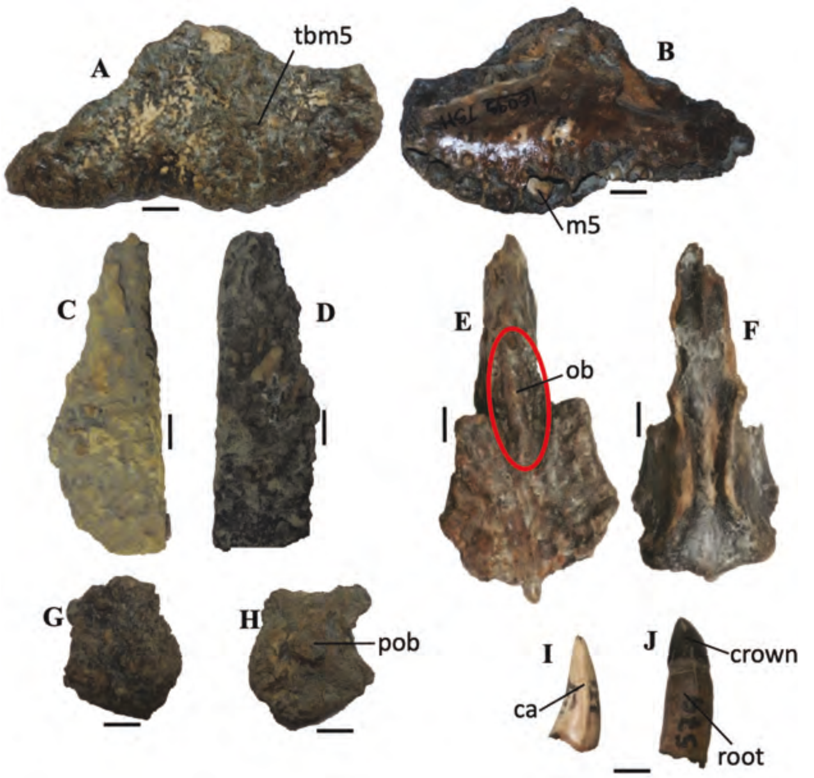

Figure 3. Specimens from Tsaramody, Sambaina. **A-B**), Right maxilla (BEC-TSM14107); **C-D**), nasal bones (BEC-TSM 16017, BEC-TSM 14008B); **E-F**), frontal bone (NIU-TSM15586); **G-H**), right postorbital (BEC-TSM 15148). **I-J**), isolated teeth (BEC-TSM15117, BEC-TSM 15579); **A**), lateral view; **B**), medial view; **C**, **D**, **E,** and **G**), dorsal view; **I**), lateral view; **J**), labial view. Abbreviations: ca, carinae; m 5, maxillary alveolus 5; ob, oval boss; pob, postorbital bar; tbm 5, swelling over the alveola of fifth maxillary tooth. Scale = 1 cm.

pterygoid. Even though much of this specimen is broken, it represents a complete right lateral wing. Its total length is 6.7 cm. The right lateral edge of this wing is thickened and rough.

The right ectopterygoid (BEC-TSM 16232) is nearly complete and robust. Whether the maxillary ramus is cleft or forked anteriorly cannot be determined given the present material.

Lower jaw bones

Teeth – At least 134 isolated teeth (Figures 3i & 3j) were collected; these are the most numerous elements recovered. They are conical in shape as is typical for crocodylian teeth.

Dentary – BEC-TSM 14002 (Figures 4a & 4b) is a partial right dentary. It preserves a portion of the mandibular symphysis and four circular alveoli; the first, second and third alveoli on this specimen are close to each other, but the fourth is isolated from the rest. The diastema between the third and the fourth alveolus is approximately 0.5 cm and the diastema after the last tooth present on this specimen is approximately 1 cm. The Meckelian groove is also preserved.

Articular – BEC-TSM 14005 (Figures 5c & 5d) and TSM 16189 are both nearly complete right articular bones. BEC-TSM 14005 is bigger and thicker than BEC-TSM 16189. On both bones, the retroarticular process is preserved and its dorsal surface is concave. On the anterodorsal part, the glenoid fossa (articular surface for the quadrate) of both specimens is preserved.

Surangular – BEC-TSM 16097 (Figures 5e & 5f) is a nearly complete right surangular. It is a thick bone; its dorsal surface is flattened. In lateral view, this specimen is extremely rough and there is a pronounced groove. The articular-surangular suture is visible in medial view.

Angular – BEC-TSM 16008 (Figures 5g & 5h) is a portion of a right angular. This bone has an extremely rough lateral face; the border of the external mandibular fenestra is also preserved; the external mandibular fenestra is definitely constricted. The medial surface is quite smooth. The border of the

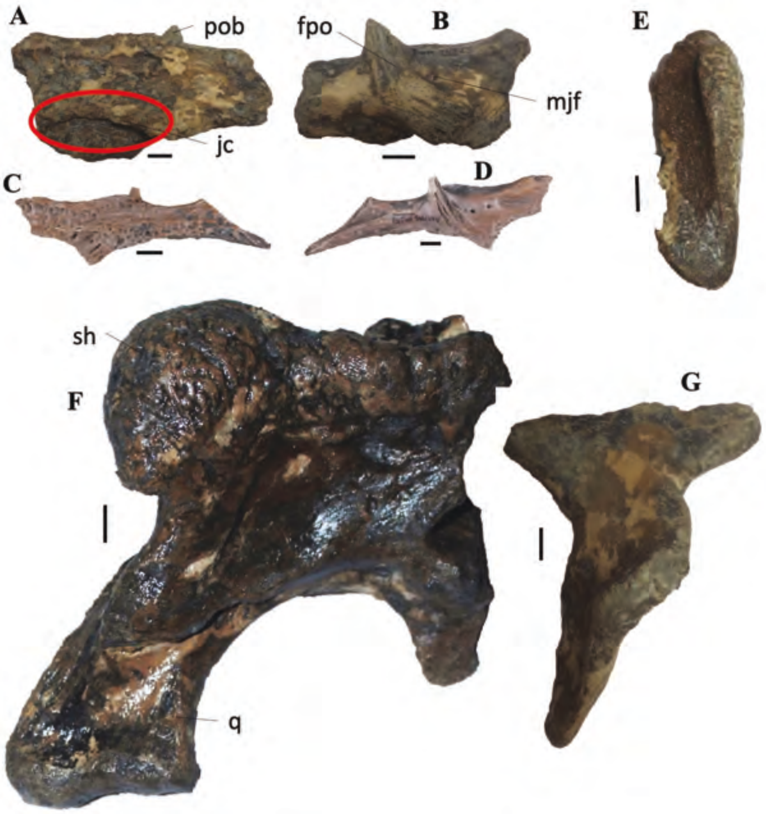

Figure 4. Specimens from Tsaramody, Sambaina. **A-B**), left jugal (BEC-TSM 16225); **C-D**), left jugal (NIU-AMPAS18561); **E**), right pterygoid wing (BEC-TSM 15017); **F**), BEC-TSM 16223; **G**), ectopterygoid (BEC-TSM 16232). **A** and **C**), lateral view; **B** and **D**), medial view; **E** and **F**), occipital view; **G**), ventral view. Abbreviations: fpo, facet receiving the postorbital; jc, jugal crest; mjf, medial jugal foramen; q, quadrate, sh, squamosal horn. Scale = 1 cm.

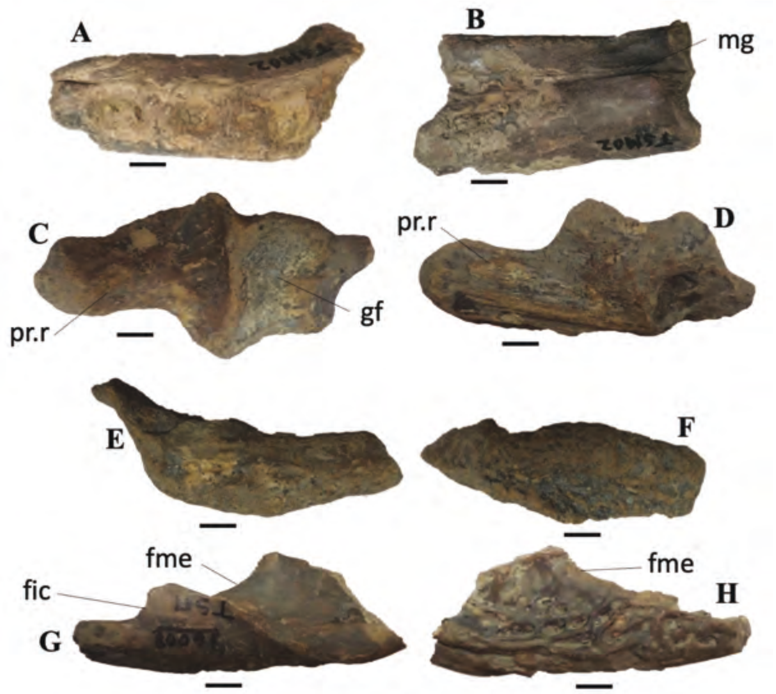

Figure 5. Specimens from Tsaramody, Sambaina. **A-B**), Right dentary (BEC-TSM 14002); **C-D**), right articular (BEC-TSM 16008); **E-F**), right surangular (BEC-TSM 16097); **G-H**), right angular (BEC-TSM 16008); **A**, **C**, and **D**), dorsal view; **B** and **G**), medial view; **D**, **F** and **H**), lateral view. Abbreviations: fic, foramen intermandibularis caudalis, fme, external mandibular fenestra; gf, glenoid fossa of articular; mg, Meckel's groove; pr.r, retroarticular process. Scale = 1 cm.

foramen intermandibularis caudalis is also preserved. Posterior to this foramen, there is a deep sulcus.

Postcranial elements

Ilium – BEC-TSM 15064 (Figure 6e) is a well-preserved right ilium. It bears the entire acetabulum and lacks the dorsal constriction or "wasp waisting" which is characteristic of the extant *Crocodylus* (Brochu, 2007). BEC-TSM 15027 is a well-preserved ilium, larger than BEC-TSM 15064 but similar in overall shape.

Radius – BEC-TSM 14087 (Figures 6f & 6g) is a well-preserved right radius. Its total length is approximately 3.5 cm. The width of the proximal articular surface is the same as its total length, although the distal articular surface is approximately 2.7 cm.

Femur – NIU-TSM 15044 (Figures 6c & 6d) is a nearly complete left femur. NIU-TSM 18049 (Figure 6 a-b) and NIU-TSM 18048 (Figures 6a' & 6b') are both partial left femora; they fit perfectly with each other, indicating that they belong to the same element. This individual was larger than that of NIU-TSM 15044. Both left femora are robust. Their proximal heads are flattened, and the fourth trochanter is well developed and prominent in both.

Osteoderms – Four osteoderms are referred in this manuscript (BEC-TSM 14559; BEC-TSM 17193; BEC-TSM 18202; BEC-TSM18102), but more than 50 of varying preservation have been collected from this site. Some osteoderms possess a more prominent keel (Figures 7a, 7c & 7d) than others (Figure 7b). Many of them are square and thin with a less prominent keel (Figure 7b), although some are sub-rounded (Figure 7d) or triangular (Figures 7a & 7c) in shape with a robust prominent keel. They originate from different regions of the lateral and dorsal armor. Despite their differences in the shape and keel, osteoderms do not possess clearly defined and rounded pits in their dorsal surface.

Analytical results

Most of all crocodile bones found at Tsaramody exhibit characters diagnostic of *Voay robustus* described by Brochu (2007) (Table 2), such as possessing a constricted supratemporal fenestrae, squamosal "horn", and oval boss on the frontal bone.

Figure 6. Specimens from Tsaramody, Sambaina. **A-D**), Left femora (A, B: NIU-TSM 18049; A', B': NIU-TSM 18048; C, D: NIU-TSM 15044); **E**), right ilium (BEC-TSM 15064); **F**, **G**), right radius (BEC-TSM 14087; **A**, **C**, and **F**), dorsal view; **B**, **D**, and **G**), ventral view; **E**), lateral view. Abbreviations: ace, acetabulum; aip, anterior iliac process; pip, posterior iliac process; 4th, fourth trochanter of femur. Scale = 1 cm.

Figure 7. Osteoderms in dorsal view. **A**), BEC-TSM 14559, **B**), BEC-TSM 17193, **C**), BEC-TSM 18202, and **D**), BEC-TSM18102, from Tsaramody, Sambaina; **E**, **F**, and **G**), from Taolambiby, **H**), NIU-AMPAS 18592 from Ampasambazimba; **I**), UABEC-0373 from Tsimanampesotse. Scale = 1 cm.

Moreover, the jugal of *V. robustus* presents a notable jugal crest; in contrast none of the four skulls of *Crocodylus niloticus* examined share this character. However, many recovered elements do not appear to contain diagnostic characters, such as the nasal bone and ectopterygoid (Table 3).

Discussion

General

The frontal bone, postorbital, jugal, and the specimen BEC-TSM 16223 from Tsaramody share many characteristics with the neotype (MCZ 1006) of *Voay robustus*, as well as other material referred to this species, suggesting their generic identification is correct (Tables 2 & 3). *Voay robustus* (MCZ 1006) has a triangular squamosal horn at the posterolateral corner of the squamosal (Brochu, 2007; Bickelmann & Klein, 2009); MB.R.4127.3, AMNH 3101, and three uncatalogued UA specimens also share this character. When comparing (Figures 8a & 8b) the two squamosal horns (BEC-TSM 16223, BEC-TSM 16226) from Tsaramody to squamosal horns from Tsimanampesotse (Figures 8d & 8e, UABEC 0369), and an uncatalogued specimen from Antsirafaly, near Soalara (Figure 8c, both of which are sites in the southwest), there are slight differences in shape. For example, the squamosals recovered from Tsaramody are rounded, while the others are triangular. Moreover, MCZ 1006 (from near Antsirabe), UABEC 0369 (from Tsimanampesotse), AMNH 3101 and three uncatalogued specimens at the Université d'Antananarivo have a pair of oval bosses on the frontal bone (Figures 9a & 9b), while the frontal bone from Tsaramody and MB.R. 4128.1 (unknown origin, bought by the Museum fűr Naturkunde Berlin in 1889) has only one oval boss.

All the *V. robustus* skulls and jugal elements (NIU-AMPAS18561, UABEC 0369) examined present a notable "jugal crest" (Figures 9c, 9e & 9g); in contrast none of the *Crocodylus niloticus* skulls have this characteristic. This suggests that the jugal crest may distinguish *V. robustus* from *C. niloticus.* Additionally, the presence of the jugal crest on the specimen from Tsaramody (BEC-TSM 16225) suggests that these specimens should be referred to *V. robustus*.

The premaxilla (BEC-TSM 14107) lacks a pit for the first dentary tooth (Table 3); this character was also reported by Grandidier & Vaillant (1872) but this character is also recognized to vary ontogenetically in most types of crocodylians (Brochu, 2007), and may not be a good diagnostic character. Moreover, the maxilla (BEC-TSM 16099) bears 13 alveoli without a diastema, while the *Voay* neotype (MCZ 1006) bears 12 alveoli (Brochu, 2007). Even though there is a difference between the number of the alveoli

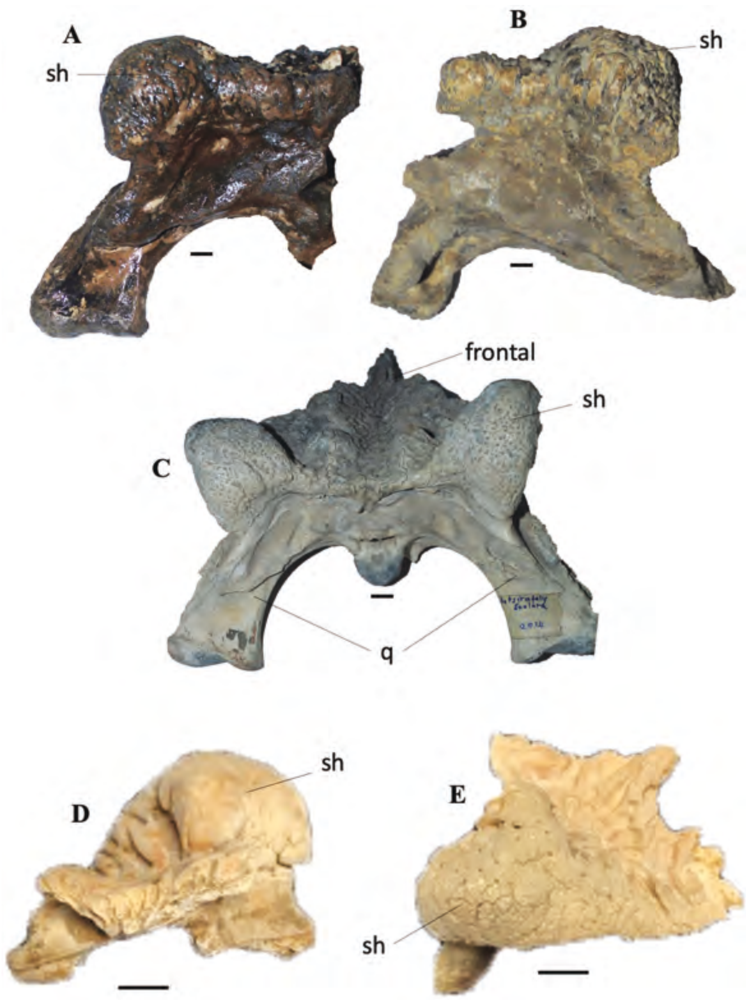

Figure 8. Comparison of squamosa. **A**), BEC-TSM 16223 and **B**), BEC-TSM 16226 from Tsaramody Sambaina; **C**), UABEC 1440 from Antsirafaly in the region of Soalara; **D-E**), UABEC 0369 from Tsimanampesotse. **A-C**), occipital view, **D**), right medial view, **E**), dorsal view. Abbreviations: q, quadrate, sh, squamosal horn. Scale = 1 cm.

on the maxilla (fsmd1 is absent in the Tsaramody specimen, but present in the one from Antsirafaly and Tsimanampesotse), it may not be a reliable diagnostic character for distinguishing these two genera (Iordanski, 1973).

The maxilla also has varying numbers of alveoli (13 in the Tsaramody specimen, and 12 in both Antsirafaly and Tsimanampesotse), and there is a diastema in the specimen from Tsaramody, but not in those from the other sites.

With regards to the postcrania, the ilium (BEC-TSM 15064) lacks the dorsal constriction or "wasp waisting" characteristic of *C. niloticus*, supporting referral to *Voay*. Osteoderms from Tsaramody are large and deep with a pronounced dorsal crest, this might suggest that *Voay* from Tsaramody spent more time on land than water, requiring more effective protection against evaporation. However, it could also indicate that Tsaramody was a cooler, high-altitude subfossil site (Samonds *et al*., 2019) as osteoderms function in aiding temperature regulation (Chen *et al*., 2014; Clarac *et al*., 2018), and crocodylians may develop larger thicker osteoderms to maintain an appropriate temperature. Osteoderms from Tsaramody also lack a defined pit in the dorsal view, in contrast to osteoderms from Tsimanampesotse (Figure 7I) and Taolambiby (Figures 7e-7g) which possess a defined pit in dorsal view. Osteoderms from Ampasambazimba (Figure 7h), also in the Central Highlands, contain more pits than specimens from Tsaramody, but less than those recovered from Tsimanampesotse and Taolambiby. All osteoderms from Tsaramody resemble osteoderms of *V. robustus* described by Brochu (2007) and by Bickelmann & Klein (2009) more than they resemble those from Tsimanampesotse and Taolambiby.

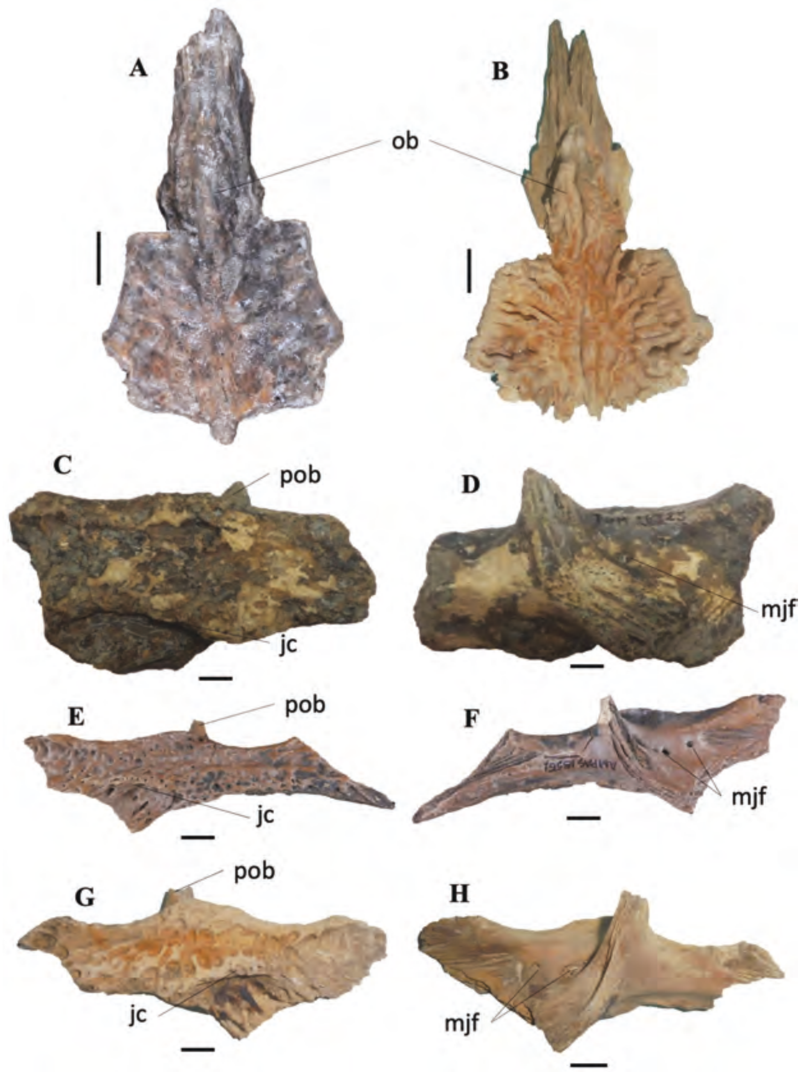

Figure 9. A-B. Frontal bones in dorsal view. **A**), NIU-TSM 15586 from Tsaramody Sambaina; **B**), UABEC 0369 from Tsimanampesotse; **C-D**), BEC-TSM 16225 left jugal from Tsaramody; **E-F**), NIU-AMPAS18561 left jugal from Ampasambazimba; **G-H**), UABEC 0369 right jugal from Tsimanampesotse; **C, E,** and **G**), lateral view; **D, F,** and **H**), medial view. Abbreviations: pob, postorbital bar; jc, jugal crest; mjf, medial jugal foramen; ob, oval boss. Scale = 1 cm.

Paleoenvironment

The local geology and sediments deposited in this region support a river or lake at Tsaramody during the Plio-Pleistocene (Lenoble, 1934). This kind of low energy environment is preferred by crocodiles (Glaw & Vences, 1994; Kuchling *et al*., 2003; Raxworthy, 2003), and many other aquatic animals (e.g., hippopotami) have also been recovered at this site (Samonds *et al*., 2019). The high elevation (1658 m) of Tsaramody suggests this region had a cooler climate than other known subfossil sites.

During the time these bones were deposited, the central and the southern portions of Madagascar represented different biomes, which suggests that there may have been "clines" within *Voay* in body size or "robusticity" or perhaps even additional lineages of horned crocodile on the island. Given the relatively few specimens of *V*. *robustus* in collections worldwide, it is reasonable to assume that the range of variation found in this taxon has yet to be fully explored. Future excavations, and a more comprehensive analysis of subfossil crocodylian bones throughout the entire island is the best way to rigorously test this hypothesis and, when possible, overlaid on genetic comparisons.

Conclusion

To summarize, the site of Tsaramody has many preserved crocodile bones, the majority of which can be referred to the extinct *Voay robustus*.

However, there are some elements that we were unable to definitively identify. Additionally, there are subtle differences between characters of subfossil bones and those of the *V. robustus* neotype (MCZ 1006) possibly suggesting more variation within this genus than is currently recognized; this has also been discussed by Brochu (2007) and Bickelmann & Klein (2009). The most striking differences between subfossil crocodile bones from Tsaramody and other subfossil sites are within the cranial anatomy, including distinct variants of the frontal and squamosal bones. Furthermore, the osteoderms from Tsaramody have a distinct form. Future discoveries, and a more comprehensive island-wide analysis of subfossil crocodylian morphometrics will help to determine the full range of variation in *Voay* and whether this genus comprises a single species or currently unrecognized taxa.

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