Journal of Vertebrate Paleontology e1570223 (15 pages)

DOI: 10.1080/02724634.2019.1570223

ARTICLE

NEW MIOCENE SIRENIANS FROM NOSY MAKAMBY, NORTHWESTERN MADAGASCAR

KAREN E. SAMONDS,*[1] REBEKAH A. ERNAT,[1,2] TSIORY ANDRIANAVALONA,[3] and DARYL P. DOMNING[4]
[1]Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115, U.S.A., ksamonds@niu.edu;
[2]Department of Anthropology, University of Wisconsin–Milwaukee, Milwaukee, Wisconsin 53201, U.S.A., raernat@uwm.edu;
[3]Domaine des Sciences et Technologies, Mention Bassins Sédimentaires Évolution Conservation, Université d'Antananarivo, Antananarivo 101, Madagascar, tsioryandrianavalona@gmail.com;
[4]Laboratory of Evolutionary Biology, Department of Anatomy, Howard University College of Medicine, Washington, D.C. 20059, U.S.A., ddomning@Howard.edu

ABSTRACT—The near lack of vertebrate fossils from the Cenozoic of Madagascar has left many of the details regarding the origin and evolution of the island's extant faunas unknown. However, recent fossil discoveries from Madagascar's nearshore marine deposits have begun to elucidate this mystery. These finds include sharks, bony fish, turtles, crocodylians, a middle Eocene sirenian (*Eotheroides lambondrano*), and the island's first fossil dolphin. We report here at least three (possibly four) different early (or possibly later) Miocene dugongid sirenians recovered from the island of Nosy Makamby, Mahajanga Basin, northwestern Madagascar. These include (1) a fragmentary braincase originally attributed to the genus *Halitherium* but here reidentified as a previously named species known only from Libya (*Rytiodus heali*; Dugonginae); (2) a newly named genus and species (*Norosiren zazavavindrano*) interpreted as a primitive relative of *Xenosiren* (Dugonginae); (3) a probable dugongine not yet identified with any known species; and (4) a taxon reported here as *Metaxytherium* cf. *krahuletzi* (Halitheriinae), the first Neogene halitheriine credibly reported from the Indian Ocean basin. This pattern of shallow marine environments harboring multispecies sirenian paleofaunas is seen elsewhere in the world, and these three or four contemporaneous sirenians represent the first glimpse into Madagascar's sea cow diversity during the Miocene. This specific time period is a poorly known and critical interval for interpreting Madagascar's past, and these specimens are potentially highly significant for reconstructing sirenian evolutionary and biogeographic history. Surprisingly, this sirenian fauna, so far, shares no genera with the roughly contemporaneous and relatively nearby one from Kutch, western India.

FRENCH ABSTRACT—La quasi-absence de fossiles de vertébrés datant du Cénozoïque à Madagascar laisse planer beaucoup d'incertitudes sur l'origine et l'évolution de sa faune actuelle. Toutefois, de récentes découvertes de fossiles marins littoraux malagasy, notamment des fossiles de poissons osseux, requins, crocodiles, tortues, un sirénien de l'Éocène moyen (*Eotheroides lambondrano*) et un dauphin, ont commencé à donner des éléments de réponse. Nous rapportons ici au moins trois, peut-être quatre, différents siréniens miocènes retrouvés dans les formations sédimentaires d'origine marines de Nos Makamby (Bassin de Mahajanga, Nord-Ouest de Madagascar). Les spécimens récoltés incluent: (1) un fragment de crâne auparavant attribué incorrectement au genre *Halitherium* mais réattribué ici à une espèce précédemment nommée: le dugonginé *Rytiodus heali*, connu seulement en Libye; (2) un nouveau genre et espèce (*Norosiren zazavavindrano)* que nous interprétons comme étant un parent primitif de *Xenosiren* (Dugonginae); (3) un présumé dugonginé qui n'est semblable à aucune espèce connue; (4) et un taxon identifié comme *Metaxytherium* cf. *krahuletzi* (Halitheriinae), c'est-à-dire le premier halitheriiné rapporté de manière crédible pour l'Océan Indien. Ce modèle de milieu marin peu profond abritant une paléo-faune sirénienne multi-spécifiques est observé ailleurs dans le monde, et les trois ou quatre siréniens contemporains rapportés ici représentent le premier aperçu de la diversité des siréniens malagasy du Miocène. Comme cette période est mal connue et représente un intervalle critique dans l'interprétation du passé de Madagascar, ces spécimens sont très significatifs pour reconstruire l'histoire évolutive et biogéographique des siréniens. Il est cependant surprenant que cette faune sirénienne ne présente aucun genre en commun avec celle approximativement contemporaine et relativement proche de Kutch (Inde occidentale).

http://zoobank.org/urn:lsid:zoobank.org:pub:6AA2F70F-1385-45D6-9553-F728031DDFC8

Citation for this article: Samonds, K. E., R. A. Ernat, T. Andrianavalona, and D. P. Domning. 2019. New Miocene sirenians from Nosy Makamby, northwestern Madagascar. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2019.1570223.

INTRODUCTION

How, when, and from where Madagascar's spectacular modern vertebrate faunas arrived on the island has mostly remained a mystery, largely due to the virtual absence of Cenozoic fossils (Krause et al., 1997; Krause, 2010). Although the island currently lies close to Africa, it had a long-shared history with other landmasses as part of Gondwana and has been isolated from all other landmasses for ca. 90 million years (Storey et al., 1995), the time period when most of the island's living groups are thought to have evolved and arrived.

Madagascar's currently recognized fossil record is mainly constrained to two major time periods: the middle–late Triassic to late Cretaceous (230–66 Ma; Krause et al., 1997; Flynn et al., 2010) and the late Pleistocene/Holocene, the latter extending

---

*Corresponding author.
Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/ujvp.

back a mere 80,000 years (Samonds, 2007). These terrestrial records have received the majority of attention, yet almost all mapped Cenozoic sediments are marine. These marine deposits have been previously overlooked, even though similar Cenozoic deposits have yielded significant finds elsewhere in the world (e.g., Marivaux et al., 2014).

Madagascar has already contributed a significant glimpse into sirenian evolution during the Cenozoic: *Eotheroides lambondrano* was described from middle Eocene nearshore marine deposits in the Mahajanga Basin of northwestern Madagascar; referred specimens include a nearly complete adult skull and several portions of pachyosteosclerotic ribs (Samonds et al., 2009). The age and relatively primitive morphology of *E. lambondrano* suggest that it may represent the ancestral form from which more northerly species of its genus were derived.

Here, we report a multispecies fauna of Miocene sirenians from northwestern Madagascar. The fossils were recovered from the small island of Nosy Makamby, 4 km off the coast of northwestern Madagascar (Fig. 1). This site is known for having produced a partial sirenian braincase attributed to the genus *Halitherium* nearly a century ago (Collignon and Cottreau, 1927). This braincase was reported as recovered from a nummulitic marl unit on the eastern side of the island. Without much assignable morphology retained, its identification as *Halitherium* appears largely to have been due to the fact that this genus had historically been used as a 'wastebasket taxon.' Subsequent field work at Makamby, combined with reanalysis of that earlier collection housed at the Muséum national d'Histoire naturelle (Paris), has yielded a contemporaneous multispecies sirenian fauna, as is commonly seen elsewhere in the world (e.g., Vélez-Juarbe et al., 2012). We place these species into taxonomic context by comparing them with other described sirenian fossils (e.g., Domning, 1989a). These three or four distinct sirenians represent the first glimpse into Madagascar's sea cow diversity during the Miocene and help reconstruct details of this group's evolutionary and biogeographic history.

Institutional Abbreviations—**HMH**, Höbart-Museum, Horn, Austria; **IGM**, Instituto de Geologia, Universidad Nacional Autonoma de Mexico, Mexico City; **KÜH**, Kühnring excavation collection, Krahuletz-Museum, Eggenburg, Austria; **MHNBx**, Muséum d'Histoire Naturelle de Bordeaux, Bordeaux, France; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **NHMUK**, Natural History Museum, London, U.K.; **UA**, Université d'Antananarivo, Antananarivo, Madagascar.

GEOLOGY AND AGE

Nosy Makamby (= Mahakamby) is a small (~1.6 km × 0.4 km) island located near the delta of the Mahavavy River, in the northwestern part of Madagascar, ca. 50 km west along the coast from the regional capital of Mahajanga (Fig. 1). The only comprehensive description of the island's fossils is the result of reconnaissance work done in the early part of the last century (Collignon and Cottreau, 1927). Nosy Makamby presents one of the most complete marine Miocene sedimentary sequences reported from Madagascar, and also has lateral extensions that crop out in the regions of Cap Tanjona, Cap Sada, and Amparafaka to the west (Collignon and Cottreau, 1927). Sedimentary facies of the Miocene rocks suggest a nearshore depositional environment.

A diverse assemblage of both invertebrates and vertebrates has been reported from this site, including benthic foraminiferans, crabs (Crustacea, Decapoda, Brachyura), bivalves, gastropods, echinoids, sharks, rays, bony fish, reptiles including crocodyliform teeth and large pieces of turtle carapace and plastron, and dolphins (Collignon and Cottreau, 1927; Besairie, 1972; Samonds et al., 2007; Charbonnier et al., 2012; Ramihangihajason et al., 2014; Andrianavalona et al., 2015; Gottfried et al., 2017; Samonds and Fordyce, 2019). Based on the fossil mollusks, Collignon and Cottreau (1927) originally interpreted the age of nearshore marine beds of Nosy Makamby as early Miocene (younger than Aquitanian), ranging between the Burdigalian and Helvetian (the older term Helvetian approximately equates to the Langhian–Serravallian interval). Miliolid foraminiferans are abundant in nearly all of the deposits of Makamby and also suggest a Miocene tropical nearshore paleoenvironment (Lavocat et al., 1960; Ramihangihajason et al., 2014). Recent work on strontium isotopes suggests that some of the sediments may be as late as early Tortonian in age (~10 Ma; Samonds and Fordyce, 2019).

Additional Abbreviations—**c.**, character state as described and numbered by Domning (1994), Bajpai and Domning (1997), Domning and Aguilera (2008), Vélez-Juarbe et al. (2012), and/or Springer et al. (2015) (e.g., [c. 42(2)] refers to state 2 of character 42); **e**, estimated (for measurements).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order SIRENIA Illiger, 1811
Family DUGONGIDAE Gray, 1821
Subfamily DUGONGINAE (Gray, 1821) Simpson, 1932
Genus *RYTIODUS* Lartet, 1866

Rytiodus Lartet, 1866:682. [Incorrect transliteration, but 'correct original spelling.']

Rhytiodus Delfortrie, 1872:282. [Unjustified emendation of *Rytiodus* Lartet, despite correctness of transliteration. Junior homonym of *Rhytiodus* Kner, 1858 (Pisces).]

Thelriope Pilleri, 1987:65. [Unnecessary replacement name for *Rhytiodus* 'Lartet.']

Type Species—*Rytiodus capgrandi* Lartet, 1866.

Included Species—*Rytiodus capgrandi* Lartet, 1866; *Rytiodus heali* Domning and Sorbi, 2011.

Range—Aquitanian–Burdigalian and possibly Langhian; southwest France, Libya, Madagascar, and possibly Atlantic coast of Brazil.

Emended Diagnosis—*Rytiodus* is a genus of dugongine dugongids characterized by large tusks [c. 140(2)] that are broad and extremely flattened mediolaterally [c. 141(3)], with enamel mainly on medial side [c. 142(1)]; premaxillae with nasal processes that are broadened and bulbous at their posterior end, having a more or less vertical joint surface with frontal [c. 6(3)]; thick, strongly downturned supraorbital process of frontal [c. 36(1 or 3)]; lacrimal inserted between posterior extremity of nasal process of premaxilla and anterior extremity of supraorbital process of frontal [c. 93(2)]; temporal crests closely approximated in midline; and posterior process of jugal long [c. 89(0)], a retained state that is primitive for dugongines.

RYTIODUS HEALI Domning and Sorbi, 2011
(Fig. 2)

Halitherium sp., Collignon and Cottreau, 1927:33. [MNHN 1924-2 from Madagascar.] New synonymy.

"Flat-tusked dugongid," Savage, 1975:824.

"*Rytiodus* sp. from Libya," Domning, 1978:577, 1989b:424, 1997:409; Toledo and Domning, 1991:133; Bajpai and Domning, 1997:224; Domning and Aguilera, 2008:499; Clementz et al., 2009:appendix 1; Bajpai et al., 2010:43.

Rytiodus heali Domning and Sorbi, 2011:1340.

Holotype—NHMUK M45674 (formerly numbered M19101a–c), skull, endocranial cast, associated vertebrae and ribs of subadult.

Type Locality—Jabal Zaltan, Libya.

Type Formation—The Garat Jahanam (Qaret Jahannam) Member, the basal part of the Marada Formation (Gaziry, 1987).

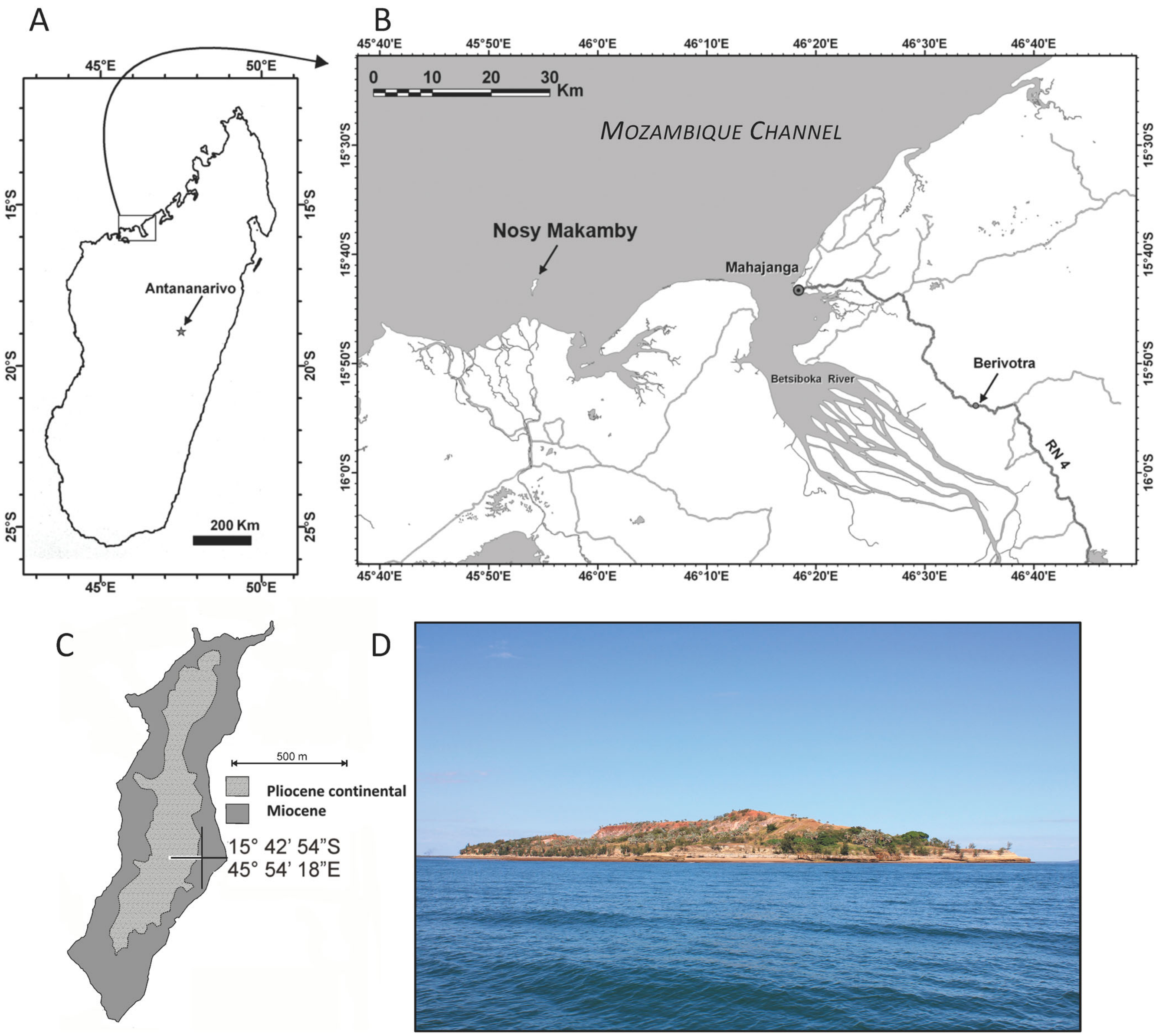

FIGURE 1. **A**, map of Madagascar showing location of the study site. **B**, regional map of the island of Nosy Makamby. **C**, map showing location of Pliocene and Miocene sediments. **D**, photograph of Nosy Makamby showing central red Pliocene continental rocks ringed by nearshore marine Miocene sediments.

Age at Type Locality—Probably in the interval from Burdigalian to Langhian (19–14 Ma).

Newly Referred Specimen—MNHN 1924-2, partial skull, vertebrae, and ribs described by Collignon and Cottreau (1927); from ?early Miocene deposits on Ile (= Nosy) Makamby, Madagascar.

Range—Known previously only from the Burdigalian–Langhian deposits of Jabal Zaltan, Libya.

Emended Diagnosis—Dugongine dugongid differing from *Rytiodus capgrandi* (the only other species of the genus) in having the following apomorphies: premaxillae with nasal processes that circumscribe an almost rectangular anterior end of the mesorostral fossa; narrower temporal fossa; more elevated processus retroversus of squamosal; blunter and less recurved supraorbital process [c. 36(1)]; frontal roof that is shorter, narrower, concave, and sloping ventrad [c. 42(2)]; large nasal with prominent triangular dorsal exposure; vertical butt joint between premaxilla and nasal, with almost no overlap or contact between premaxilla and frontal [c. 9(2)]; and loss of contact between exoccipitals [c. 66(1)].

DESCRIPTION

Skull

The skull of MNHN 1924-2 comprises only the braincase, without the rostrum, palate, jugals, or dentition (Table 1). Preserved at least in part are the ethmoid, frontals, parietals, supraoccipital, exoccipitals, a fragment of ?sphenoid, squamosals (left zygomatic and posttympanic portions, fragment of right posttympanic portion), right periotic and mastoid portion of left periotic, both tympanics, and some unidentified fragments.

TABLE 1. Cranial measurements (in mm) of *Rytiodus*, *Metaxytherium*, and Dugongidae, sp. indet., from Madagascar and other representatives from Libya and Austria.

Cranial dimension	*Rytiodus heali* (Madagascar) MNHN 1924-2[a]	*Rytiodus heali* (Libya) NHMUK M45674	*Rytiodus heali* (Libya) NHMUK M82415	*Metaxytherium* cf. *krahuletzi* (Madagascar) UA-15.231[a]	*Metaxytherium krahuletzi* (Austria) KÜH 88	*Metaxytherium krahuletzi* (Austria) KÜH 85/85	*Metaxytherium Krahuletzi* (Austria) HMH 247	Dugonginae, sp. indet. (Madagascar) UA-15.122[a]
GG’	68e[a]	75e[b]	66e[c]	69[a]	76	—	—	58[a]
OP	>>105[a]	133e	139	—	—	—	—	—
LFr	46e[a]	54e	76	—	—	—	—	—
PL	113[a]	117e	—	95e[a]	93	80	103	52[a]
PW	74[a]	60	—	73[a]	90e	87	98	67[a]
HSo	56[a]	66	—	58[a]	50	52	59	—
WSo	40e × 2 = 80e[a]	50 × 2 = 100e	—	77[a]	73	85	82	—
SPa	122°[a]	115°	—	130°[a]	127°e	136°	126°	—

Abbreviations: **e**, estimated; **GG’**, breadth of cranium at frontoparietal suture; **HSo**, height of supraoccipital; **LFr**, length of frontals in midline; **OP**, length of zygomatic process of squamosal; **PL**, length of parietals (frontoparietal suture to rear of external occipital protuberance in midline); **PW**, maximum width of parietals (in front of nuchal line); **SPa**, angle between supraoccipital and parietal; **WSo**, width of supraoccipital (ventrally).

[a] Specimens described in this paper.

[b] Measured low on sides of braincase.

[c] Measured at level of braincase roof.

Ethmoidal Region—The dorsal end of the perpendicular plate of the ethmoid is thickened to a width of ca. 3 cm where it fits into a socket in the frontals (Fig. 2B). It is roughly almond-shaped with pointed ends (i.e., vesica piscis) in transverse cross-section, with the crista galli forming a vertical ridge on the posterior side, extending up into the braincase roof and projecting back into a small pointed ridge in the anterior portion of the braincase. Other details are mostly destroyed.

Frontal—The supraorbital processes are broken; a part of the right process that was illustrated by Collignon and Cottreau (1927:fig. 2) is now also missing. The anterior frontal border is damaged in the midline. On the dorsal surface, the frontoparietal suture is obscure. The frontal roof has no median ridge or knob-like bosses [c. 45(0)] and is deeply concave between broadly rounded temporal crests, sloping steeply anteroventrad at an angle of ca. 42° to the parietal roof [c. 42(2)]. The intracranial interfrontal suture slopes posterodorsad from the cribriform plate and crista galli; it is 1.5 cm long, much shorter than the approximately 3 cm length of the frontal roof dorsal to the nasal cavity. The frontal roof is ca. 41 mm thick at the frontoparietal suture, and the breadth of the cranium at the frontoparietal suture and at the level of the braincase roof is 52 mm.

Parietal—The parietals bear distinct temporal crests with their lateral sides concave. The crests diverge anteriorly and are in continuity with the prominent frontal ridges, whereas posteriorly they diverge equally sharply and apparently met the nuchal crest. In their middle sections, the crests meet in the midline and run parallel for ca. 5 cm with only a shallow groove separating them; they are jointly 8 mm wide and form a pseudosagittal crest. A true sagittal crest is absent [c. 51(1)]. In lateral view, the profile of the crests dips downward slightly where the crests diverge posteriorly (Fig. 2C). This divergence also creates a triangular dorsal depression with a slightly raised center, as in Libyan *R. heali*.

Internally, the internal occipital protuberance is blunt but prominent; the bony falx cerebri is sharp posteriorly but short, ending ca. 4 cm from the frontoparietal suture (Fig. 2B). The intracranial frontoparietal suture is straight and transverse. The tentorium cerebelli is weak. The thickness of the skull roof is ca. 39 mm at the transverse sulcus and 34 mm at the anterior end of the parietals. The lateral surfaces of the parietals are steeply sloped, giving this part of the braincase a maximum width of 81 mm and a minimum width of 60 mm.

Supraoccipital—The supraoccipital is subrectangular, as in *R. heali*. It is wider in its dorsal half (80e mm) than at the ventral extremities of its lateral borders (76e mm) [c. 64(0)]. The round insertions for the semispinalis capitis muscles and the distinct, posterad-concave nuchal crest are also like in *R. heali* (Fig. 2D). The external occipital protuberance is broadly triangular, blunt, with a broad but poorly developed median ridge below it that is slightly broken along the midline. The parietal-supraoccipital angle is 122°. The sutural surfaces for the exoccipitals meet at an angle of ca. 149°, separated by a distinct median crevice 5 mm deep; together with the gap between the exoccipitals themselves, this crevice at the top of the foramen magnum is ca. 15 mm deep. Endocranially, there is a shallow transverse sulcus posterior to the internal occipital protuberance.

Exoccipital—The exoccipitals are separated in the midline by ca. 6 mm [c. 66(1)]. The dorsolateral border is ca. 14 mm thick, rounded, smooth, and not flange-like [c. 70(1)]. Shallow supracondylar fossae are present.

Sphenoid—A fragment of bone may represent part of the basisphenoid-alisphenoid complex; it bears a large groove, possibly representing the sphenorbital canal. However, its orientation is uncertain.

Squamosal—Represented by fragments, including the left zygomatic process. The squamosal reaches the level of the temporal crest and the roof of the parietal and indents the latter’s outline posterolaterally [c. 76(1)]. The sigmoid ridge is preserved

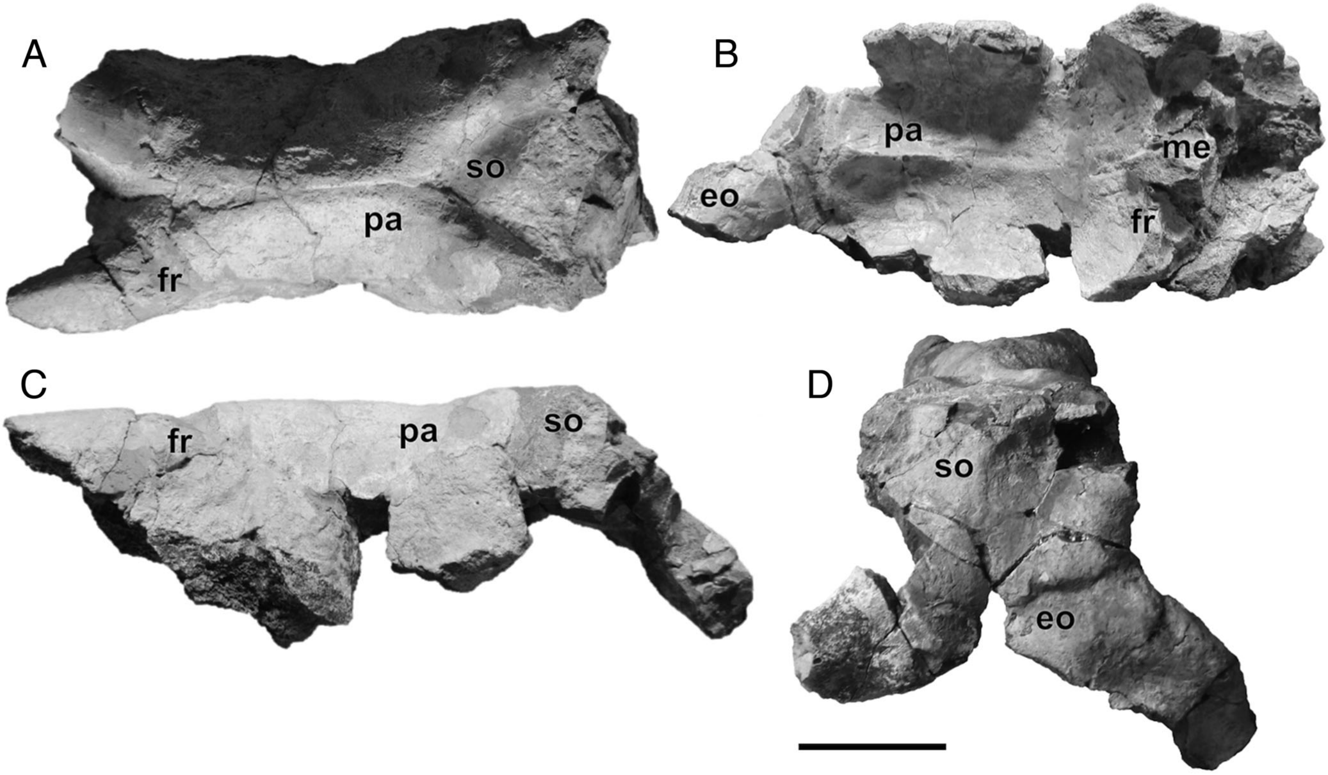

FIGURE 2. *Rytiodus heali*, MNHN 1924-2, partial skull in **A**, dorsal, **B**, ventral, **C**, left lateral, and **D**, posterior views. Anterior to the left in **A**. **Abbreviations**: **eo**, exoccipital; **fr**, frontal; **me**, mesethmoid; **pa**, parietal; **so**, supraoccipital. Scale bar equals 5 cm.

on the left; it is more or less straight in its midsection, between the dorsal and ventral curvatures, and prominent [c. 74(2)]. The external auditory meatus is <1 cm long mediolaterally [c. 75(1)] and was about as wide as high [c. 82(1)]. The posttympanic process projects anteroventrally [c. 73(0)]. The root of the zygomatic process is inclined strongly anteriad and may have been dorsally somewhat concave. The zygomatic process is damaged anteriorly but appears narrower dorsoventrally than in Libyan *R. heali*; it is mediolaterally thin, not medially swollen [c. 84(0)], with its lateral surface concave in its midsection. The shape of its anterior tip is uncertain [c. 81(?)]. Its posterodorsal border is straight and scarcely convex laterad. The processus retroversus is moderately inflected [c. 77(1)] and appears to have been elevated above the plane of the squamosal-jugal suture, although this suture is not substantially preserved. The temporal condyle is prominent in lateral view. The maximum dorsoventral height of the zygomatic process (measurement WX) is 46 mm.

Ear Region—The height of the pars temporalis (= tegmen tympani) of the right periotic is 19 mm; that of the pars mastoideus is 35 mm. The latter has a more or less sharp vertical ridge that protrudes into the mastoid fenestra [c. 118(1)]. The periotic was not fused to other bones [c. 115(1 or 2)] and is largely complete, with only the tip of the pars temporalis and the promontory missing. The overall shape is very squared off, with a maximum length of ca. 50 mm. The anterior parts of both tympanics are preserved and are approximately 2 cm high by 2 cm wide with a smooth surface and a blunt tip.

Postcranial Skeleton

Ribs—Several rib fragments of MNHN 1924-2 are also preserved: the proximal part of right rib 1, three rib fragments respectively numbered '1,' '2,' and '4,' nine other rib fragments collectively numbered '21,' and a large piece consisting mostly of matrix numbered '20.' The most distinctive is the right rib 1, with its anteriorly directed ventral process of the neck; its diameters where broken are 32 × 24 mm. The largest of the more posterior ribs has diameters of 30 × 23 mm.

Vertebrae—MNHN 1924-2 includes centra of two thoracic vertebrae (additionally numbered '18' on their label). These are similar in shape to the thoracics of Libyan *R. heali* (Domning and Sorbi, 2011:fig. 12c, d). The larger one has an anterior width of 49e mm, height in midline of 37 mm, and anteroposterior thickness of 29 mm.

COMPARISON

With reference to the diagnoses provided in Domning and Sorbi (2011), the imperfectly preserved MNHN 1924-2 resembles the genus *Rytiodus* on the basis of its temporal crests being closely approximated in the midline. It can be referred to *R. heali* (as distinct from *R. capgrandi*, the only other species in the genus) on the basis of its apparently elevated processus retroversus of the squamosal, shorter and narrower frontal roof, and loss of contact between exoccipitals [c. 66(1)].

Further differences from *R. capgrandi* can now be established (and the diagnoses revised), based on Domning's unpublished observations on the unique long-missing, recently relocated skull of that species (MHNBx 2006.PG.308; Delfortrie, 1880; Rocher et al., 2015): *R. heali* has a concave, steeply sloping frontal roof [c. 42(2)], whereas that of *R. capgrandi* is nearly flat with no anterior slope [c. 42(0)]. *Rytiodus capgrandi* has pronounced, recurved posterolateral corners of the supraorbital processes [c. 36(3)] and slightly developed bilateral longitudinal ridges on the frontal roof [c. 45 (1)], whereas *R. heali* does not [c. 36(1), 45(0)]. Where it can be scored for these characters, MNHN 1924-2 agrees with Libyan *R. heali* [c. 42(2), 45(0)].

With regard to the distinctive temporal crests of MNHN 1924-2, which are fully in contact for a distance of ca. 5 cm, this would appear to be at least a subtle difference from the Libyan specimens of *R. heali*, in which the midline contact (if fully present at all) is proportionately shorter by some centimeters. However, the form of the temporal crests is well known to be variable intraspecifically in sirenians; in fact, in *R. capgrandi*, this contact is ca. 4 cm long (Delfortrie, 1880:pl. 6, fig. 2) and most similar to the Madagascar form.

Also to be considered are the other adequately known fossil sirenians (all of them dugongines) from the Indian Ocean basin, specifically Kutch, India: *Bharatisiren indica* Bajpai et al. (2006); *B. kachchhensis* Bajpai and Domning (1997); *Domningia sodhae* Thewissen and Bajpai (2009); and *Kutchisiren cylindrica* Bajpai et al. (2010). The only one of these that resembles the Madagascar specimen in the form of the temporal crests is *K. cylindrica*, but they differ in characters 42, 64, and 66. Besides having dissimilar temporal crests, *B. indica* differs from the Madagascar skull in characters 42, 66, and 70; *B. kachchhensis* in characters 64, 66, and 70; and *D. sodhae* in character 66. On the whole, none of the known species from the Indian Ocean basin matches the Madagascar form as well as the Libyan *R. heali* does. However, *K. cylindrica* has some intriguing resemblances to *R. heali* (temporal crests of the frontals, form of nasals and frontal roof) that may help to demonstrate a close relationship when the former becomes more completely known.

Therefore, we see no morphological evidence that would necessarily bar the Madagascar specimen from referral to *Rytiodus heali*, and we regard this as the most parsimonious assignment. The present inconclusive dating of some of the Nosy Makamby sediments (not necessarily the ones that yielded *R. heali*) suggests an age (possibly ca. ~10 Ma) younger than that of the Libyan material.

Subfamily DUGONGINAE (Gray, 1821) Simpson, 1932
NOROSIREN ZAZAVAVINDRANO, gen. et sp. nov.
(Fig. 3)

Holotype—UA-14.139, a partial left maxilla.

Type Locality—Recovered from the locality 2010-09, Nosy Makamby, northwestern Madagascar. Locality is on the northeastern tip of the island.

Age at Type Locality—Miocene.

Etymology—‘*Noro*’ (NOO-roo) refers to the water spirit Ranoro in the lore of the Malagasy Merina tribe; Latin ‘*siren*’ = siren (f.), from Greek ‘*Seiren*.’ ‘*Zazavavindrano*’ (ZA-za-va-vin-DRA-noo; noun in apposition) refers to the ‘daughters of water’ or water spirits in Madagascan mythology, who first owned cattle and gave them to human beings.

Diagnosis—Alveolar process of maxilla dorsolaterally concave and thin dorsoventrally, but with dorsal side not pierced by apices of the cheek tooth alveoli. Zygomatic-orbital bridge short anteroposteriorly, with its dorsal surface crossed by a low, rounded, nearly transverse ridge [c. 14(2)] partly obstructing the infraorbital canal [c. 20(1)].

DESCRIPTION

Maxilla—UA-14.139 is a partial left maxilla comprising much of the alveolar process but no teeth (Fig. 3). The palatal gutter anterior to the alveoli is narrow relative to the posterior palate including the teeth [c. 23(0)]. The alveolar row is short, including vacant alveoli for one or two small molariform teeth anteriorly and two larger, three-rooted teeth posteriorly; the maximum width of a set of alveoli is ca. 25 mm. The bone is broken at the rear, so it is not clear whether the last of these teeth was really the last of the series. If the transverse ridge in *Norosiren* (see below) has the same position relative to the tooth row as in *Xenosiren yucateca* Domning (1989a), then the two posterior tooth sockets in the former represent M1–2.

The lateral profile of the maxilla is ventrally concave throughout the alveolar row. The alveolar process itself is broken laterally but is thin dorsoventrally (~11 mm) at the level of the last preserved molar alveolus; this vertical compression is a feature in common with *Xenosiren*. However, unlike *Xenosiren*, the process is not so thin that its dorsal side is pierced by apices of the cheek tooth alveoli.

The zygomatic-orbital bridge is very thin dorsoventrally (~4 mm) near its anterior edge, thick posteriorly [c. 22(0?)], and of uncertain length anteroposteriorly. The underside of the posterior part of the bridge (~labial border of alveoli) is nearly level with the palate [c. 11(0)], also as in *Xenosiren*. At the front end of the maxilla, the palatal surface is recessed 5 mm above the palate's rounded lateral border. At and anterior to the level of the anterior alveoli, the lateral surface of the maxilla is broadly concave, facing anteroventrad. The dorsoventral thickness of the zygomatic-orbital bridge (measurement T) is strikingly deep where broken (~28 mm), due to a low, rounded, more or less transverse ridge on its dorsal side that crosses the posterior part of the bridge [c. 14(2)]. This transverse ridge corresponds in its location with the much higher and thinner vertical transverse wall that characterizes the maxilla of *Xenosiren yucateca* (Domning, 1989a:fig. 4; Fig. 3 here). Thus, it partly obstructed the infraorbital canal [c. 20(1)]. At its posteromedial end, this ridge curves backward and intersects a thin (5 mm) vertical wall atop the posterior part of the maxilla's alveolar process. The latter wall corresponds to the even thinner medial vertical wall in *X. yucateca*. This wall in the Madagascan specimen is continued anteriorly by a lower, fainter longitudinal ridge; taken together, these posterior and anterior parts form a nearly continuous longitudinal ridge that is slightly concave medially.

The palatal process is thick (~25 mm) [c. 16(1)] near its posterior end, compared with 35 mm in *X. yucateca*. The rear end of the intermaxillary suture was at the level of the transverse ridge in the infraorbital canal, but the sutural surface itself seems not to be preserved; the rough surface now existing is probably erosional. The palatine bones evidently extended anteriorly beyond the posterior edge of the zygomatic-orbital bridge [c. 99 (0)], but the anterior extent of the palatal incisure is not determinable [c. 97(?)].

COMPARISON

The vertical compression of the maxillary alveolar process is shared with *Xenosiren*, but in *Xenosiren* this region is even thinner and is pierced by apices of the cheek tooth alveoli, which is not seen in *Norosiren*. The extremities of the zygomatic-orbital bridge are not preserved here, but its cross-section, seen where broken at the level of the transverse ridge on its dorsal side, gives the impression of its having been (like *Xenosiren*) shorter anteroposteriorly than in most sirenians. In any case, the most extraordinary feature of the *Norosiren* maxilla is this same transverse ridge, which has no counterpart in any other known sirenian except *Xenosiren* (an apparently later [late Miocene or early Pliocene?] and much more derived form). The ridge obstructs the infraorbital canal (modestly in *Norosiren* and dramatically in *Xenosiren*), posing the questions of (1) where the large neurovascular bundle that traverses this canal in other sirenians was accommodated and (2) what stresses (possibly of tusk use; Domning, 1989a; Domning and Beatty, 2007) occasioned such a radical change in cranial architecture.

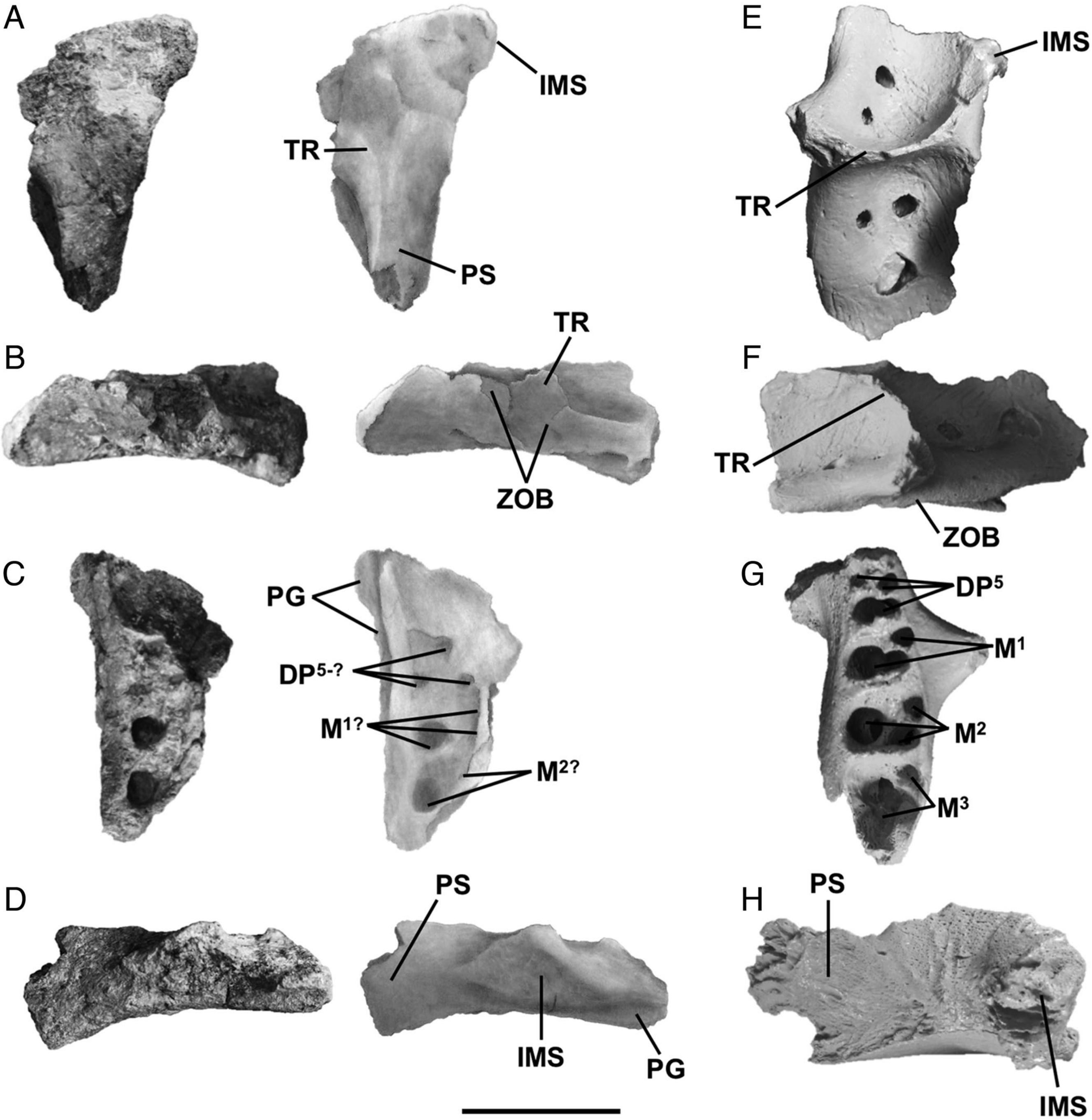

FIGURE 3. *Norosiren zazavavindrano*, gen. et sp. nov., and *Xenosiren yucateca* maxillae. *Norosiren zazavavindrano*, gen. et sp. nov., UA-14.139, left maxilla (photos on left and drawings at right) in **A**, dorsal, **B**, medial, **C**, ventral, and **D**, lateral views. *Xenosiren yucateca*, IGM 4190, holotype, replica of left maxilla in **E**, dorsal, **F**, medial, **G**, ventral, and **H**, lateral views. **Abbreviations**: **DP**$^{\mathbf{5}}$, deciduous 5th premolar alveoli; **DP**$^{\mathbf{5?}}$, **M**$^{\mathbf{1?}}$, **M**$^{\mathbf{2?}}$, groups of alveoli thought to represent DP$^{\mathbf{5}}$–M^{2}, respectively; **IMS**, intermaxillary suture; **M**$^{\mathbf{1}}$, **M**^{2}, **M**$^{\mathbf{3}}$, groups of alveoli representing M^{1}–M^{3}, respectively; **PG**, palatal gutter; **PS**, surface in contact with palatine bone; **TR**, transverse ridge; **ZOB**, broken surface of zygomatic-orbital bridge. Scale bar equals 5 cm.

This resemblance would be less surprising if *Xenosiren yucateca* were, like *Norosiren*, known to have occurred in the Indian Ocean; but the unique type specimen of the former species and genus is, as its name reveals, from Yucatan in Mexico. The fossils in hand therefore present as much of a puzzle for paleozoogeography as for functional anatomy. Phylogenetically, the derivation of *Xenosiren* from *Norosiren* or a similar form is the obvious initial hypothesis, although parallel evolution of separate dugongine lineages cannot be ruled out, given the inadequacy of the present material and our ignorance regarding the adaptive value (if any) of the transverse ridge.

Subfamily DUGONGINAE (Gray, 1821) Simpson, 1932

DUGONGINAE, gen. et sp. indet.

(Fig. 4)

Referred Specimen—Partial braincase (skullcap) with both parietals (UA-15.122; Fig. 4) recovered from the locality 2010-09.

DESCRIPTION

Skull

One partial parietal-supraoccipital skullcap (UA-15.122; Fig. 4) represents a different animal than *Metaxytherium* or *Rytiodus*, possessing a short, square, concave parietal roof somewhat similar to that of the dugongine *Corystosiren* Domning, 1990. The dorsal concavity of the parietals is bordered on all sides by prominent, thick, concave-outward ridges: an anterior one following the line of the frontal-parietal suture, the temporal crests on either side, and the nuchal crest posteriorly. Adjoining the nuchal crest anteriorly is a raised triangular area. The skullcap is 21 mm thick at the frontal-parietal suture. The ventral surface is slightly eroded.

COMPARISON

Skullcaps of this general pattern have so far been found only among dugongines. *Corystosiren* is the only such genus to have been named, but new, similar dugongine material from the early Miocene Pirabas Formation of Pará, Brazil, may represent a different taxon (Domning and H. Moraes, in prep.). In any case, UA-15.122 resembles neither *Metaxytherium* nor *Rytiodus*, nor does it closely resemble any of the taxa so far known from India; it comes closest to *Domningia*, but the latter has a proportionately much longer parietal roof. It could conceivably represent *Norosiren*, whose skullcap is unknown; but all that can now be said is that UA-15.122 is highly likely to represent a dugongine, possibly a new one.

Subfamily HALITHERIINAE (Carus, 1868) Abel, 1913
GENUS *METAXYTHERIUM* Christol, 1840

METAXYTHERIUM KRAHULETZI Depéret, 1895

For synonymy, see Domning and Pervesler (2001).

Type Series—KME nos. GII 21, 22, 25, 26, 29, 34, six isolated molars.

Type Locality—Schindergraben, Eggenburg, Austria.

Type Formation—Burgschleinitz Formation.

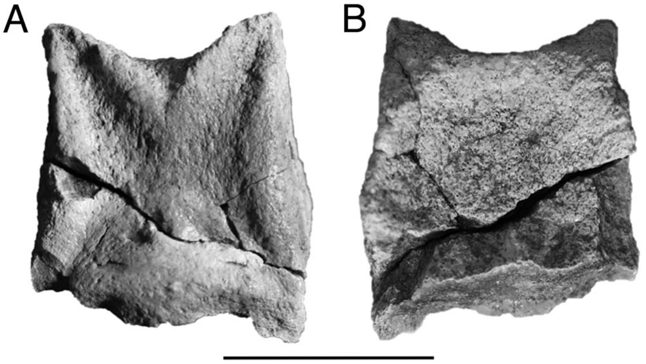

FIGURE 4. Dugonginae, gen. et sp. indet., UA-15.122, partial parietal-supraoccipital skullcap in **A**, dorsal and **B**, ventral views. Scale bar equals 5 cm.

Age at Type Locality—Early Miocene (Eggenburgian).

METAXYTHERIUM cf. KRAHULETZI Depéret, 1895
(Fig. 5)

Newly Referred Specimen—Partial braincase (skullcap) comprising both parietals and supraoccipital (UA-15.231; Fig. 5A–D) recovered from the locality 2010-10-'East Annex' on the northern central part of the island.

DESCRIPTION

Skull

Parietal—The interparietal suture is faintly visible (Fig. 5A). The sides of the braincase are vertical, descending at a ca. 90° angle from the braincase roof. On each side, directly below the parietal-supraoccipital suture, is an indentation roughly 2 cm in diameter and 0.75 cm deep for the squamosal. This indentation barely reaches the level of the temporal crest [c. 76(1)] and negligibly indents the outline of the skull roof in dorsal view, except for a notch marking the parietal-supraoccipital intersection. The top of the parietals is relatively flat between the temporal crests, with a slightly elevated, backward-pointed triangular area anteriorly and another slightly elevated, broader, and forward-pointed area posteriorly that is continuous with the nuchal crest. The endocranial surface displays a bony falx cerebri extending anteriorly from the internal occipital protuberance (Fig. 5B); the falx nearly flattens out before reaching the frontoparietal suture. The roof of the braincase is relatively thick (~3 cm), whereas the sides are much thinner, approaching 0.5 cm ventrally.

Supraoccipital—The border between the supraoccipital and parietals is marked by a strong nuchal crest (Fig. 5C). The top of the nuchal crest and external occipital protuberance is pierced by a small emissary foramen. A perpendicular ridge extends posteriorly along the midline and tapers off near the bottom of the supraoccipital (Fig. 5C, D). Two rounded depressions (insertions for the semispinalis capitis muscles; ~1.4 cm in diameter) exist on either side of this ridge, directly below the nuchal crest. The lateral edges of the supraoccipital are convex and overhanging [c. 64(0)]. The sutural surfaces for the exoccipitals are continuous, indicating that the exoccipitals met in the midline [c. 66(0)].

COMPARISON

There are eight valid species of *Metaxytherium* described from Africa, Europe, North America, and South America (de Muizon and Domning, 1985; Domning and Thomas, 1987; Aranda-Manteca et al., 1994; Carone and Domning, 2007; Sorbi et al., 2012; Domning and Pervesler, 2013; Vélez-Juarbe and Domning, 2014). Of these, the ones closest geochronologically and geographically to the Madagascan specimen, and thus most appropriate for comparison, are *M. krahuletzi* Depéret, 1895, from the early Miocene (upper Eggenburgian to Ottnangian, early to middle Burdigalian-correlative) and *M. medium* (Desmarest, 1822) (see also Hooijer, 1952) from the middle–late Miocene (Serravallian–Tortonian), both from the European-Mediterranean region (Domning and Pervesler, 2001, 2013).

Specimen UA-15.231 is very similar in size and morphology to skullcaps of *M. krahuletzi*. Particularly relevant is the juvenile Austrian specimen KÜH 88 (Domning and Pervesler, 2001:pl. 1, fig. 2a, b; pl. 2, fig. 2; tables 2, 3; Table 1 here). With widely open interparietal and parietal-supraoccipital sutures, it is less osteologically mature than UA-15.231, which shows only a trace of the interparietal suture (in almost all sirenian skullcaps, even

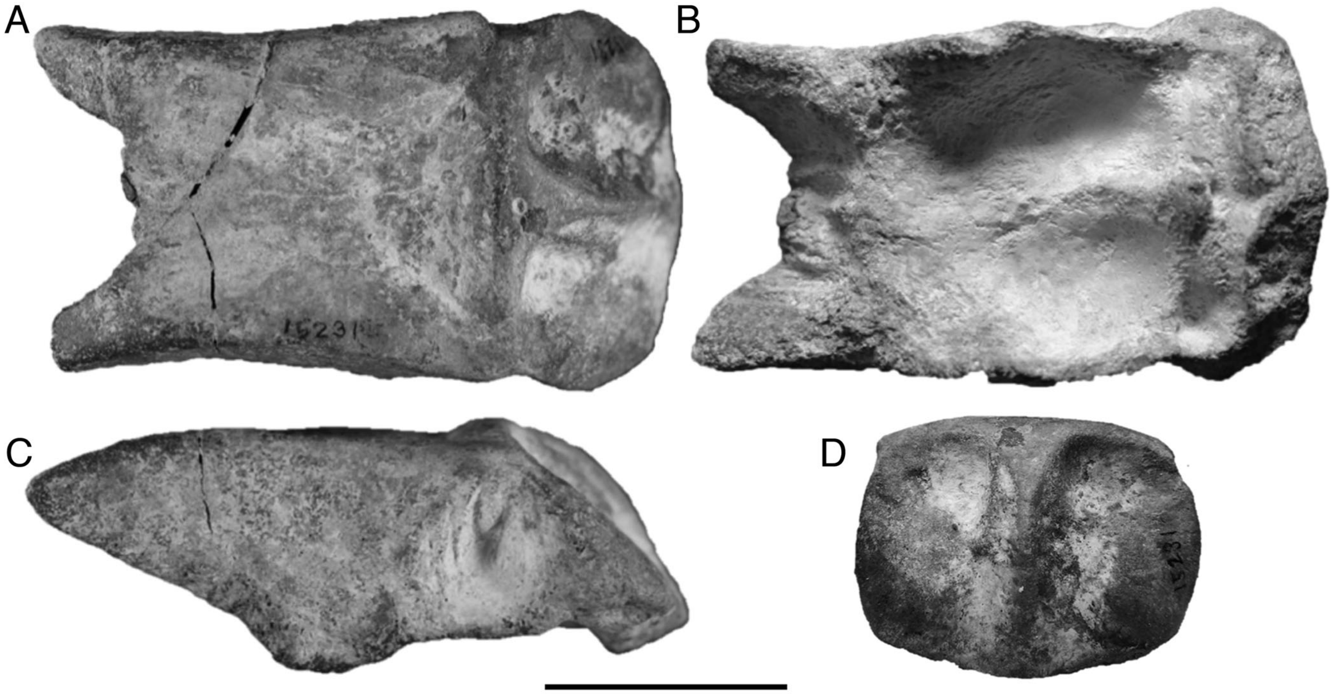

FIGURE 5. *Metaxytherium* cf. *krahuletzi*, UA-15.231, partial parietal-supraoccipital skullcap in **A**, dorsal, **B**, ventral, **C**, left lateral, and **D**, posterior views. Anterior to the left in **A** and **B**. Scale bar equals 5 cm.

neonates, this suture is obliterated). Proportions of still more mature specimens of *M. krahuletzi* vary somewhat, but UA-15.231 falls within this range of variation for most measurements, as exemplified in Table 1.

Midline contact of the exoccipitals [c. 66(0)] is a primitive sirenian state not seen in most *Metaxytherium*, but it does occur in about a third of studied specimens of *M. krahuletzi*, which is one of the earliest species of the genus (Domning and Pervesler, 2001:21). Also primitive, and unusual for *Metaxytherium*, is a supraoccipital narrower at its bottom than in its midsection [c. 64(0)]. However, this condition is also seen in some *M. krahuletzi*, including the juvenile KÜH 88 (Domning and Pervesler, 2001:pl. 1, fig. 2b).

Given that at least some of the Madagasacan sirenians may possibly be as young as early Tortonian (ca. 10 Ma), we must consider the possibility that UA-15.231 represents *M. medium*, the successor chronospecies to *M. krahuletzi* in the European-Mediterranean region. However, based on available data, these two chronospecies cannot be unambiguously distinguished, on either morphology (Domning and Pervesler, 2001, 2013) or body size (Bianucci et al., 2008). Certainly, there are no diagnostic characters of the parietal that would permit such a distinction; but because the primitive states of the supraoccipital and exoccipitals [c. 64(0) and 66(0)] have not been observed in *M. medium*, their presence in UA-15.231 argues for a relatively early date for the Madagascan *Metaxytherium*. Consequently, UA-15.231 should most appropriately be identified as *M.* cf. *krahuletzi*.

We think it plausible that this European species might be represented in Madagascar—especially because a similar if not identical species of *Metaxytherium* occurs in association with *Rytiodus heali* in Libya (Domning and Pervesler, 2001). Of even greater importance is the fact that this is the first credible record of a Neogene halitheriine dugongid in the Indian Ocean, where all the Neogene fossil sirenians hitherto studied adequately have been dugongines.

Family DUGONGIDAE Gray, 1821
DUGONGIDAE subfam., gen. et sp. indet.
(Figs. 6–8)

Referred Specimens—UA-14.177, a partial mandible (from locality 2010-10; Fig. 6); UA-10.213, an atlas (from locality 2005-25); UA-14.194 and UA-15.130, two axes (from localities 2005-25 and 2010-09, respectively; Fig. 7). Twenty-one other vertebrae, including UA-14.230A and UA-15.289, two neural arches of cervical vertebrae; UA-14.226, UA-14.230, UA-15.289.1 to UA-15.289.8, 10 thoracic vertebrae; UA-14.231-3, one lumbar vertebra; and UA-05404.1 to UA-05404.7 and UA-14.231, eight caudals. Twenty ribs (from localities 2005-25, 2013-12, 2013-16, and 2014-01): UA-05.404.18, UA-05.404.8, UA-05.404.5, UA-05.404.6, UA-05.404.10, UA-05.404.2, UA-05.404.25, UA-05.404.21, UA-05.404.11B, nine left ribs; UA-05.404.1A, UA-05.404.27, UA-05.404.7, UA-05.404.17, UA-05.404.14, UA-05.404.4, UA-05.404.20, UA-05.404.19, UA-05.404.13, UA-05.404.12, UA-05.404.15, 11 right ribs (Fig. 8).

DESCRIPTION

Mandible

The partial mandible (UA-14.177) is broken inferiorly but contains two teeth on each side, m2 and m3 (Fig. 6). The symphysis is missing; what appears in Figure 6A to be the symphysis and masticating surface consists almost entirely of sediment, which holds together the two horizontal rami (therefore, the profile of the damaged anterior part of the mandible in lateral view [Fig. 6C] does not reflect the original shape.) This sediment preserves a natural mold of the internal (median) parts of the anterior jaw. The underside of this mold displays a median ridge that is an impression of the symphyseal suture on the dorsal side of the

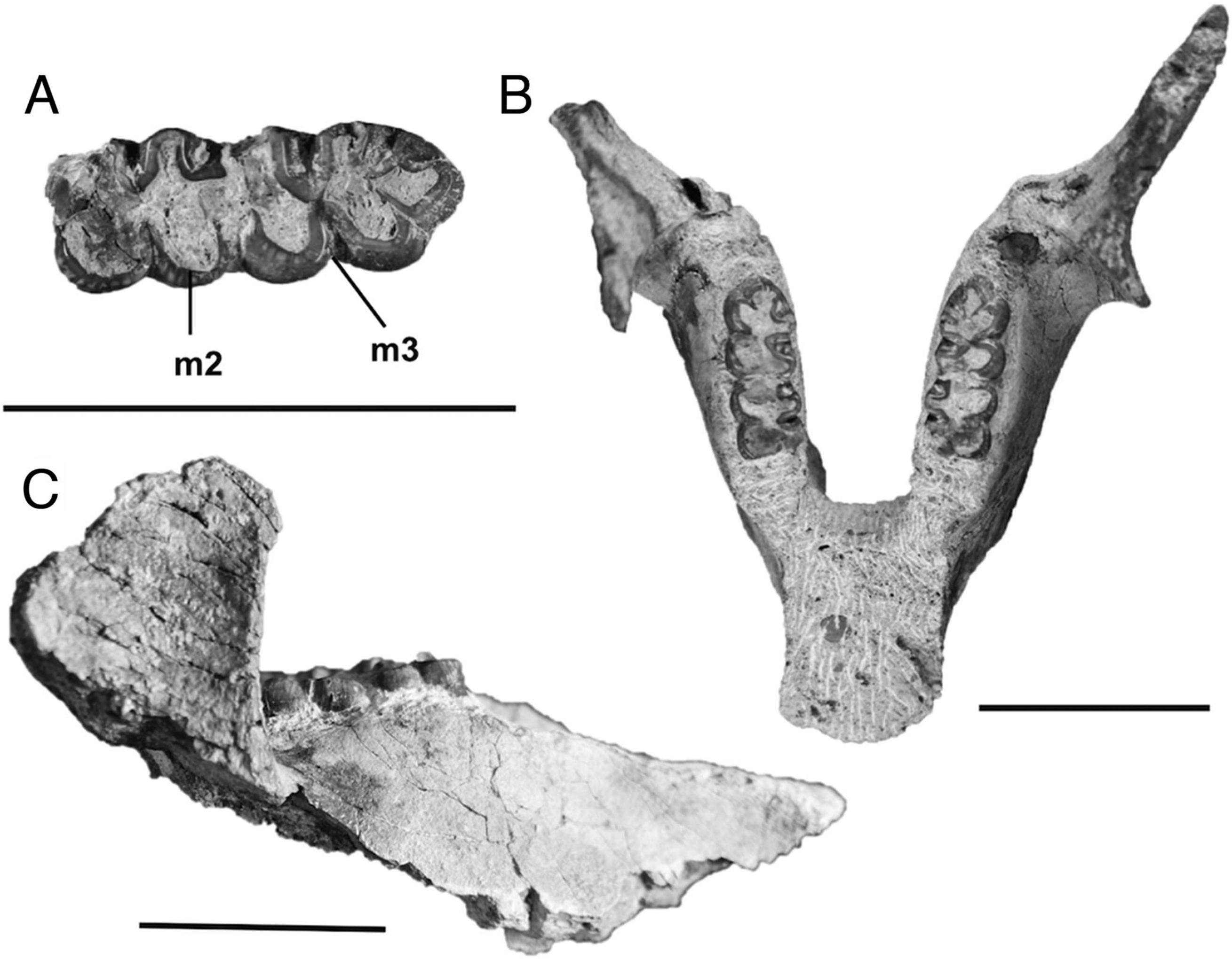

FIGURE 6. Dugongidae, sp. indet., UA-14.177, mandible. **A**, close-up of left molars in occlusal view. Mandible in **B**, occlusal and **C**, right lateral views. Scale bar equals 5 cm.

symphysis. Also visible, on the undersides of the broken horizontal rami, are the roots of the right m3 and sediment filling the anterior part of the left mandibular canal. The identity of m3 is confirmed by the dissimilar shapes of its roots (the posterior root larger and rounder in cross-section than the anterior one, which is flattened anteroposteriorly). Posteriorly, the lower parts of the ascending rami are partly preserved; the anterior border of the coronoid process extends slightly anterior to its base [c. 126(1)].

The molars are all heavily worn. Of the cusp pattern, m2 reveals only the coalesced protolophid and hypolophid. On m3, the dentine lakes of the lophids have coalesced on the right tooth but not quite on the left. Connected to the center of the hypolophid is a single large, mesiodistally elongated hypoconulid; it does not show any subdivision into cuspules, nor is it 'Y'-shaped as commonly seen in *Metaxytherium*.

Maximum width between labial edges of left and right alveoli = 64 mm. Left m2 is slightly broken on its anterior surface, mesial–distal length = 17 mm, anterior width = 13 mm, posterior width = 14 mm; left m3 mesial–distal length = 22 mm, anterior width = 15 mm, posterior width = 13 mm. Right m2 is slightly broken on the anterior aspect, but length is estimated as 18e mm, anterior width = 15 mm, posterior width = 14 mm. Right m3 mesial–distal length = 23 mm, anterior width = 15 mm, posterior width = 12 mm.

Postcranial Skeleton

Vertebrae—The atlas (UA-10.213; Fig. 7A, B) is well preserved, with a total breadth of 109 mm. The dorsolateral edges of the anterior cotyles are relatively thin and possess a transversely oriented canal for the first cervical spinal nerve. The transverse processes are relatively gracile and directed posteriorly and slightly dorsally. A vertebrarterial canal is absent. Processes for the transverse ligament are present, separated by 34 mm. External height = 68 mm; internal height = 39 mm; width across anterior cotyles = 79 mm; width across posterior cotyles = 70 mm; length in dorsal midline = 18 mm, in ventral midline = 19 mm.

An axis (UA-14.194; Fig. 7C) is largely complete but preserved in two pieces and is missing most of the odontoid process. Two well-formed rounded knobs are present on the anterior aspect of the neural arch. The profile of the arch is steeply inclined anteroinferiorly. Maximum height of axis = 98e mm; maximum width of axis (measured at anterior cotyles) = 66 mm; breadth of cotyle = 18 mm; height of cotyle = 24 mm; posterior breadth of centrum

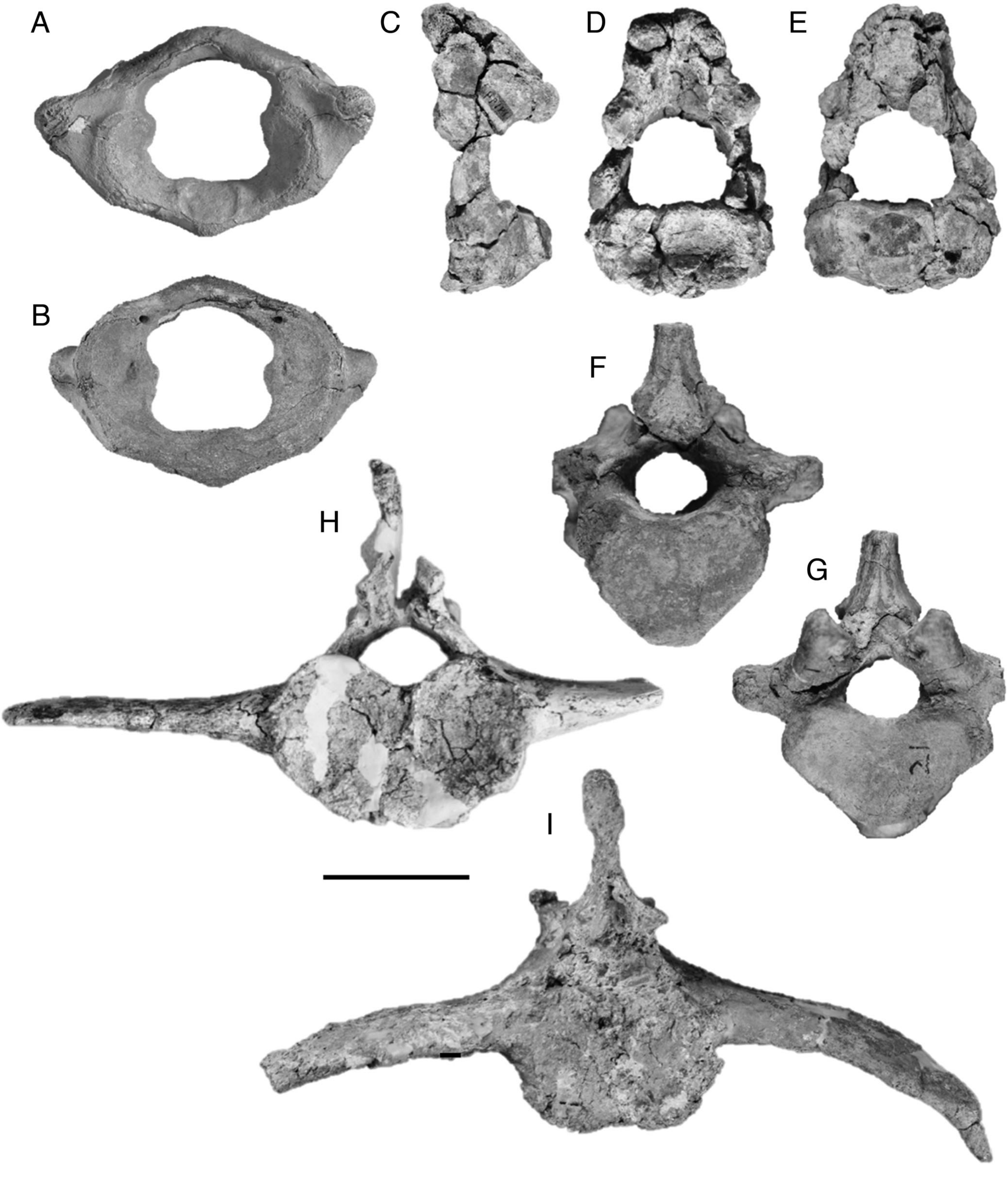

FIGURE 7. Dugongidae, sp. indet., representative vertebrae. UA-10.213, atlas, in **A**, posterior and **B**, anterior views. **C**–**E**, UA-14.194, axis, in **C**, lateral, **D**, posterior, and **E**, anterior views. UA-15.154, thoracic vertebra, in **F**, posterior and **G**, anterior views. **H**, UA-14.231-3, lumbar vertebra, in posterior view. **I**, UA-05.404.2, caudal vertebra, in posterior view. Scale bar equals 5 cm.

= 66 mm; posterior height of centrum = 33 mm; width of neural canal = 35 mm; height of neural canal = 32 mm; length of neural arch in midline = 42 mm; width of facet on odontoid process = 17 mm. Another axis (UA-15.130) is missing the neural arch but includes most of the odontoid process and anterior cotyles. The orientation and size of the anterior cotyles are different than in

UA-14.194, with a broader facet of the odontoid process (24 mm) and a more concave depression on the anteroventral articular surface.

Two other partial cervical vertebrae were recovered. UA-14.230-1 consists of just the isolated neural arch. The articular surfaces of the postzygapophyses are oriented posteriorly. Breadth of arch (outsides of postzygapophyses) = 77e mm. Mediolateral width of a postzygapophysis = 16 mm; anteroposterior width of a postzygapophysis = 16 mm. Specimen UA15-289 is larger but has the same general morphology.

Ten thoracic vertebrae (UA-14.226, UA-14.230B, UA-15.289.1 to UA-15.289.8) are preserved but vary greatly in size. Specimen UA-14.230B is from the anterior part of the column and is relatively small (width across transverse processes = 126e mm). Only one-half of the arch is present, with the spinous process completely missing. The centrum is dorsoventrally flattened (= oblong) and relatively small compared with the estimated size of the neural canal. The transverse process is relatively small and oriented slightly caudally. Anterior breadth of centrum = 59 mm; posterior breadth of centrum = 55 mm; centrum height in midline = 32 mm; centrum thickness in midline = 23 mm; width of neural canal = 48e mm. Specimen UA-14.226 is larger and the most posterior in the column. The arch is complete (except for the neural spine); the neural canal is relatively round (width = 40 mm; height = 32 mm). The transverse processes are robust, thick, and squared off, oriented only very slightly caudally. Breadth across transverse processes = 145 mm. The centrum is more rounded than seen in UA-14.230B (anterior breadth = 80 mm; posterior breadth = 74 mm; height in midline = 52 mm; thickness in midline = 45 mm). There is a prominent lip across the rim of the anterior and lateral aspect of the centrum. A large costal facet (length = 26 mm; width = 13 mm) is present at the junction between centrum and arch; this complete costal facet is consistent with this specimen being one of the most posterior thoracic vertebrae. Distinct depressions are present on the posterior aspect of the vertebral arch lateral to the midline (region of spinous process).

Specimen UA-14.231-3 is a relatively complete lumbar vertebra missing only the distal half of the right transverse process (Fig. 7E). The centrum is lima-bean-shaped and relatively massive (height in midline = 45 mm; thickness in midline = 52 mm; anterior breadth of centrum = 78 mm; posterior breadth of centrum = 84 mm). The neural canal is small (width = 28 mm; height = 22 mm). The transverse processes are oriented laterally with a slight caudal inclination. The tip of the process is slender and relatively pointed. The arch is broad, and the zygapophyses are quite angular with distinct projections, oriented halfway between the coronal and sagittal planes (distance from front of prezygapophysis to back of postzygapophysis = 67 mm). The spinous process is relatively wide and squared off (height = 55 mm). A prominent lip extends along the rims of both the anterior and posterior aspects of the centrum; it is especially prominent along the posterior face.

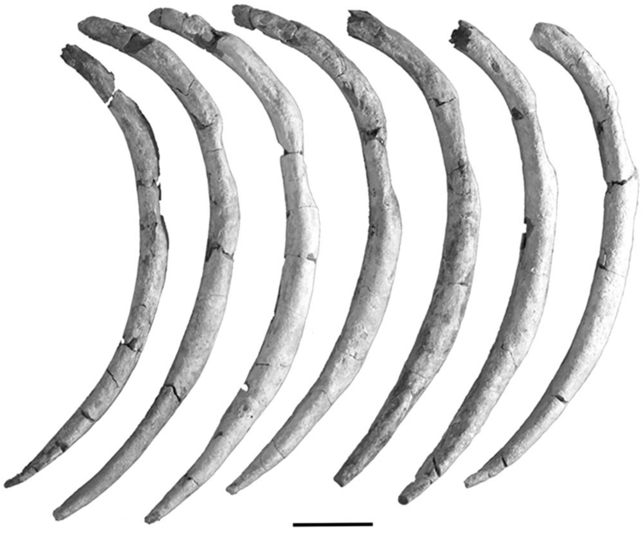

FIGURE 8. Dugongidae, sp. indet., representative ribs. Scale bar equals 5 cm.

On the more anterior caudals (e.g., UA-05.404.2 [Fig. 7F], UA-05.404.5), the transverse processes are long and tapered, located relatively inferiorly on the centra and anteroventrally inclined. The centra are dorsoventrally compressed, with heights ranging from 44 to 52 mm. Anterior and posterior breadths of the centra range from 59 to 68 mm and 61 to 67 mm, respectively. The thicknesses of the centra along the midline range from 50 to 57 mm. The neural canals are relatively small and triangular, with heights and widths ranging from 15 to 21 mm and 22 to 29 mm, respectively. The zygapophyses are oriented along the coronal plane. The maximum lengths from the front of the prezygapophysis to the rear of the postzygapophysis range from 44 to 72 mm.

On the more posterior caudals (UA-05.404.1, UA-05.404.3, 05.404.4, UA-14.231), the transverse processes are located much higher on the neural arch and are narrower, shorter, and more squared off. The centra are rounder and smaller, with the heights of the centra ranging from 41 to 51 mm. Anterior and posterior breadths of the centra range from 52 to 68 mm and 54 to 71 mm, respectively. The thicknesses of the centra along the midline range from 47 to 51 mm. The maximum lengths from the front of the prezygapophysis to the rear of the postzygapophysis range from 50 to 71 mm. The spinous processes are shorter, broader, and more squared off, and the transverse processes are much shorter than seen on the anterior caudals.

Ribs–Twenty nearly complete ribs were recovered (Fig. 8), as well as many other fragmentary ones. All ribs exhibit the characteristic sirenian pachyosteosclerotic morphology, but they are subelliptical in cross-section, rather than cylindrical as seen in the Malagasy Eocene species *Eotheroides lambondrano* (Samonds et al., 2009). Most ribs were broken into several segments, with the gaps between them filled with clay. Anteroposterior thickness is relatively constant along the shaft's length except for the proximal extremity. In contrast, the mediolateral thickness varies: at about one-third of its length (from the proximal extremity), the shaft is mediolaterally compressed over a distance of ca. 3–4 cm, then thickens again to reach its maximum at about half its length, then thins again at the distal extremity. This lateral concavity marks the attachment area of the iliocostalis thoracis muscle. Average length along the external arc ranges from 33 to 44 cm (n = 18) on the most complete specimens. Maximum anteroposterior shaft thickness (just distal to the mediolateral thinning) ranges from 31 to 40 mm, and maximum mediolateral shaft thickness ranges from 16 to 23 mm. Even at its thickest point, the shaft is not cylindrical; rather, the anteroposterior thickness is almost twice the mediolateral thickness. Minimum mediolateral thicknesses range from 13 to 17 mm.

DISCUSSION

The occurrence of *Rytiodus* in Madagascar demonstrates a much larger geographic (and possibly temporal) range for this genus than previously appreciated (Domning and Sorbi, 2011): Nosy Makamby is ca. 6,000 km southeast of the only other known locality of *R. heali* (Jabal Zaltan, Libya) and ca. 8,500 km southeast of Lot-et-Garonne (France), the locality of *R. capgrandi* Lartet, 1866, the only other species recognized within this genus. In addition, because the Libyan *Rytiodus* *heali* is incompletely known, future field work in Madagascar may yield elements of this taxon not currently described.

The oldest occurrence of *Metaxytherium* is from the Oligocene, but it is also reliably reported from the Miocene of North America, South America, Europe, and northern Africa (de Muizon and Domning, 1985; Domning and Thomas, 1987; Aranda-Manteca et al., 1994; Domning and Pervesler, 2001, 2013; Sorbi et al., 2012; Vélez-Juarbe and Domning, 2014); a specimen reported from Kutch, India (Savage and Tewari, 1977), is almost certainly a dugongine. Given this geographic range, the presence of *Metaxytherium* in Madagascar is especially significant because it represents the first Neogene occurrence from the Indian Ocean, not only of this genus but also of the subfamily Halitheriinae itself, showing that both were more widely distributed during the Miocene than previously appreciated. Because the final closure of the ancient Tethys Sea (and subsequent end of exchange between the Indian Ocean and the Mediterranean) is thought to have occurred during the Miocene (Hamon et al., 2013), this large range expansion can illuminate past dispersal routes for both *Metaxytherium* and *Rytiodus*. Of particular interest is that the co-occurrence of *M.* cf. *krahuletzi* and *R. heali* in Madagascar duplicates the association of a similar and possibly identical species of *Metaxytherium* with *R. heali* at the latter's type locality in Libya. Thus, the early Miocene sirenian fauna of the Mediterranean seems to have extended around the east coast of Africa as well. This does away with the apparent mystery of why no post-Eocene halitheriines were found in the Indian Ocean, but it substitutes the opposite mystery of why the diverse dugongine fauna of India apparently did not reach the Mediterranean (or even Madagascar). However, even the latter apparent anomaly might be explained by the possibly later date of the Madagascan fauna relative to that of Kutch.

Norosiren is a new genus of dugongine with what we interpret to be closest affinities to the Mexican genus *Xenosiren*. Zoogeographically, this is a truly startling result; but given our far-from-adequate and still rapidly growing knowledge of dugongine diversity (including the fact that each of these two genera is known from only a single fragmentary specimen), surprises like this are to be expected.

The presence of three (possibly four) sympatric Miocene sea cow species from Nosy Makamby indicates a substantial level of diversity. However, shallow marine environments of the same geological interval elsewhere in the world also have been demonstrated to harbor multispecies sirenian paleofaunas (e.g., Domning and Sorbi, 2011; Vélez-Juarbe et al., 2012). In particular for the taxa recovered from Nosy Makamby, *Rytiodus* appears to have lived sympatrically with *Metaxytherium* over a wide area (from Libya to Madagascar; Domning and Sorbi, 2011).

CONCLUSIONS

This study provides the first comprehensive description of Miocene sirenians from the island of Nosy Makamby, Mahajanga Basin, northwestern Madagascar. These include the dugongine dugongid *Rytiodus heali* (previously attributed incorrectly to the genus *Halitherium* and hitherto only known from Libya), a new genus and species of dugongine (*Norosiren zazavavindrano*) that we interpret as a primitive relative of the Mexican taxon *Xenosiren*, and *Metaxytherium* cf. *krahuletzi*, the first Neogene halitheriine dugongid credibly recorded from the Indian Ocean basin. This pattern of shallow marine environments harboring multispecies sirenian paleofaunas is seen elsewhere in the world; and because this specific time period is poorly known for Madagascar and represents a critical interval for interpreting the island's past, these specimens are potentially highly significant for reconstructing sirenian and Madagascan evolutionary and biogeographic history.

Finally, the presence of sirenians, crocodiles, and turtles, which are generally associated with nearshore marine environments, suggests that this site also has the potential to yield fossils of terrestrial and freshwater vertebrates, which are well documented to occur in these types of mixed facies (Gingerich, 1977; Cunningham et al., 1993; Rogers and Kidwell, 2000; Marivaux et al., 2014). Therefore, future work at this site has great potential to yield fossils that can help reconstruct aspects of how, when, and from where the basal stocks of Madagascar's extant terrestrial clades arrived on the island.

ACKNOWLEDGMENTS

We thank the government of Madagascar for permission to conduct this research and the Département de Paléontologie et Anthropologie Biologique, Université d'Antananarivo, specifically A. Rasoamiaramanana, H. Andriamialison, and T. Rakotondrazafy, for the opportunity to collaborate. Field work was performed under a collaborative accord between Northern Illinois University and the Université d'Antananarivo, Madagascar.

We thank J. Groenke, J. Mathews, and K. Ababio, all of whom prepared fossils described in this article; and G. Hegyi and J. Seuntjens for help with CT scanning. We especially thank J.-L. Raharison and Sadabe Madagascar for logistical support, as well as M. Irwin, J. Ali, C. Botou (Ramiaramila), D. Branch, M. Gottfried, S. Ostrowski, J. Mathews, T. N. Ramihangihajason, L. Raharivony, Z. Rakotomalala, N. Rasolofomanana, and I. Zalmout for their hard work in the field. We also thank O. Devergne for help translating the French abstract. Domning thanks C. Sagne and G. Billet for access to the Madagascar specimen at the MNHN, Paris; L. Charles and P. Rocher of the MHNBx, F. Meunier and F. Bordessoule of the Association Paléontologique du Bassin Aquitaine and the Resérve Naturelle Géologique de Saucats–La Brède, B. Cahuzac of the Université de Bordeaux, and J.-J. Cladères of Saint-Martin-d'Oney, France, for access to the specimens of *Rytiodus capgrandi* and other sirenians in various collections and for many courtesies and assistance in the study of these specimens. The drawings of *Norosiren zazavavindrano* were done by R. Ernat. We thank reviewers B. Beatty and I. Zalmout and editor O. Lambert for their constructive comments on the manuscript. Finally, we thank the local Malagasy villagers who received our teams with immeasurable hospitality. This research was supported by grants from the National Geographic Society Committee for Research and Exploration to K.E.S. D.P.D.'s visit to France was funded by National Geographic Society Waitt Grant no. W466-16.

ORCID

Karen E. Samonds http://orcid.org/0000-0003-3597-9215

LITERATURE CITED

Abel, O. 1913. Die eocänen Sirenen der Mittelmeerregion. Erster Teil: Der Schädel von *Eotherium aegyptiacum*. Palaeontographica 59:289–360.

Andrianavalona, T. H., T. N. Ramihangihajason, A. Rasoamiaramanana, D. J. Ward, J. R. Ali, and K. E. Samonds. 2015. Miocene shark and batoid fauna from Nosy Makamby (Mahajanga Basin, Northwestern Madagascar). PLoS ONE 10:e0129444. doi: 10.1371/journal.pone.0129444.

Aranda-Manteca, F. J., D. P. Domning, and L. G. Barnes. 1994. A new middle Miocene sirenian of the genus *Metaxytherium* from Baja California and California: relationships and paleobiogeographic implications. Proceedings of the San Diego Society of Natural History 29:191–204.

Bajpai, S., and D. P. Domning. 1997. A new dugongine sirenian from the Early Miocene of India. Journal of Vertebrate Paleontology 17:219–228.

Bajpai, S., D. P. Domning, D. P. Das, J. Vélez-Juarbe, and V. P. Mishra. 2010. A new fossil sirenian (Mammalia, Dugonginae) from the Miocene of India. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 258:39–50.

Bajpai, S., J. G. M. Thewissen, V. V. Kapur, B. N. Tiwari, and A. Sahni. 2006. Eocene and Oligocene sirenians (Mammalia) from Kachchh, India. Journal of Vertebrate Paleontology 26:400–410.

Besairie, H. 1972. Géologie de Madagascar, Volume I. Les terrains sédimentaires. Tananarive Imprimerie Nationale, Antananarivo, Madagascar, 463 pp., 89 pls.

Bianucci, G., G. Carone, D. P. Domning, W. Landini, L. Rook, and S. Sorbi. 2008. Peri-Messinian dwarfing in Mediterranean *Metaxytherium* (Mammalia: Sirenia): evidence of habitat degradation related to the Messinian Salinity Crisis. Garyounis Scientific Bulletin, Special Issue 5:145–157.

Carone, G., and D. P. Domning. 2007. *Metaxytherium serresii* (Mammalia: Sirenia): new pre-Pliocene record, and implications for Mediterranean paleoecology before and after the Messinian Salinity Crisis. Bollettino della Società Paleontologica Italiana 46:55–92.

Carus, J. 1868. Handbuch der Zoologie. 1ster Band. Wirbelthiere, Mollusken und Molluscoiden. Wilhelm Engelmann, Leipzig, ix + 894 pp.; Sirs., 163–168.

Charbonnier, S., A. Garassino, and G. Pasini. 2012. Review of the crabs (Crustacea, Decapoda, Brachyura) from the Miocene of the Mahakamby Island (Mahajanga, NW Madagascar) collected during the Waterlot's Mission (1922). Geodiversitas 34:873–881.

Clementz, M. T., S. Sorbi, and D. P. Domning. 2009. Evidence of Cenozoic environmental and ecological change from stable isotope analysis of sirenian remains from the Tethys-Mediterranean region. Geology 37:307–310.

Collignon, M., and J. Cottreau. 1927. Paléontologie de Madagascar: fossiles du Miocene marin. Annales de Paleontologie 16:135–170.

Cunningham, C., H. Feldman, E. Franseen, R. Gastalso, G. Mapes, C. Maples, and H. Schultze. 1993. The Upper Carboniferous Hamilton fossil-lagerstätte in Kansas—a valley-fill, tidally influenced deposit. Lethaia 26:225–236.

Christol, J. de. 1840. Recherches sur divers ossements fossiles attribués par Cuvier à deux phoques, au lamantin, et à deux espèces d'hippopotames, et rapportés au *Metaxytherium*, nouveau genre de cétacé de la famille des dugongs. *L'Institut*, Année 8, Sect. 1, No. 352:322–323.

Delfortrie, E. 1872. Étude sur les restes fossiles de siréniens du genre *Halitherium* dans le bassin de la Garonne. Actes de la Société Linnéenne de Bordeaux 28:281–316.

Delfortrie, E. 1880. Découverte d'un squelette entier de *Rytiodus* dans le falun Aquitanien. Actes de la Société Linnéenne de Bordeaux 34:131–144.

Depéret, C. 1895. Über die fauna von miocänen Wirbelthieren aus der ersten Mediterranstufe von Eggenburg. Sitzungsberichte der Akademie der Wissenschaften, Wien, mathematisch-naturwissenschaftliche Classe 104:395–416.

Desmarest, A. G. 1822. Mammalogie ou description des espèces de Mammifères. Seconde Partie. Mme. Veuve Agasse, Paris, pp. 277–556.

Domning, D. P. 1978. Sirenia; pp. 573–581 in V. J. Maglio and H. B. S. Cooke (eds.), Evolution of African Mammals. Harvard University Press, Cambridge, Massachusetts.

Domning, D. P. 1989a. Fossil Sirenia of the West Atlantic and Caribbean Region. III. *Xenosiren yucateca*, gen. et sp. nov. Journal of Vertebrate Paleontology 9:429–437.

Domning, D. P. 1989b. Fossil Sirenia of the West Atlantic and Caribbean Region. II. *Dioplotherium manigaulti* Cope, 1883. Journal of Vertebrate Paleontology 9:415–428.

Domning, D. P. 1990. Fossil Sirenia of the West Atlantic and Caribbean Region. IV. *Corystosiren varguezi*, gen. et sp. nov. Journal of Vertebrate Paleontology 10:361–371.

Domning, D. P. 1994. A phylogenetic analysis of the Sirenia. Proceedings of the San Diego Society of Natural History 29:177–189.

Domning, D. P. 1997. Fossil Sirenia of the West Atlantic and Caribbean region. VI. *Crenatosiren olseni* (Reinhart, 1976). Journal of Vertebrate Paleontology 17:397–412.

Domning, D. P., and O. A. Aguilera. 2008. Fossil Sirenia of the West Atlantic and Caribbean Region. VIII. *Nanosiren garciae*, gen. et sp. nov. and *Nanosiren sanchezi*, sp. nov. Journal of Vertebrate Paleontology 28:479–500.

Domning, D. P., and B. L. Beatty. 2007. Use of tusks in feeding by dugongid sirenians: observations and tests of hypotheses. Anatomical Record 290:523–538.

Domning, D. P., and P. Pervesler. 2001. The osteology and relationships of *Metaxytherium krahuletzi* Depéret, 1895 (Mammalia: Sirenia). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 553:1–89.

Domning, D. P., and P. Pervesler. 2013. The sirenian *Metaxytherium* (Mammalia: Dugongidae) in the Badenian (Middle Miocene) of Central Europe. Austrian Journal of Earth Sciences 105:125–160.

Domning, D. P., and S. Sorbi. 2011. *Rytiodus heali*, sp. nov., a new sirenian (Mammalia, Dugonginae) from the Miocene of Libya. Journal of Vertebrate Paleontology 31:1338–1355.

Domning, D. P., and H. Thomas. 1987. *Metaxytherium serresii* (Mammalia: Sirenia) from the early Pliocene of Libya and France: a reevaluation of its morphology, phyletic position, and biostratigraphic and paleoecological significance; pp. 205–232 in N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelin, and D. D. Boaz (eds.), Neogene Paleontology and Geology of Sahabi. Alan R. Liss Publishers, New York.

Flynn, J. J., S. J. Nesbitt, J. M. Parrish, L. Ranivoharimanana, and A. R. Wyss. 2010. A new species of *Azendohsaurus* (Diapsida: Archosauromorpha) from the Triassic Isalo Group of southwestern Madagascar: cranium and mandible. Palaeontology 53:669–688.

Gaziry, A. W. 1987. New mammals from the Jabal Zaltan site, Libya. Senckenbergiana Lethaea 68:69–89.

Gingerich, P. 1977. A small collection of fossil vertebrates from the Middle Eocene Kuldana and Kohot formations of Punjab (Pakistan). Contributions from the Museum of Paleontology, The University of Michigan 24:190–203.

Gottfried, M. D., K. E. Samonds, S. A. Ostrowski, T. H. Andrianavalona, and T. N. Ramihangihajason. 2017. New evidence indicates the presence of barracuda (Sphyraenidae) and supports a tropical marine environment in the Miocene of Madagascar. PLoS ONE 12: e0176553. doi: 10.1371/journal.pone.0176553.

Gray, J. E. 1821. On the natural arrangement of vertebrose animals. The London Medical Repository Monthly Journal and Review 15:296–310.

Hamon, N., P. Sepulchre, V. Lefebvre, and G. Ramstein. 2013. The role of eastern Tethys seaway closure in the Middle Miocene Climatic Transition (ca. 14 Ma). Climate of the Past 9:2687–2702.

Hooijer, D. 1952. Fact and fiction in hippopotamology (sampling the history of scientific error). Osiris 10:109–116.

Illiger, J. K. W. 1811. Prodromus systematis mammalium et avium: additis terminis zoographicis utriusque classis, eorumque versione Germanica. Sumptibus C. Salfeld, Berlin, 302 pp.

Kner, R. 1858. Beiträge zur Familie der Characinen. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Wien 30:75–80.

Krause, D. W. 2010. Biogeography: washed up in Madagascar. Nature 463:613–614.

Krause, D. W., J. H. Hartman, and N. A. Wells. 1997. Late Cretaceous vertebrates from Madagascar: implications for biotic change in deep time; pp. 3–43 in S. M. Goodman and B. D. Patterson (eds.), Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington, D.C.

Lartet, E. 1866. Notes sure deux nouveaux sireniens fossiles des terrains tertiaires du bassin de la Garonne. Bulletin de la Société Géologique de France 2:673–686.

Lavocat, R., P. Marie, and J. Sigal. 1960. La faune de foraminifères du Miocène de l'ile Mahakamby (Madagascar). Compte Rendu sommaire des Séances de la Société Géologique de France 11: 211–213.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordinus, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Impensis Direct. Laurentii Salvii, Stockholm, 824 pp.

Marivaux, L., E. M. Essid, W. Marzougui, H. Khayati Ammar, S. Adnet, B. Marandat, G. Merzeraud, A. Ramdarshan, R. Tabuce, M. Vianey-Liaud, and J. Yans. 2014. A morphological intermediate between eosimiiform and simiiform primates from the late middle Eocene of Tunisia: macroevolutionary and paleobiogeographic implications of early anthropoids. American Journal of Physical Anthropology 154:387–401.

Muizon, C. de, and D. P. Domning. 1985. The first records of fossil sirenians in the southeastern Pacific Ocean. Bulletin du Muséum National d'Histoire Naturelle, Section C, 4ème Série 7:189–213.

Pilleri, G. 1987. Sirenia of the Swiss Molasse with a Descriptive Catalogue of the Fossil Sirenia Preserved in Swiss Collections. Brain Anatomy Institute, Ostermundigen, Switzerland, 114 pp.

Ramihangihajason, T., T. Andrianavalona, R. Razafimbelo, L. J. Rahantarisoa, J. Ali, and K. E. Samonds. 2014. Miocene benthic foraminifera from Nosy Makamby and Amparafaka, Mahajanga Basin, northwestern Madagascar. Journal of African Earth Sciences 100:409–417.

Rocher, P., L. Charles, and N. Mémoire. 2015. Redécouverte du crâne de *Rytiodus capgrandi* Lartet, 1866 (Mammalia : Dugongidae) du Plantat (Saint-Morillon, Gironde). Bulletin de la Société Linnéenne de Bordeaux 43:13–18.

Rogers, R., and S. Kidwell. 2000. Associations of vertebrate skeletal concentrations and discontinuity surfaces in terrestrial and shallow marine records: a test in the Cretaceous of Montana. The Journal of Geology 108:131–154.

Samonds, K. E. 2007. Late Pleistocene bat fossils from Anjohibe Cave, northwestern Madagascar. Acta Chiropterologica 9:39–65.

Samonds, K. E., and R. E. Fordyce. 2019. The first Pre-Pleistocene cetacean from Madagascar, western Indian Ocean. Journal of African Earth Sciences 151:184–188.

Samonds, K. E., I. S. Zalmout, M. T. Irwin, and L. L. Raharivony. 2007. Sirenian postcrania from Nosy Mahakamby, northwestern Madagascar. Journal of Vertebrate Paleontology 27(3, Supplement):139A.

Samonds, K., I. Zalmout, M. Irwin, D. Krause, R. Rogers, and L. Raharivony. 2009. *Eotheroides lambondrano*, new middle Eocene seacow (Mammalia, Sirenia) from the Mahajanga Basin, northwestern Madagascar. Journal of Vertebrate Paleontology 29:1233–1243.

Savage, R. J. G. 1975. *Prorastomus* and new Early Tertiary sirenians from North Africa. American Zoologist 15:824.

Savage, R. J. G., and B. S. Tewari. 1977. A new sirenian from Kutch, India. Journal of the Paleontological Society of India 20:216–218.

Simpson, G. G. 1932. Fossil Sirenia of Florida and the evolution of the Sirenia. American Museum of Natural History Bulletin 59:419–503.

Sorbi, S., D. P. Domning, S. C. Vaiani, and G. Bianucci. 2012. *Metaxytherium subapenninum* (Bruno, 1839) (Mammalia, Dugongidae), the latest sirenian of the Mediterranean Basin. Journal of Vertebrate Paleontology 32:686–707.

Springer, M. S., A. V. Signore, J. L. A. Paijmans, J. Vélez-Juarbe, D. P. Domning, C. E. Bauer, K. He, L. Crerar, P. F. Campos, W. J. Murphy, R. W. Meredith, J. Gatesy, E. Willerslev, R. D. E. MacPhee, M. Hofreiter, and K. L. Campbell. 2015. Interordinal gene capture, the phylogenetic position of Steller's sea cow based on molecular and morphological data, and the macroevolutionary history of Sirenia. Molecular Phylogenetics and Evolution 91:178–193.

Storey, M., J. J. Mahoney, A. D. Saunders, R. A. Duncan, S. P. Kelley, and M. F. Coffin. 1995. Timing of hot spot-related volcanism and the breakup of Madagascar and India. Science 267:852–855.

Thewissen, J. G. M., and S. Bajpai. 2009. A new Miocene sirenian from Kutch, India. Acta Palaeontologica Polonica 54:7–13.

Toledo, P. M., and D. P. Domning. 1991. Fossil Sirenia (Mammalia: Dugongidae) from the Pirabas Formation (Early Miocene), northern Brazil. Boletim do Museu Paraense Emílio Goeldi, Série Ciências da Terra 1:119–146.

Vélez-Juarbe, J., and D. P. Domning. 2014. Fossil Sirenia of the West Atlantic and Caribbean region. IX. *Metaxytherium albifontanum*, sp. nov. Journal of Vertebrate Paleontology 34:444–464.

Vélez-Juarbe, J., D. P. Domning, and N. D. Pyenson. 2012. Iterative evolution of sympatric seacow (Dugongidae, Sirenia) assemblages during the past ~26 million years. PLoS ONE 7:e31294. doi: 10.1371/journal.pone.0031294.

Submitted August 6, 2018; revisions received December 18, 2018; accepted December 28, 2018.
Handling editor: Olivier Lambert.