

EOTHEROIDES LAMBONDRANO, NEW MIDDLE EOCENE SEACOW (MAMMALIA, SIRENIA) FROM THE MAHAJANGA BASIN, NORTHWESTERN MADAGASCAR

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ABSTRACT—The first diagnostic sirenian material from Madagascar and, more broadly, the first diagnostic pre-Pleistocene Cenozoic mammal material recovered from the island is reported. *Eotheroides lambondrano* is a new species of sirenian collected from middle Eocene nearshore marine deposits in the Mahajanga Basin of northwestern Madagascar. The recovered material consists of a nearly complete adult skull (including the first complete rostrum known for *Eotheroides*) and several portions of pachyosteosclerotic ribs. Diagnostic features of *E. lambondrano* include: primitive upper dental formula of 3.1.5.3, relatively large occlusal area of M2 and M3, long and narrow nasals, weak rostral deflection compared to other Eocene Dugongidae, well developed supraorbital processes, short infraorbital canal, anteroposteriorly short zygomatic-orbital bridge of maxilla, and a palate that is narrow anteriorly, creating a strongly bell-shaped maxillary dental arcade. The cranium of *E. lambondrano* is similar to that of *E. aegyptiacum* from the middle Eocene of Egypt in aspects of both morphology and size but the upper molars of *E. lambondrano* are considerably longer and wider and it has longer, narrower nasals. The age and relatively primitive morphology of *E. lambondrano* suggests that it may represent the ancestral form from which more northerly species were derived.

INTRODUCTION

Madagascar's extant vertebrate fauna is one of the most unique and endemic on the planet, and exploring its biogeographic origins has been the focus of considerable recent research (e.g., see articles and references in compendium by Goodman and Benstead, 2003). The virtual absence of a Cenozoic terrestrial fossil record has left the origins of Madagascar's extant vertebrate clades shrouded in mystery; interpretations have been drawn largely from the negative evidence provided by a growing Late Cretaceous fossil record (e.g., Krause et al., 2006) and from molecular systematic analyses and the resulting estimated divergence dates (e.g., Raxworthy, 2003; Poux et al., 2005; Yoder and Nowak, 2006). These indirect lines of evidence indicate that the basal stocks of nearly all of the major extant groups of vertebrate animals colonized the island after the Cretaceous.

Only two collections of mammalian fossils have been described from within the 65-million-year post-Cretaceous gap in Madagascar's fossil record. The first is a poorly-dated collection of rodents, insectivores, and bats, purported to be of Plio-Pleistocene age (Sabatier and Legendre, 1985), and the second is a fragmentary and largely undiagnostic specimen of a Miocene dugong (Collignon and Cottreau, 1927). This specimen consists of the top and posterior portions of a braincase; its attribution to the genus *Halitherium* is based on superficial similarities and is therefore only weakly supported.

Here we report the first diagnostic remains of a sirenian from the Eocene of Madagascar. This material consists of a nearly complete cranium and fragmentary ribs and is assigned to the small to medium-sized dugongid genus *Eotheroides*. *Eotheroides* was first described from the famous nummulitic limestone hills near Cairo; it represents the earliest and most primitive known dugong adapted to life in marine habitats. The Malagasy material represents a new species of *Eotheroides*, *E. lambondrano*, which we place in taxonomic context by comparing it with other Eocene sirenian material (consisting primarily of fragmentary cranial and postcranial remains, and isolated teeth) from the Indian and East African Tethyan regions (Sahni and Mishra, 1975; Savage and Tewari, 1977; Sahni and Kumar, 1980; Sahni et al., 1980; Gingerich et al., 1995; Zalmout et al., 2003; Bajpai et al., 2006).

Institutional Abbreviations—**UA**, Université d'Antananarivo, Antananarivo, Madagascar; **IITR**, Indian Institute of Technology, Roorkee, India; **BSPM**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany.

GEOLOGY AND AGE

Along the northwest coast of Madagascar, where the Mahajanga Basin borders the Mozambique Channel, the strata consist primarily of varicolored clastic sediments intercalated with marine carbonates (Besairie, 1969). In the vicinity of the port city of Mahajanga, these strata are exposed discontinuously along local small-scale faults (Besairie, 1972). The variety of

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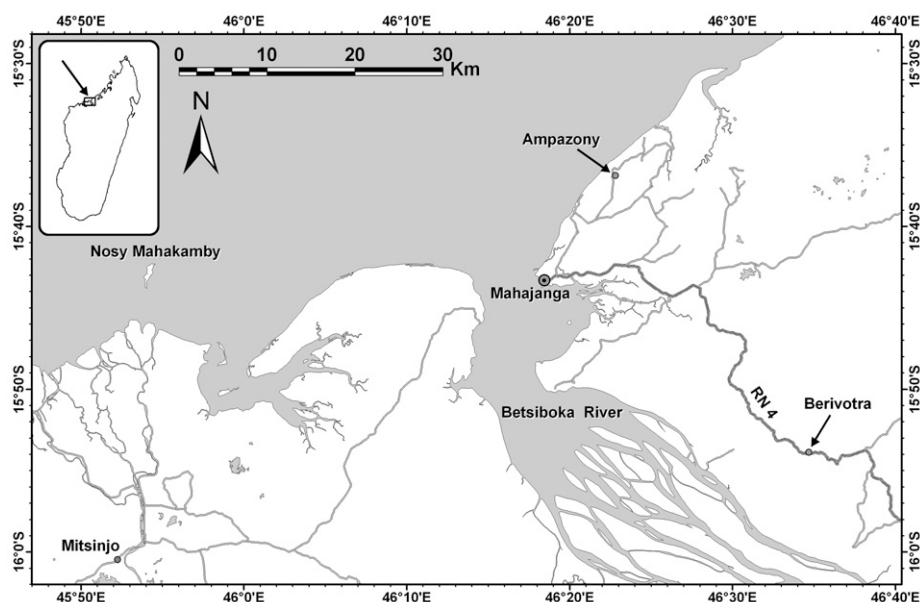


FIGURE 1. Map showing location of Ampazony, northwestern Madagascar. Also indicated are the port city of Mahajanga, the Cretaceous fossil-bearing locality of Berivotra (Krause et al., 2006), and the previously known Miocene sirenian locality of Nosy Mahakamby (Collignon and Cottreau, 1927).

facies represented in the region indicate that conditions shifted from coastal/paralic to open marine, presumably due to small-scale transgressions and regressions.

The sirenian fossils described in this report were recovered from a local exposure near the small village of Ampazony, approximately 15 km northeast of Mahajanga (Fig. 1). The rocks at this locality consist of interbedded sandy claystones, mudstones, siltstones, and marly limestones that accumulated in low-lying coastal and shallow marine environments (Fig. 2A). Nearby underlying exposures display large-scale mudcracks that are consistent with subaerial exposure, presumably on peritidal mudflats (Fig. 2B). The sirenian specimens were recovered from two distinct marly limestone beds separated by approximately 3 m of section. These beds also yielded numerous invertebrate fossils, including alveolinid foraminifera, echinoids, gastropods, and

bivalves, as well as fragmentary remains of sharks, rays, bony fishes, and reptiles (fragments of turtle carapace and plastron and crocodyliform teeth) (Samonds et al., 2001, 2005; Samonds and Zalmout, 2002). The numerous fragments of the holotype skull of *Eotheroides lambondrano* were recovered from the uppermost unit, along a small exposure spanning approximately 10 m². Rib fragments were recovered from the lower marly unit, where they were found scattered throughout the bed. They do not appear to be associated with the skull material. The overall sedimentologic context of the two fossil-producing beds and the taphonomic quality of the fossil material suggest that they accumulated under high-energy conditions in shallow marine waters along ancient coastlines. Whether they represent accumulations of fossils that formed due to storm events or marine transgressions (ravinement beds) is difficult to resolve given the limited exposures.

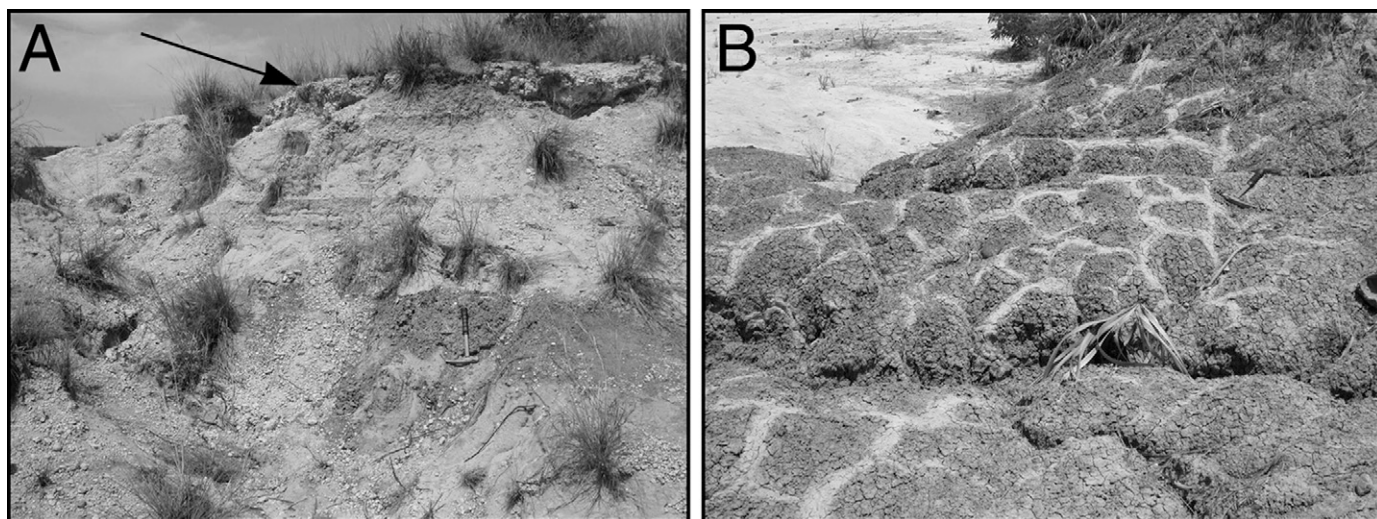


FIGURE 2. Ampazony, northwestern Madagascar. **A**, Local exposure of paralic facies that yielded the specimens of the sirenian described in this report. Cranial elements were recovered from the shell and bone-bearing limestone bed that caps the exposure (marked by arrow); **B**, Large-scale mudcracks indicative of subaerial exposure crop out below the bone-producing horizons, and are consistent with a coastal setting.

With regard to age, rocks in the study area were previously mapped as Pliocene (Besairie, 1969). However, the selachian assemblage recovered from the same bed as the sirenian described here includes teeth of *Galeocерdo eaglesomi* (D. Ward, pers. comm., Dec. 2008), a shark species currently restricted to the middle Eocene (White, 1955; Cappetta, 2004, 2006). We therefore reinterpret the age of the exposures near Ampazony as middle Eocene; micropaleontological analyses are in progress to more precisely constrain the age of the deposits.

SYSTEMATIC PALEONTOLOGY

Order SIRENIA Illiger, 1811

Family DUGONGIDAE Gray, 1821

Subfamily HALITHERIINAE (Carus, 1868) Abel, 1913

GENUS *EOTHEROIDES* Palmer, 1899

EOTHEROIDES LAMBONDRANO sp. nov.

(Figs. 3–7, Tables 1, 2)

Holotype—Université d'Antananarivo (UA) 9046, adult skull including left and right premaxillae, left maxilla with M3 and distobuccal corner of M2; right maxilla with M2 and distal half of M3 (all other teeth represented by alveoli); left and right nasals, lacrimals, frontals, and parietals; supraoccipital; partial basioccipital; partial left and right pterygoids; right jugal and squamosal; virtually complete left periotic; partial right periotic; and left tympanic (Figs. 3–6).

Type Locality—The holotype and all referred elements were recovered as isolated specimens from a single locality, AMP-11, near the village of Ampazony in northwestern Madagascar, approximately 15 km northeast of the port city of Mahajanga (Fig. 1).

Referred Specimens—Eight rib fragments (UA 9562–9567, 9593–9594; Fig. 7).

Etymology—*lambondrano* (lam-boon-DRA-noo, Malagasy), a contraction of “lambo” (wild pig) and “rano” (water); the Malagasy common name for *Dugong dugon*.

Diagnosis—Differs from all known species of *Eotheroides* in possessing long and narrow nasals (180–210% longer than wide), well developed supraorbital process with distinct flared ledge superiorly and depressed dorsal surface, anteroposteriorly short zygomatic-orbital bridge of maxilla, short infraorbital canal, strongly bell-shaped maxillary dental arcade, primitive dental formula of 3.1.5.3, and relatively large occlusal area of M2 and M3. Shares with other species of genus banana-shaped, pachyosteosclerotic ribs, premaxillary-maxillary suture below the premaxillary symphysis, and temporal portion of periotic smaller than the mastoid portion. Resembles *E. aegyptiacum* in having nasals joined along midline and possessing three-rooted DP5 that is retained and not replaced, but differs in having narrow palate, longer and narrower nasals, and nasal processes of the premaxillae that extend posteriorly more than one-third of the anteroposterior length of the supraorbital process. Further differs from *E. babiae* in possessing shorter parietals and a larger supraoccipital.

DESCRIPTION

Cranial Morphology

The skull has an anterior-posterior length of 270 mm from the posterior end of the supraoccipital to the tip of the nasal rostrum (which is slightly broken), and a cranial breadth of 44 mm at the level of the frontoparietal suture (Table 1); this measurement approximates but may be slightly less than condylobasal length

TABLE 1. Measurements of cranial elements of *Eotheroides lambondrano* sp. nov. from the middle Eocene of Madagascar compared to those of *E. aegyptiacum* from the middle Eocene of Egypt and *E. babiae* from the middle Eocene of India.

Measurement	<i>Eotheroides lambondrano</i> (UA 9046)	<i>Eotheroides aegyptiacum</i> (SMNS St. III)	<i>Eotheroides aegyptiacum</i> (Senck. M4453)	<i>Eotheroides aegyptiacum</i> (BSPM 1905 XIII e1 St. VI (VII))	<i>Eotheroides babiae</i> (IITRSB 2876)
Skull length	>270	—	—	—	—
Length of the skull roof along midline (total suture lengths along nasals, frontals, parietals, and supraoccipital)	165	153	150	—	—
Zygomatic breadth	147*	—	—	—	—
Breadth across supraorbital processes	94	89	80	—	—
Breadth of cranium at frontoparietal suture	44	49	41	40	41
Length of premaxillary symphysis	50	—	—	—	—
Length of mesorostral fossa	62	—	—	—	—
Width of mesorostral fossa	30	—	—	—	—
Maximum height of rostrum	52	—	—	—	—
Deflection of rostrum from horizontal plane (degrees)	35	—	—	—	—
Length of frontals (level of tips of supraorbital processes to frontoparietal suture)	94	85	86	—	—
Anteroposterior length of zygomatic-orbital bridge of maxilla	40	52	—	—	—
Dorsoventral thickness of zygomatic-orbital bridge	10	15	—	—	—
Height of infraorbital foramen	13	20	—	—	—
Width of infraorbital foramen	14	11	—	—	—
Dorsoventral breadth of zygomatic process	40	—	—	—	—
Greatest anteroposterior length of dorsal nasal lobes	52–58	41	—	—	—
Greatest width of nasals	37	54	—	—	—
Length of parietals, frontoparietal suture to rear of external occipital protuberance	70	78	69	70	89
Height of supraoccipital	44	41	45	44	>26
Width of supraoccipital	52	55	58	53	42
Length of distal cheektooth row (DP5–M3)	53*	42	—	—	—

Measurement landmarks are after Domning (1978). All measurements in millimeters (mm).

*Estimated.

TABLE 2. Dental measurements of the upper molars of *Eotheroides lambdrano* sp. nov. from the middle Eocene of Madagascar compared with those of *E. aegyptiacum* from the middle Eocene of Egypt.

	<i>E. lambdrano</i>		<i>E. aegyptiacum</i>		<i>E. aegyptiacum</i>		<i>E. aegyptiacum</i>	
	UA 9046		SMNS St. III		SMNS St. VII (VIII)		SMNS St. XI (XIV)	
	Left	Right	Left	Right	Left	Right	Left	Right
M1								
Length	—	—	—	10.1**	—	—	—	9.8**
Mesial width	—	—	—	10.9	—	—	—	11.2
Distal width	—	—	—	11.2	—	—	—	9.6
M2								
Length	—	14.9	—	10.9**	—	11.9**	—	12.0*
Mesial width	—	14.3	—	12.6	—	12.4	—	12.3
Distal width	—	12.0	—	10.9	—	11.0	—	10.7
M3								
Length	16.9	—	—	11.8**	12.6	11.8**	—	12.7
Mesial width	14.3	—	13.1	12.4	12.5	12.6	—	11.9
Distal width	11.6	—	—	9.7	9.7	9.0	—	9.7

All measurements in millimeters (mm).

*Estimated.

**Dimension reduced by wear.

(sensu Domning, 1978). The skull is strikingly wide between the supraorbital processes (94 mm) as compared to the narrow braincase. The top of the braincase (including nasals, frontals, and parietals) is relatively flat, without vaulted nasals. Maximum skull width (zygomatic breadth) is estimated as ~147 mm. Rostral deflection from the horizontal plane (defined by the palate at M1-M3) is slight (~35°).

Premaxilla

The premaxilla contains three incisor alveoli and, as preserved, is 131 mm long (measured from the anterior tip of the symphyseal process to the posterior end of the nasal process) and 50.6 mm high (at the level of I2). At the tip of the rostrum is a small alveolus for I1 (maximum diameter = 8 mm), suggesting the lack of an enlarged tusk. The other incisors are also small (maximum alveolar diameters of I2 and I3 are 6.8 mm and 6.5 mm respectively). The I3 alveolus lies at the posterior end of the premaxilla, at its junction with the maxilla.

The nasal process is long and thick posteriorly, oval in cross section (ranging between 11 and 15 mm in diameter), and in contact with the nasal posteromedially, the frontal posterolaterally, and the lacrimal inferolaterally. It extends relatively far posteriorly (more than one-third of the anteroposterior length of the supraorbital process). The mesorostral fossa (nasal opening) is long and narrow. It is bounded posteriorly by the nasals (at the level of the anterior orbital margin) and anterolaterally by the premaxilla, with no contribution from the frontals. The premaxillary symphysis is 50 mm long, and the premaxillary-maxillary suture is below the premaxillary symphysis.

Maxilla

The maxilla houses a large infraorbital foramen (width = 14 mm; height = 13 mm) that is directed slightly inferiorly. The infraorbital canal is short (~14 mm). The incisive foramen (anterior palatine foramen) is large, bounded by the maxillae posteriorly and the premaxillae laterally, anteriorly, and superiorly), and oval in shape, measuring 20 mm wide and 29 mm long. There is a very narrow palatal gutter following the midline (width ca. 13 mm at the level of P1, its narrowest point; length = 73 mm, from the anterior edge to its articulation with the palatine), with tall but thin edges bordering the tooth row. The posterior edge of the palatal gutter (at its junction with the palatine) is approximately at the posterior border of P4. The maxillary dental arcade is strongly concave medially (bell-shaped): narrow at the level of P1 (approximately 13 mm be-

tween mesial borders of alveoli), wide at the level of M1 (34 mm), and narrower again at the level of M3 (estimated as 18 mm).

The canine alveolus has a maximum diameter of 5.8 mm and lies 8.0 mm posterior to that for I3. Posterior to the canine alveolus are alveoli for single-rooted P1-4, followed by a three-rooted alveolus for DP5. The diastemata between the alveoli for left C and P1, P1 and P2, P2 and P3, P3 and P4, and P4 and DP5, are ca 7.8, 11.1, 3.2, 2.4, and 2.0 mm, respectively. The preserved alveoli document that the molars (M1-2) each had three roots, and at the P5 position two distinct alveoli are visible. Since related taxa possess either a single-rooted P5 or a retained triple-rooted DP5, we infer the presence of a retained DP5 for which the distobuccal alveolus appears to have been partially overrun by mesial drift of the mesiobuccal alveolus of M1, leaving a single, large alveolus (Fig. 4C).

Upper Dentition

The dental formula for the upper dentition is 3.1.5.3. Tooth crowns are preserved for RM2 and LM3, as well as the distal half of RM3 and the distobuccal corner of LM2.

M2 is roughly trapezoidal in shape, with the mesial portion being much wider buccolingually than the distal portion (Table 2, Fig. 5A). The buccal margin is indented where it intersects with the furrow between the mesial and distal lophs but the mesial, lingual, and distal margins are rounded, to the extent that there are no mesiolingual or distolingual corners. There are well-developed mesial and lingual cingula. The crown is worn, with some dentin exposed along the apices of the mesial and distal lophs. On the mesial loph, which is long, transversely oriented, sloped from ventrobuccal to dorsolingual, and gently curved (convex mesially), there is a well-formed paracone; the region containing the protocone is very worn. On the distal loph, which is shorter and more strongly curved than the mesial loph (also convex mesially), there is a well-developed metacone.

M3 is longer and wider than M2 (Table 2, Fig. 5B), however it has the same essential design with mesial and distal lophs separated by a prominent transverse valley. Wear is slight and restricted to the mesial loph. The crown narrows distally more than seen in M2, resulting in a more triangular occlusal outline. M3 possesses a well-developed mesial cingulum; the lingual cingulum is slightly broken mesially but was probably continuous with the mesial cingulum, as on M2. The mesial loph is less curved than that of M2, and has two cusps, a paracone and protocone. On the distal loph, there are three distinct cusps of

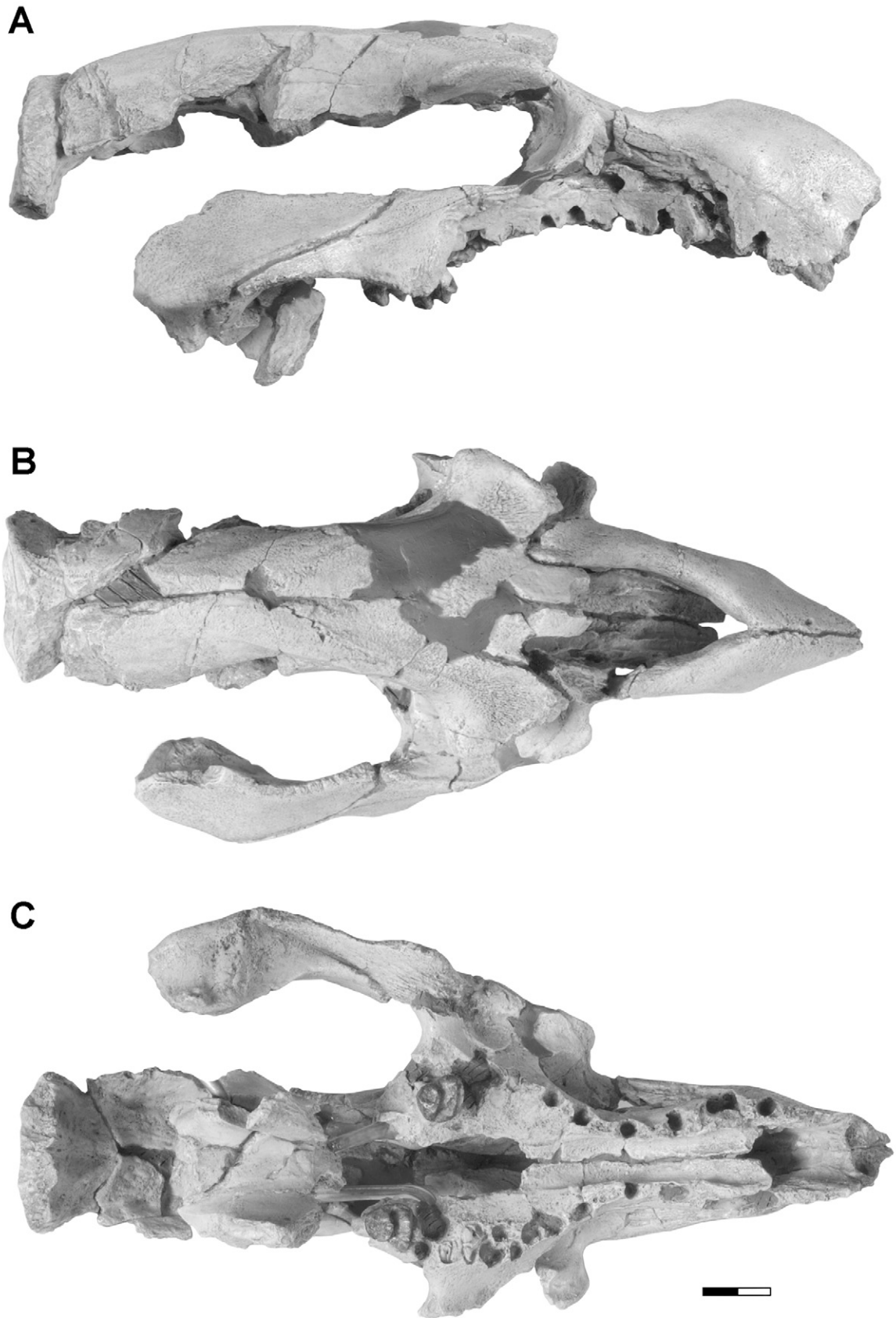


FIGURE 3. Reconstructed cast of the holotype skull (UA 9046) of *Eotheroides lambondrano* sp. nov. from the Eocene of Madagascar in **A**, right lateral, **B**, dorsal, and **C**, ventral views. Scale bar equals 2 cm.

approximately the same size: a metacone buccally, a central metaconule, and a distinct and slightly distolingually displaced hypocone.

The molars of *Eotheroides lambondrano* are substantially larger than those of *Eotheroides aegyptiacum* (Table 2). M2 in *E. lambondrano* is at least 28.5% longer mesiodistally, and is 15.0% and 10.5% wider mesially and distally, respectively, than the average dimensions of M2 of *E. aegyptiacum*. Moreover, M3 in *E. lambondrano* is 37.9% longer mesiodistally, and 14% and 21.9% wider mesially and distally, respectively, than the average dimensions of M3 in *E. aegyptiacum*.

Nasal

The nasal projects forward to the anterior border of the orbit. The anteromedial margins of both nasals are slightly broken, and, due to some missing bone on the anterosuperior aspect of the frontals, the exact shape of the posterior contact of the nasal with the frontal is uncertain. Nonetheless, the nasals are narrow and elongated anteroposteriorly: the maximum anteroposterior length of the dorsal surface can be estimated as ~52–58 mm, making the individual nasals 180–210% longer than wide. Anterolaterally, the nasal bears a concavity for the premaxilla. The dorsal surface of the nasal is flat; it does not arch upward to reach a level higher than the parietal.

Lacrimar

The lacrimal bears three projections: the first extending anteriorly toward the junction between the premaxilla superiorly and the maxilla inferiorly, the second extending posterosuperiorly and contacting the supraorbital process of the frontal laterally, and the third forming the anteroinferior border of the orbit and posteriorly contacting the maxilla and jugal. A lacrimal foramen is lacking.

Frontal

The supraorbital process of the frontal forms a distinct flared ledge projecting laterally over the orbit, with the dorsal surface possessing a shallow concavity. The lateral wall of the frontal is flat, and narrow below the coronal suture. The dorsolateral surface of the frontal is distinctly demarcated by the crista temporalis, which is oriented anterolateral-posteromedially.

Parietal

On the parietal, the crista temporalis is visible, but becomes faint as it proceeds posteromedially. The lateral edges of the left and right cristae temporalis approach each other as they move posteriorly, and are separated at their closest point by ~18 mm, just behind the coronal suture. The parietal roof is ~20 mm thick as measured across the anterior midline.

Supraoccipital

The supraoccipital is well preserved, thick and massive superiorly (relative to other cranial bones), and measures 44 mm in dorsoventral height and 52 mm in transverse breadth. The posterior surface is relatively flat, with paired, deep concavities for the rectus capitis dorsalis muscles near the superior border. The parietal-supraoccipital angle is ~120°.

Basisphenoid

There are no articulations retained between the basisphenoid and the rest of the skull, so its position in the skull reconstruction is inferred. The basisphenoid is relatively small and thin, and largely broken.

Pterygoid

The pterygoid is fused to the basisphenoid. The left pterygoid is complete, and possesses a deep groove posterolaterally. The orientation of the pterygoid appears to be anteroposterior but, as the surrounding area is missing, this reconstruction should be taken with caution.

Palatine

The palatine is missing, but its junction with the maxilla is clearly visible, as it appears to have separated at the palatomaxillary suture. The anterior border of the palatine is approximately at the posterior border of P4. The estimated width of the palatine is 7.5 mm.

Jugal

The right jugal is well preserved with a total length of ~92 mm and a maximum dorsoventral height of 34 mm below the postorbital process. The preorbital process is thin and articulates with the maxilla; its articulation with the lacrimal is slightly broken. The zygomatic (postorbital) process is oriented slightly laterally and lies against the zygomatic process of the squamosal. It has a small tubercle on its superior surface, where it articulates with the squamosal, and a much larger flange on its inferior surface, where its body forms a large triangular shelf.

Squamosal

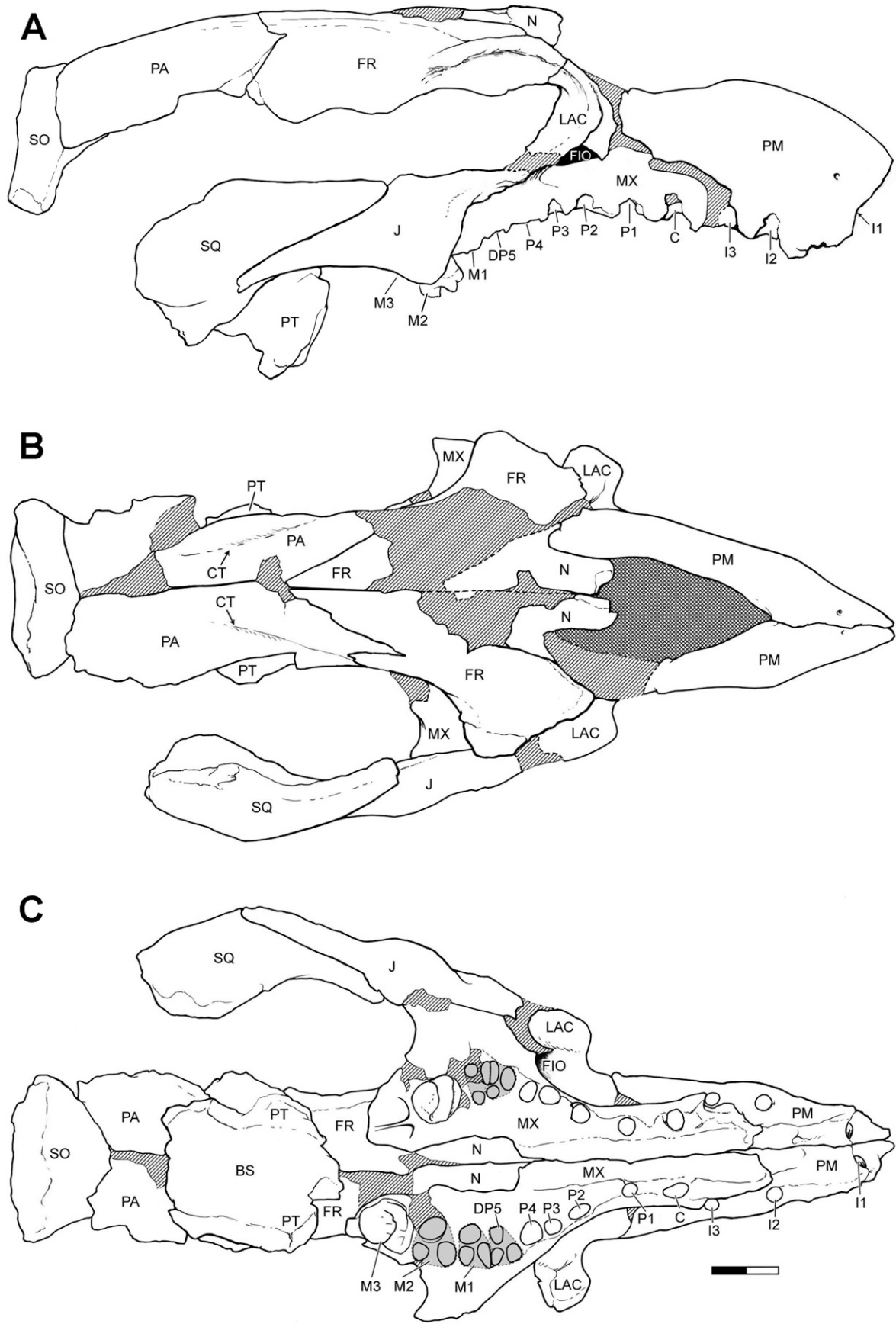
The squamosal is distinctly curved (convex laterally) in dorsal view. It is thick and deep posteriorly but narrows anteriorly and forms an obliquely oriented suture anteroinferiorly with the jugal. The processus retroversus (posterior end of the zygomatic process) is preserved. The mandibular fossa is triangular in shape and possesses a well-defined tubercle on its anteromedial edge. The portion of the squamosal posterior to the mandibular fossa (where it articulates with the parietal and supraoccipital) is missing.

Periotic

Both isolated left and right periotics were recovered. The left has excellent preservation, with only the tip of the promontory and region around the facial foramen missing, and the right is fragmentary and missing the middle of the pars temporalis, the inferior portion of the pars mastoidea, and the tip of the promontory. There is a clear separation between the pars temporalis (= tegmen tympani) and pars mastoidea (= pars petrosa) marked by a deep groove on the inferior surface, and the temporal portion is smaller than the mastoid portion (Fig. 6A). Pars mastoidea comprises two-thirds of the overall periotic, and has a rugose pyramidal posterior projection. The anteroposterior length is 45.7 mm and the maximum width is 41 mm. The overall shape of the periotic is very similar to that described by Robineau (1969) for *Dugong dugon*, but differs in having a pars temporalis with a pyramidal anteromedial projection.

Tympanic

The tympanic is dense and relatively short anteroposteriorly, and has well-ossified anterior and posterior attachments (Fig. 6B). The internal margin is roughly semicircular and its outer margin has a distinct anteroinferior projection formed halfway along its length; the short anteroposterior length and anteroinferior projection makes it distinct from all other extant sirenian tympanics described by Robineau (1969). The tympanic has a length of 17.8 mm, a maximum height of 20.5 mm, and the internal diameter of the ring is 10.6 mm.



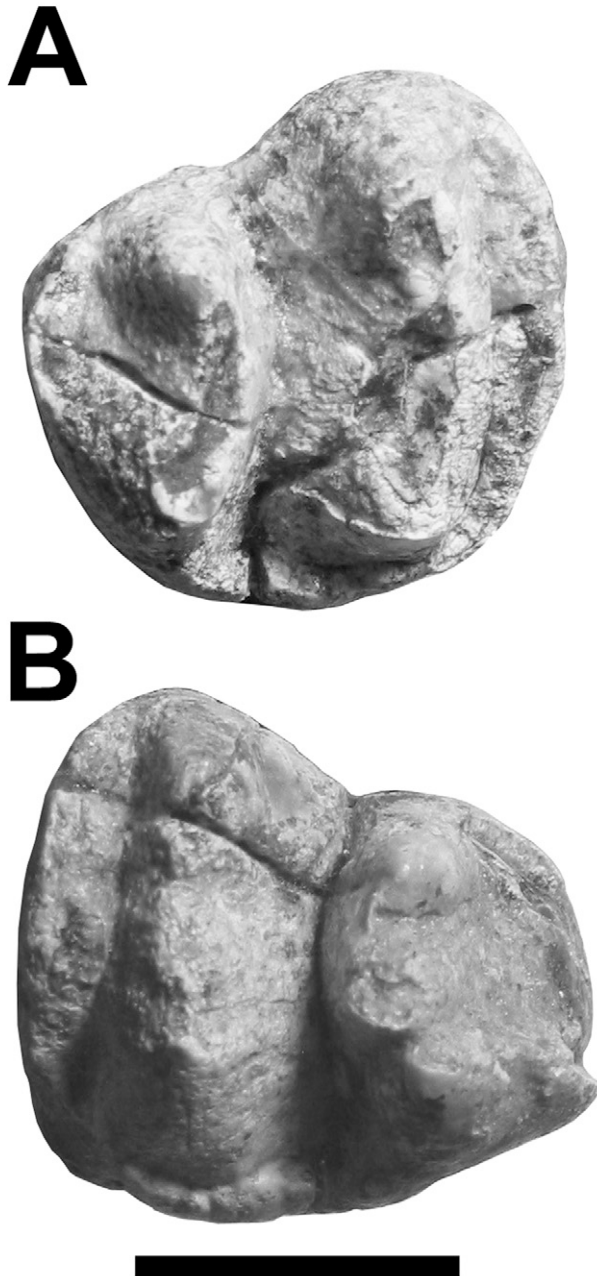


FIGURE 5. Upper molars of *Eotheroides lambondrano* sp. nov. from the Eocene of Madagascar. **A**, occlusal view of RM2, mesial to right and buccal at top; **B**, occlusal view of LM3, mesial to left and buccal at top. Scale bar equals 1 cm.

Ribs

The rib fragments recovered are pachyosteosclerotic (sensu Domning and de Buffrénil, 1991), dense, swollen, and banana-shaped (Fig. 7). The shafts are thick and no costal groove is

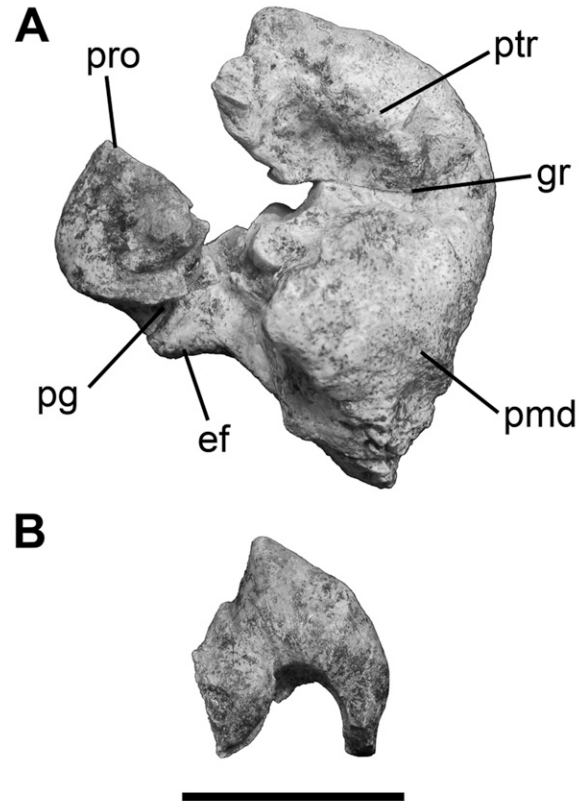


FIGURE 6. Isolated ear elements of *Eotheroides lambondrano* sp. nov. from the Eocene of Madagascar. **A**, inferior view of left periotic, anterior at top; **B**, isolated left tympanic, anterior at top. **Abbreviations:** ef, endolymphatic foramen; gr, groove separating the pars temporalis and pars mastoidea; pg, perilymphatic gutter; pmd, pars mastoidea; pro, promontory; ptr, pars temporalis. Scale bar equals 2 cm.

evident. They are circular to subcircular in cross section throughout their length.

DISCUSSION

The Malagasy sirenian described here is a member of the Dugongidae, following Sickenberg's (1934) review of European and North African Eocene Sirenia and Domning's (1994) phylogenetic analysis of the order, because it has an enlarged premaxillary symphysis, enlarged infraorbital foramen, and well developed processus retroversus of the squamosal. It represents a primitive stage for Dugongidae in retaining an upper dental formula of 3.1.5.3 and its deciduous P5 is not replaced. It is assigned to *Eotheroides* on the basis of the following characters: premaxillary-maxillary suture lies below the premaxillary symphysis, nasals long and in contact along the midline, and pachyosteosclerotic anterior ribs.

Eotheroides lambondrano is clearly not assignable to *Eosiren* (Andrews, 1902) because, unlike species of the latter genus, its nasal bones are anteroposteriorly elongate and joined along the midline; in *Eosiren* the nasal bones are short and in most cases

← FIGURE 4. Outline drawings of the holotype skull (UA 9046) of *Eotheroides lambondrano* sp. nov. from the Eocene of Madagascar in **A**, right lateral, **B**, dorsal, and **C**, ventral views. **Abbreviations:** BS, basisphenoid; CT, crista terminalis; FIO, foramen infraorbitale; FR, frontal; J, jugal; LAC, lacrimal; MX, maxilla; N, nasal; PA, parietal; PM, premaxilla; PT, pterygoid; SO, supraoccipital; SQ, squamosal. Hatching indicates missing elements, cross-hatching indicates mesorostral fossa (narial opening). Scale bar equals 2 cm.



FIGURE 7. Fragmentary ribs of *Eotheroides lambondrano* sp. nov. from the Eocene of Madagascar, demonstrating the dense, banana-shaped morphology characteristic of species of *Eotheroides*. Scale bar equals 5 cm.

are either separated from each other or have only slight contact along the midline (Domning 1994; Domning et al., 1994). Moreover, *E. lambondrano* differs from species of *Prototherium* (de Zigno, 1875) in having a greater frontal breadth with respect to the total anteroposterior length of the cranium; all *Prototherium* species have elongate and narrow skulls (de Zigno, 1875; Bizzotto 1983, 2005; Pilleri et al., 1989; Domning, 1994). The rostral deflection in *E. lambondrano* is 35° and is thus at least 10° less than in other Dugongidae that lived in the middle and late Eocene (*Eosiren* and *Prototherium*); it is close to the degree of deflection seen in members of the Protosirenidae and significantly less than that of extant *Dugong dugon* (Domning et al., 1982; Domning, 1994).

This description increases the currently known species of *Eotheroides* to three: *Eotheroides aegyptiacum* from the Lutetian of the Mokattam Hills near Cairo (Owen, 1875), *E. babiae* from the Lutetian of Kachchh, India (Bajpai et al., 2006), and *E. lambondrano* from the middle Eocene of Ampazony, Madagascar. The occurrence of *Eotheroides* in Madagascar demonstrates a much larger geographic range for the genus than previously appreciated; Ampazony is more than 5,000 km southeast of the Egyptian sites and approximately 5,000 km southwest of Kachchh in India. Recently discovered sirenian materials from the late Eocene beds of the Fayum Basin in Egypt include at least two new species of *Eotheroides* (Zalmout and Gingerich, 2007). These new taxa are more derived and have larger body sizes than the middle Eocene species of *Eotheroides* from Egypt, India, and Madagascar but detailed morphological comparisons are not made here pending description of the Egyptian material.

Eotheroides lambondrano has a skull length of only ~270 mm. This specimen is the first *Eotheroides* for which skull length can be estimated; the rostrum is lacking in all known specimens of *E. aegyptiacum* and *E. babiae*. Most of the available cranial dimensions of the holotype of *E. lambondrano* and several specimens of *E. aegyptiacum* are closely comparable. However the Malagasy taxon has longer and narrower nasals, the zygomatic-orbital bridge of the maxilla is much shorter anteroposteriorly (Table 1), and the upper molars are longer (28.45–37.9%) and wider (10.5–21.85%) than those of *E. aegyptiacum* (Table 2). *E. babiae* (Bajpai et al., 2006), which is known from an isolated mandible (IITR-SB 2775), a partial skull roof (IITR-SB 2876), and a partial scapula (IITR-SB 2815), has longer parietals and a smaller supraoccipital than those of both *E. aegyptiacum* and *E. lambondrano* (Table 1).

The morphology of the braincase of *E. lambondrano* is different than reported for the only other Malagasy sirenian fossil described, a fragmentary specimen from the island of Nosy Mahakamby consisting of the top and posterior portions of a braincase (Collignon and Cottreau, 1927). This specimen (weakly attributed to *Halitherium*) possesses pronounced temporal crests that converge to meet in the mid-line and then separate posteriorly, while *E. lambondrano* possesses weak temporal crests that gradually approach each other as they move posteriorly for their first half, and run parallel for the remainder of their length. Thus, it appears that more than one sirenian species is present in Madagascar's fossil record, and recent reconnaissance work on Nosy Mahakamby has produced associated postcranial material with rib morphology that is different than described here for *E. lambondrano* (Samonds et al., 2007).

Phylogenetically, certain characteristics of *E. lambondrano* are primitive relative to other members of the genus, most notably the presence of three incisors within the premaxilla. This character was impossible to evaluate in either *Eotheroides aegyptiacum* or *E. babiae* since the rostral areas of these species remain unknown. The retention of three incisors, as well as the general lack of other derived features, makes *E. lambondrano* a potential candidate for a basal member of the genus. If future analyses show this to be the case, this would imply a southern hemisphere origin for *Eotheroides*. A more systematic assessment of these phylogenetic relationships will necessarily require more complete material, including postcrania.

CONCLUSIONS

Madagascar has played a unique biogeographic role in Earth history, and both its fossil and living groups include some of the most diverse and unusual organisms in the world (Goodman and Benstead, 2005; Krause et al., 2006). Studies of the evolutionary history of Madagascar's mammals, however, have long been hindered by the near-complete lack of a pre-Late Pleistocene Cenozoic fossil record.

This study reports the first diagnostic mammalian material from the roughly 65 million year gap between the Late Cretaceous and Late Pleistocene, and is potentially highly significant for reconstructing the evolutionary and biogeographic history of sirenians in the southern hemisphere. The presence of *Eotheroides* in Madagascar demonstrates that members of this genus were diverse and broadly distributed within shallow marine waters of the Tethyan Realm during the middle and late Eocene.

In addition, the presence of sirenians, crocodiles, and turtles, which are generally associated with nearshore marine environments, suggests that the Ampazony region has the potential to yield fossils of terrestrial and freshwater vertebrates, which are well-documented to occur in these types of mixed facies (e.g., Gingerich, 1977; Anderson et al., 1990; Cunningham et al., 1993; Rogers and Kidwell, 2000). As the virtual absence of a Cenozoic fossil record has prevented direct and explicit testing of the biogeographic origin and colonization patterns of the modern terrestrial and freshwater vertebrate fauna of Madagascar, this new locality, and surrounding strata (which include subaerially exposed coastal mudflat deposits), have the potential to yield future fossils that at last may help us reconstruct aspects of how, when, and from where the basal stocks of Madagascar's extant clades arrived on the island.

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