



## Marine mammals from the Miocene of Panama

Mark D. Uhen<sup>a,\*</sup>, Anthony G. Coates<sup>b</sup>, Carlos A. Jaramillo<sup>b</sup>, Camilo Montes<sup>b</sup>, Catalina Pimiento<sup>b,c</sup>, Aldo Rincon<sup>b</sup>, Nikki Strong<sup>b</sup>, Jorge Velez-Juarbe<sup>d</sup>

<sup>a</sup> George Mason University, Fairfax, VA 22030, USA

<sup>b</sup> Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Ancon, Panama

<sup>c</sup> Department of Biology, University of Florida, Gainesville, FL, USA

<sup>d</sup> Laboratory of Evolutionary Biology, Department of Anatomy, Howard University, WA 20059, USA

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### ABSTRACT

Panama has produced an abundance of Neogene marine fossils both invertebrate (mollusks, corals, microfossils etc.) and vertebrate (fish, land mammals etc.), but marine mammals have not been previously reported. Here we describe a cetacean thoracic vertebra from the late Miocene Tobabe Formation, a partial cetacean rib from the late Miocene Gatun Formation, and a sirenian caudal vertebra and rib fragments from the early Miocene Culebra Formation. These finds suggest that Central America may yet provide additional fossil marine mammal specimens that will help us to understand the evolution, and particularly the biogeography of these groups.

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## 1. Introduction

Central America includes an abundance of marine sedimentary rock units that have produced many fossil marine invertebrates (Jones and Hasson, 1985), as well as marine vertebrates, including fishes (Gillette, 1984; Martin and Dunn, 2000), and turtles (Webb and Perrigo, 1984). Despite these abundant fossils, only recently have the first marine mammals been noted from Central America, from the Pliocene El Salto Formation of Nicaragua (a partial skeleton of a mysticete whale (Lucas et al., 2008)). Here we describe the first fossil marine mammals found in Panama: a cetacean vertebra discovered in 1999 by Anthony G. Coates, a partial cetacean rib discovered by Douglas Jones and Gary S. Morgan in 2009, a sirenian vertebra discovered in 2008 by Aldo Rincon, and several sirenian rib fragments discovered between 2007 and 2009 by Aldo Rincon and others.

## 2. Stratigraphic setting

### 2.1. Tobabe cetacean

The whale vertebra was found in a sandy pebble conglomerate in the Tobabe Formation on Small Plantain Cay in the Bocas del Toro

archipelago, Panama (Fig. 1A). The Tobabe Formation is the basal unit of the Late Miocene–Early Pliocene (~7.2–~3.5 Ma) Bocas del Toro Group, an approximately 600 m thick succession of volcanoclastic marine sediments (Fig. 2). (Note that all ages in Ma are with reference to the time scale of Gradstein et al., 2004.) In Bocas del Toro the Tobabe Formation outcrops in the Plantain Cays to the east and Toro Cay to the west of the Valiente Peninsula where it unconformably overlies Late Miocene (~11.5 Ma) volcanic arc columnar basalts (Fig. 2). The Tobabe Formation in the Plantain Cays consists of a poorly sorted pebble and cobble conglomerate comprised of a variety of subangular to rounded sedimentary and volcanic clasts at its base that fines upward into a massive bioturbated, fossiliferous, coarse-grained, quartz sandstone containing abundant echinoids, various mollusks, fossil wood bored by teredonid “shipworms”, and numerous infaunal burrow structures (Coates, 1999b; Collins and Coates, 1999).

Although the upper part of the Tobabe Formation is not visible on Small Plantain Cay because it is covered with thick tropical vegetation, we know from laterally equivalent deposits of the Tobabe Formation on Toro Cay (~16 km west of the Plantain Cays, on the western side of the Valiente Peninsula), the Tobabe Formation is well-exposed and conformably overlain by the Late Miocene Nancy Point Formation. At Toro Cay the Nancy Point Formation stratigraphically overlies the Tobabe Formation and is comprised mostly of bioturbated, muddy sandstones and siltstones with scattered mollusks and organic matter (Coates, 1999b). At Toro Cay, Lower Nancy Point Formation fauna (Finger Island facies)

\* Corresponding author. Tel./fax: +1 205 348 2319.

E-mail address: [muhen@gmu.edu](mailto:muhen@gmu.edu) (M.D. Uhen).

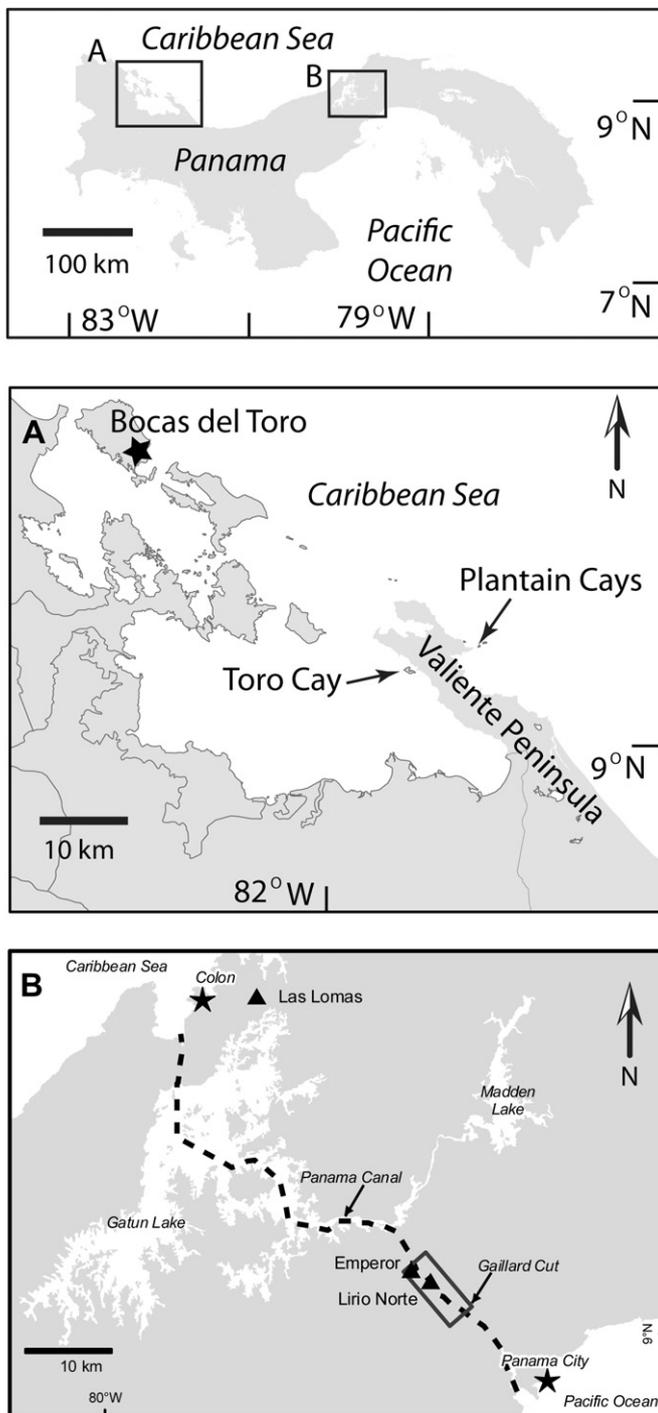


Fig. 1. Map showing the whale and sirenian fossil localities. A, Bocas del Toro Basin. B, Gaillard Cut Reach, Panama Canal Basin.

indicate a middle neritic (60–100 m) water depth (Aubry and Berggren, 1999). Up section changes in invertebrate fossil assemblages (Coates, 1999b; Collins and Coates, 1999), benthic foraminifera (Collins and Coates, 1999), and sedimentary facies (Coates, 1999b) in the Tobabe Sandstone indicate that it was deposited in a transgressive near-shore marine environment, that at Toro Cay, graded into the middle neritic facies of the Nancy Point formation (Collins, 1993). Planktonic foraminifera from the Tobabe Formation on Toro Cay and planktonic foraminifera from the Nancy Point Formation suggest that the Tobabe and Nancy Point formations are

Messinian in age, together spanning a time period from  $\sim 7.25$  to  $\sim 5.33$  Ma (Collins, 1993).

#### 2.1.1. *Gatun cetacean*

The partial rib was collected in Neogene marine sediments of the lower part of the Gatun Formation at Las Lomas (Fig. 1). This formation crops out in a large area of north-central Panama, extending along the northern coast of Lake Gatun, 15 km northward to the Caribbean Sea, and east and west of Colon, within the Panama Canal basin.

The Gatun Formation is highly fossiliferous, with diverse molluscan assemblages (Woodring, 1957, 1959, 1964). Vertebrate macrofossils consist typically of shark, ray and osteichthyan teeth. In addition, microfossil assemblages include ostracodes (Borne et al., 1999), benthic foraminifera (Collins, 1999), osteichthyan otoliths (Aguilera and Rodrigues de Aguilera, 1999), and small shark taxa (Gillette, 1984; Pimiento et al., 2010).

The lower Gatun Formation is late middle Miocene in age (Coates, 1999a; Collins et al., 1996). Studies of different taxa indicate that the Gatun Formation represents a shallow-water environment ( $\sim 25$  m depth) with higher salinity, mean annual temperature variations, seasonality and productivity relative to modern systems in this region (Coates and Obando, 1996; Collins et al., 1996; Gussone et al., 2004; Haug et al., 2001; Teranes et al., 1996). The Gatun Formation was located within a productive marine strait that connected the Pacific Ocean and the Caribbean Sea during the late Miocene (Collins et al., 1996).

#### 2.2. *Culebra sirenians*

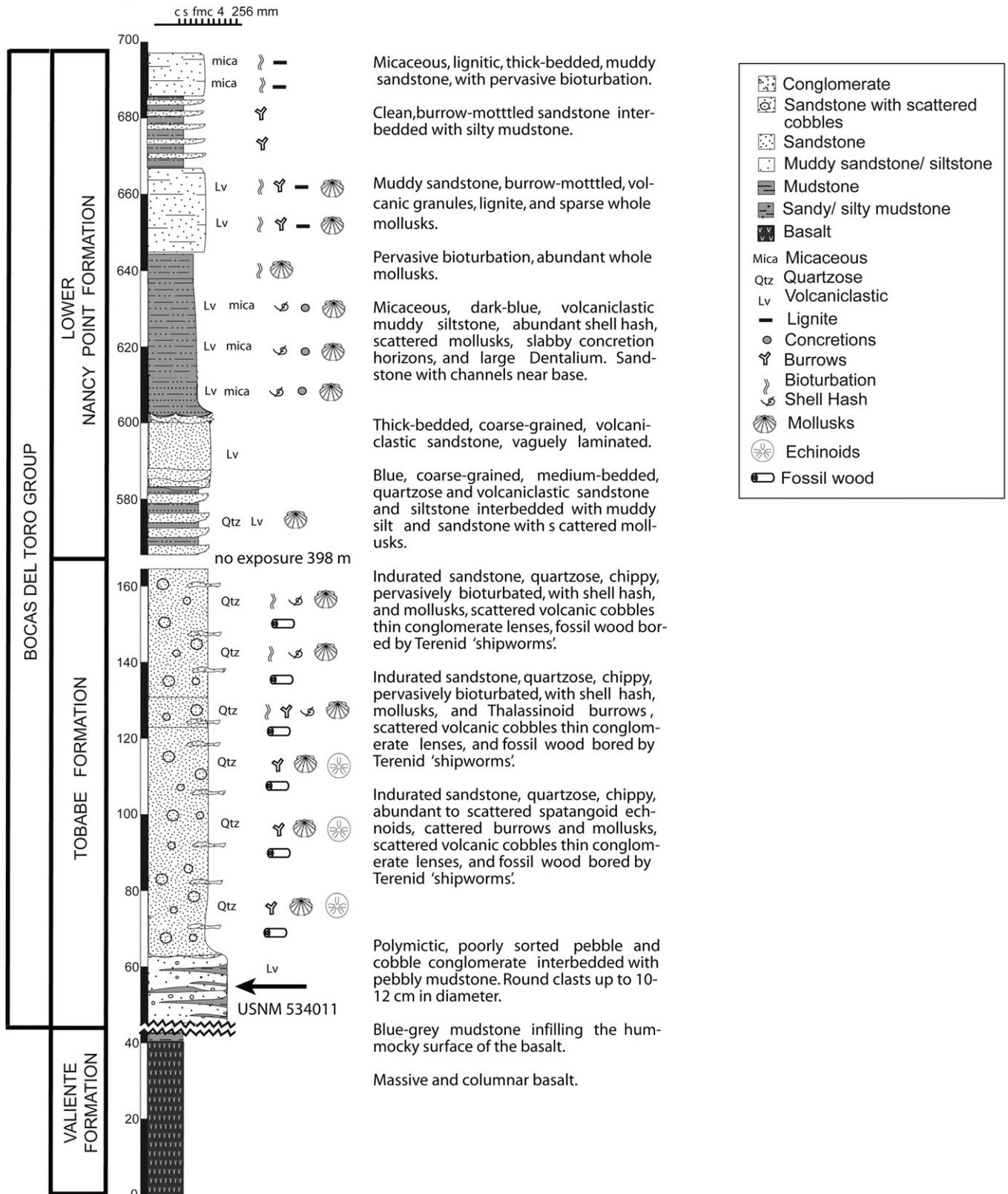
The sirenian vertebra and additional sirenian rib fragments were found in a volcanoclastic pebble conglomerate in the Upper Culebra Formation (Fig. 3) in the El Lirio Norte reach of the Panama Canal in the Panama Canal Basin (Fig. 1B). The Culebra Formation is comprised of a  $\sim 200$  m thick section (Woodring, 1957) of mixed siliciclastic and carbonate marine sediments. Together with the predominantly terrestrial Cucaracha Formation, that conformably overlies it, they comprise what is thought to be a transgressive–regressive sequence with environments of deposition that include fringing reef, neritic, upper bathyal (Lower Culebra) and lagoonal to fluvial-deltaic (Upper Culebra–Cucaracha) (Kirby et al., 2008; Moron et al., 2008; Strong et al., 2008; Woodring and Thompson, 1949).

The Culebra Formation sits unconformably on the terrestrial Las Cascades Formation, an Early Miocene sequence of predominantly volcanic agglomerates, tuffs, and paleosols. The Las Cascades, Culebra, and Cucaracha Formations, together with the overlying volcanic Pedro Miguel Formation comprise what Woodring and Thompson (1949) referred to as the Gaillard Group, a sequence of volcanic rock, and marine to terrestrial sediments and paleosols that fill the southeastern part of the Panama Canal Basin, a Tertiary structural and depositional basin that formed in response to the convergent tectonics of the eastern Pacific subduction zone and associated arc volcanism (Coates, 1999a).

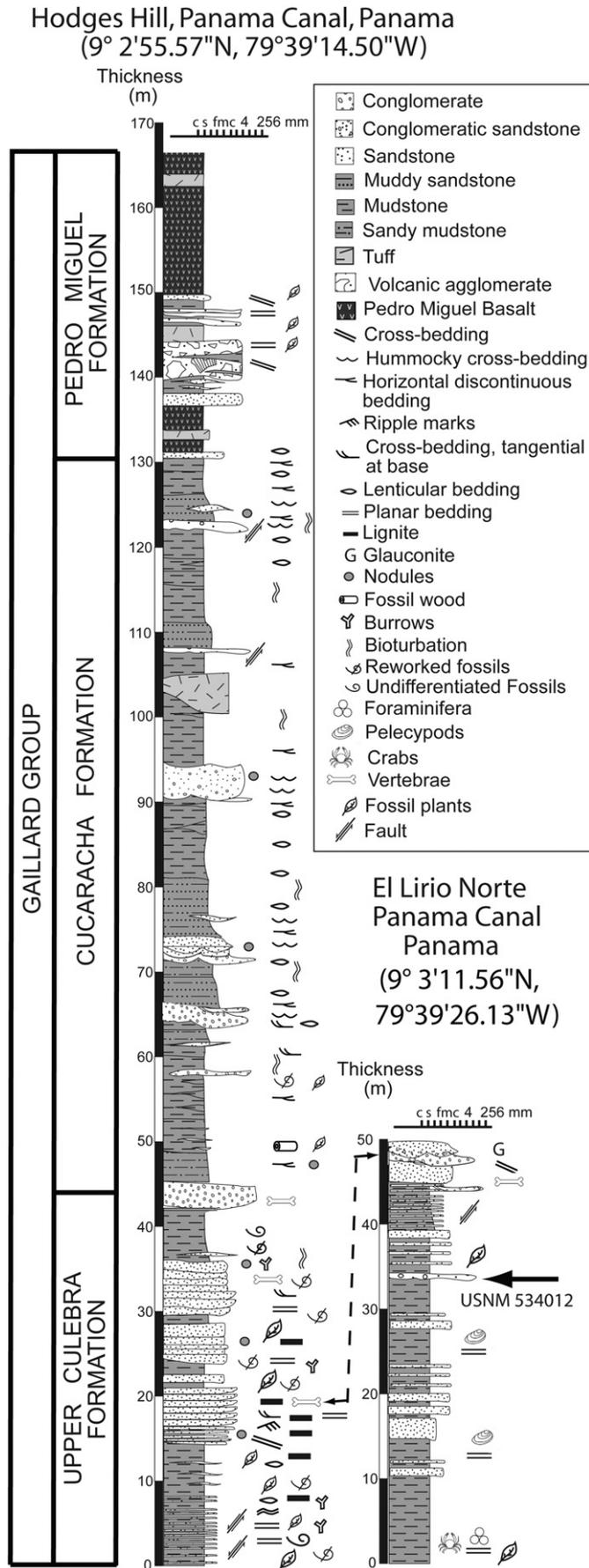
The sirenian rib fragments were found in both the Lower and Upper Culebra Formation. The sirenian vertebra was found in the Upper Culebra Formation (Fig. 3) approximately 40 m below the upper contact with the Cucaracha Formation. The vertebra was found in a volcanoclastic, clast-supported, pebble conglomerate located within a section of interbedded shallow marine marls and lignitic shales that contain abundant relic plant material, including carbon compressions of sea grasses (Johnson and Kirby, 2006), wood and scattered individual ostreids, ostreid beds, and crabs, and some thin beds of volcanoclastic sandstone. Together these sedimentary facies and fossils indicate a relatively shallow marine

## Little Plantain Cay to the Valiente Peninsula Bocas del Toro, Panama

Thickness (m) (9° 7'41.00"N, 81°48'36.25"W to ~ 9° 7'11.45"N, 81°49'50.68"W)



**Fig. 2.** Stratigraphic section from Little Plantain Cay to the Valiente Peninsula in the Bocas del Toro Basin (Modified from Collins and Coates, 1999). Arrow indicates the cetacean specimen (USNM 534011) collection level.



lagoonal or estuarine environment of deposition (Johnson and Kirby, 2006; Kirby et al., 2008; Strong et al., 2008). The clast-supported pebble conglomerate that the vertebra was found in suggests that it was likely deposited as depositional lag in a near-shore fluvial-deltaic distributary-channel. Assuming minimal transport of the sirenian fossil, its presence in the strata also indicates a coastal marine, estuarine, or fluvial environment of deposition (MacFadden et al., 2004). The Lower Culebra has been dated as lower Miocene (Aquitanian, ~23 Ma) with benthic foraminifera (Blacut and Kleinpell, 1969) and Sr chemostratigraphy (Kirby et al., 2008). The Upper Culebra Formation is likely anywhere from 17 to 19 Ma (Burdigalian, Early Miocene), based on Sr chemostratigraphic analyses of Upper Culebra marine bivalves (Kirby et al., 2008) and Upper Culebra ostracodes correlation with known planktonic foraminifera zones (Blow, 1969; Van den Bold, 1972).

### 3. Systematic paleontology

CETACEA Brisson, 1762

NEOCETI Muizon and Fordyce, 2001

ODONTOCETI Flower, 1867

Family indet. gen. et. sp. indet.

**Material**—UF 247257, rib, partial.

**Locality**—Las Lomas (9°21'15.66"N, 79°50'11.34"W) of north-central Panama in the Panama Canal Basin (see Fig. 1), PaleoDB collection 96700.

**Formation**—Lower Gatun Formation.

**Age**—Late middle Miocene, Serravallian.

**Description**—The specimen consists of a portion of a rib 16.4 cm long, 2.1 cm wide, and 0.3–1.5 cm thick. As the distal and proximal extremities are lacking, the exact length of the rib is uncertain, nevertheless, the costal angle and part of the shaft are distinguishable. The bone is slightly curved, with the anterior face flat and the posterior concave. The dorsal surface is thicker than the ventral. The proximal end is flattened and wider than the distal end, however, the shaft increases its thickness distally. The external bone is compact, while the internal is spongy.

MYSTICETI Cope, 1891

CHAEOMYSTICETI Mitchell, 1989

BALAENOPTEROIDEA? Gray, 1868

Family indet. gen. et. sp. indet. (Table 1; Fig. 4)

**Material**—USNM 534011, posterior thoracic vertebra.

**Locality**—Small Plantain Cay (9°7'41.00"N, 81°48'36.25"W) in the Bocas del Toro archipelago See Fig. 1A, PaleoDB collection 96701.

**Formation**—Tobabe Formation. Matrix adhering to the specimen is a sandstone pebble conglomerate. (see Stratigraphic Setting above; Fig. 2)

**Age**—The Tobabe Formation is considered late Miocene (Messinian) in age (Coates, 1999a).

**Description**—The specimen consists of a single, heart-shaped vertebral body including the neural arch, a broken neural spine, much of the left transverse process and the base of the right transverse process. Both anterior and posterior epiphyses are missing. The left transverse process is present, with a slight distal swelling, but missing the distal tip. The bases of the transverse processes are placed very high on the lateral side of the vertebral body. The transverse processes angle slightly dorsally, forming an

Fig. 3. Stratigraphic columns of the Hodges Hill and El Lirio Norte filed locations in the Gaillard Cut reach of the Panama Canal Zone. Arrow indicates the sirenian specimen (USNM 534012) collection level.

**Table 1**

Measurements cetacean vertebra, USNM 534011. Both epiphyses are missing. All measurements are in millimeters.

Anterior breadth	Anterior height	Ventral length	Posterior width	Posterior height	Dorsal length
142.0	98.7	108.9	–	–	–

angle with the neural spine slightly less than  $90^\circ$ . The neural arch is triangular in shape, with a neural spine broken on the distal end. The vertebral body itself lacks a ventral keel, or any additional processes. Nutrient foramina are present on the ventral surface. The heart-shaped body indicates that the vertebra is a thoracic vertebra, and the length of the transverse processes indicate it is from the posterior part of the thoracic region.

SIRENIA Illiger, 1811

DUGONGIDAE Gray, 1821 gen. et. sp. indet. (Table 2; Fig. 5)

**Material**—USNM 534012, one anterior caudal vertebra, possibly Ca3; FLMNH 244758, 244759, 249194, 249195, 249198, rib fragments.

**Locality**—El Lirio Norte reach ( $9^\circ 3' 11.56''\text{N}$ ,  $79^\circ 39' 26.13''\text{W}$ ) of the Panama Canal in the Panama Canal Basin. See Fig. 1B Paleodb collection 96702.

**Formation**—Upper Culebra Formation. (see Stratigraphic Setting above; Fig. 3).

**Age**—Burdigalian (19–17 Ma) in age (see Stratigraphic Setting above).

**Description**—USNM 534012 consists of an anterior caudal vertebra, missing the right transverse process and distal portion of

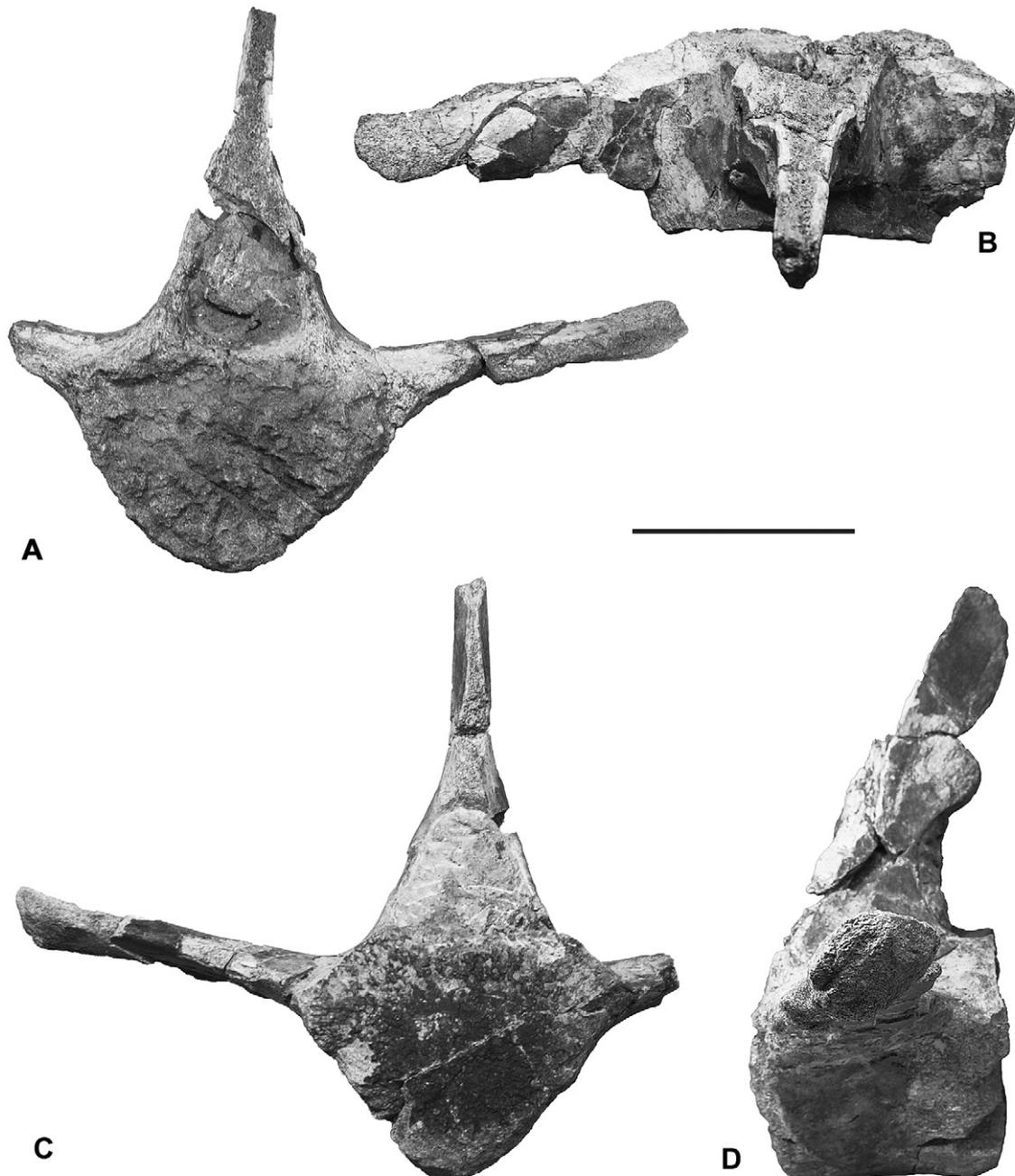


Fig. 4. USNM 534011, Balaenopteroidea? gen. et. sp. indet. posterior thoracic vertebra in A, anterior; B, dorsal; C, posterior; and D, lateral views. Scale bar equals 10 cm.

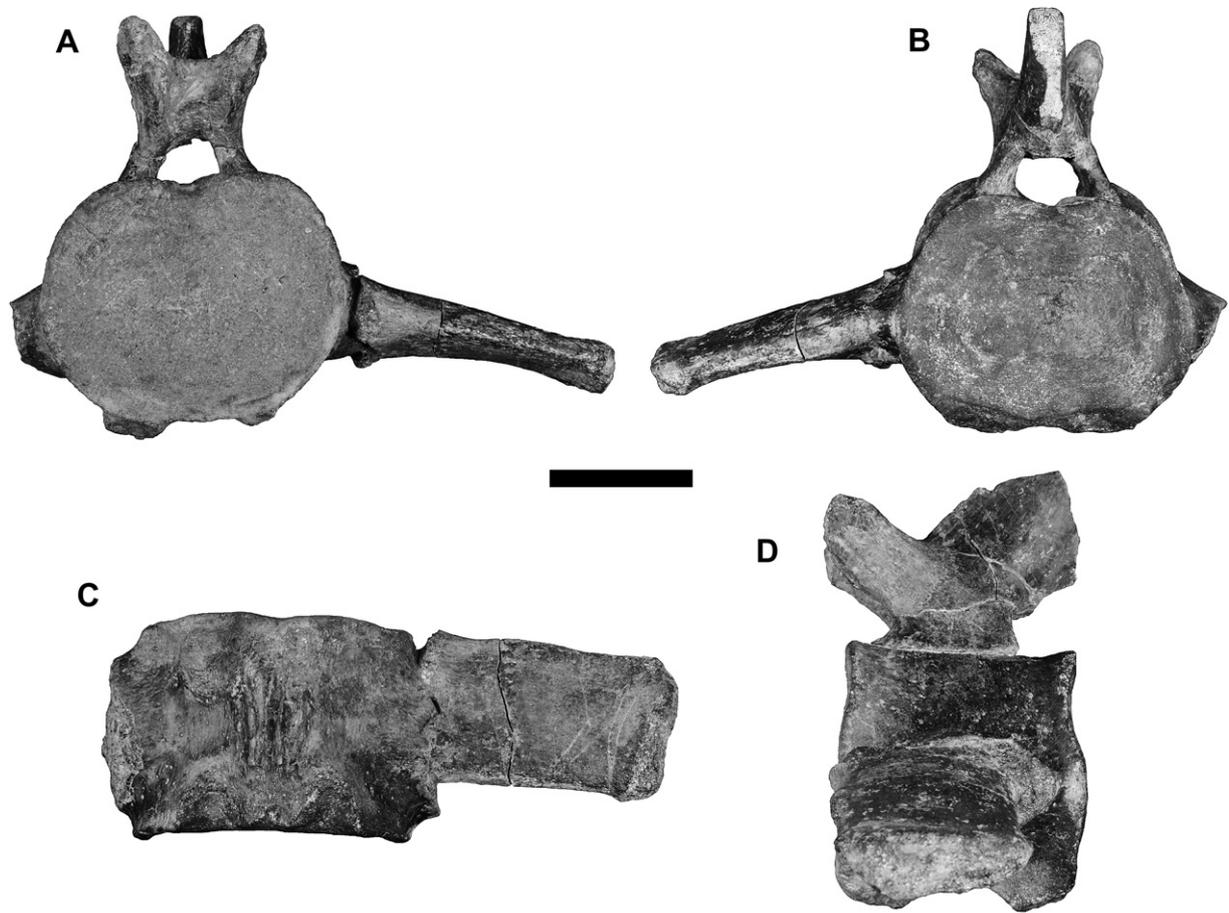


Fig. 5. USNM 534012. Dugongidae gen. et. sp. indet. third caudal vertebra in A, anterior; B, posterior; C, ventral; D, lateral views. Scale bar equals 4 cm.

the spinous process. Centrum, hexagonal in outline, with midline depression on dorsal surface; cranial and caudal articular surfaces slightly concave; surfaces above and below transverse processes slightly concave. Small nutrient foramina present throughout the centrum, but more numerous near the base of the transverse process and on the ventral surface lateral to the midventral keel. Ventral surface contains two pairs of demifacets, for articulation of chevrons, separated by about 14 mm; anterior demifacets unequal in size, with left being smaller than right, the latter being more than twice as large and thus more similar to posterior demifacets which are about 10 mm long. A low midventral keel is present which disappears posteriorly where it turns into a flat surface between the posterior demifacets; anteriorly it turns into a gently convex surface between the demifacets. Transverse processes located at about the middle of the lateral surface of the centrum; both were broken near their bases with only the left one preserved and displaced about 9 mm anteriorly; directed ventrolaterally; distal end of process rugose and slightly expanded dorsoventrally. Anterior border of transverse process thinner and sinuous when viewed dorsally, posterior border thicker and straight. Neural canal wider than high, apex rounded anteriorly and with a small (3 mm high) keel posteriorly. Pedicles with anterior border thicker than posterior. Prezygapophyses directed anterodorsally, nearly vertical and mediolaterally flattened; mammillary processes present, articular surface possibly faced dorsomedially, although feature obscured by sediment. Postzygapophyses absent. Spinous process with thin, keeled anterior border, posterior border broken above wider, square base. Process directed posteriorly, with angles to the horizontal of about 45° and

30° on anterior and posterior borders, respectively, giving the impression that it was expanded dorsally.

The ribs are pachyosteosclerotic as in most sirenians (de Buffrénil et al., 2010). Of these, only FLMNH 244758 and 249195, two right ribs, are nearly complete, both missing the proximal end from about the level just proximal of the angle; their preserved lengths are 243 mm and 230 mm, respectively. The ribs are mediolaterally flattened, with midshaft diameters of 29 × 13 mm for FLMNH 244758 and 26 × 18 mm for FLMNH 249195. They taper gradually towards the distal end; this is more pronounced in the distalmost 25 mm of FLMNH 244758 where it becomes rounder. Distal to the angle the ribs are curved inwards and slightly posteriorly. The area just distal to the angle has a flange on the posterior border for the origin of *m. iliocostalis thoracis* (Domning, 1977). The other rib fragments (FLMNH 244759, 249194) consist of fragments of the shaft, they are pachyosteosclerotic and mediolaterally flattened. FLMNH 249198 is rounder; the medullar region is open and near the medial surface.

**Material**—FLMNH 249196, 249197, rib fragments.

**Locality**—Emperor area (9° 4'17.62"N, 79°40'28.99"W) of the Panama Canal in the Panama Canal Basin. See Fig. 1B, PaleoDB collection 96703.

**Formation**—Lower Culebra Formation. (see Stratigraphic Setting above).

**Age**—Aquitian (23–20.4 Ma) in age.

**Description**—FLMNH 249196 consists of two fragmentary ribs missing most of the areas proximal and distal to the angles; these are pachyosteosclerotic and mediolaterally flattened, becoming rounder near the angle. FLMNH 249197 consists of an eroded fragment, it is pachyosteosclerotic and round in cross section.

## 4. Discussion

### 4.1. *Tobabe cetacean*

The poor preservation of the vertebra and lack of distinguishing morphological features makes a precise identification impossible. The lack of anterior and posterior epiphyses on the body of the vertebra suggest that it is from an immature individual. The size of the vertebra, its overall morphology, and its presence in marine strata indicate that it is a cetacean. The age of the fossil makes it unlikely that it came from a toothed mysticete, all of which are known from the Oligocene or early Miocene. The size also indicates that it is a large cetacean, suggesting a mysticete or physeterid. It is unlikely to belong to a physeterid (sperm whale) due to the length of the transverse processes, which are shorter in physeterids. The thoracic vertebrae of physeterids are also much less heart-shaped than the Tobabe specimen, and physeterids also have much antero-posteriorly shorter pedicles than the Tobabe specimen.

All large baleen-bearing mysticetes from the Miocene are in the Chaemysticeti, so assignment to this group is almost certain. Three superfamilies of Chaemysticeti are represented in the late Miocene: Balaenoidea (sensu Geisler and Sanders, 2003; Steeman, 2007), Cetotherioidea (sensu Steeman, 2007), and Balaenopteroidea (sensu Geisler and Sanders, 2003; Steeman, 2007). A single characteristic of thoracic vertebrae, other than number, has been used for phylogenetic purposes within Neoceti, the capitular articulation faces of the posterior vertebrae (Geisler and Sanders, 2003). Unfortunately, this character does not vary among the mysticete superfamilies. The transverse processes and neural spines of the thoracic vertebrae of modern balaenids are much thicker than those of balaenopteroids, and also much thicker than those of the Tobabe specimen. The thoracic neural spines in modern balaenids are distally thickened, a feature lacking in the Tobabe specimen. In addition, the transverse processes of the thoracic vertebrae of modern balaenids are angled slightly down, vs. slightly up in the Tobabe specimen. Finally, the bodies of thoracic vertebrae in modern balaenids are much more round when compared to the heart-shaped body of the Tobabe specimen.

The orientation of the transverse processes and neural spines, along with the shape of the vertebral body and relative length of the pedicles on the Tobabe specimen all compare favorably with the posterior thoracic vertebrae of several Miocene stem balaenopteroids. When compared to a range of relatively complete thoracic vertebrae from Miocene mysticetes in the collection of the USNM, it compares most favorably in size and shape with the posterior thoracic vertebrae of *Pelocetus* (Kellogg, 1965). The taxonomy of Miocene mysticetes remains in flux (Bouetel, 2005; Deméré et al., 2005; Steeman, 2007), but at least a questionable assignment to the Balaenopteroidea (Balaenopteridae plus stem taxa previously classified in the Cetotheriidae) is warranted.

### 4.2. *Gatun cetacean*

Based on the small width and thickness of the partial rib, it is most likely from an odontocete, rather than a mysticete. Cetacean ribs, even when complete, are not often diagnostic even to family, so no more particular identification can be made for this specimen.

### 4.3. *Culebra sirenians*

The Panamanian sirenian vertebra is most likely a third caudal based on: 1) absence of postzygapophyses, which are otherwise present in Ca1–2 of *Metaxytherium serresii*, although they could have been completely absent from the caudal region as in *Dusisiren jordani*; 2) presence of large anterior and posterior demifacets; Ca2

of *D. jordani* has weakly developed anterior and large posterior demifacets, whereas both pairs are large from Ca3 to 20; 3) laterally directed transverse processes as in Ca1–5 of *D. jordani* and *M. serresii* (Carone and Domning, 2007; Domning, 1978).

The posterior orientation of the spinous process is noteworthy. A strongly posteriorly oriented spinous process has only been described for *D. jordani* (Domning, 1978) but the Panamanian material seems to have been more extreme. In overall morphology USNM 534012 is most similar to Ca3 of *D. jordani* (Domning, 1978:pl.12c) with the main difference being that the former is about 35% smaller; its size (Table 2) is most similar to anterior caudals of *Metaxytherium krahuletzii* and *M. serresii* (Carone and Domning, 2007:table 8; Domning and Pervesler, 2001:table 12).

The vertebra cannot be assigned to known dugongines from northern or western South America. The dugongine *Nanosiren sanchezii*, from the Late Miocene of Venezuela, and *Nanosiren* sp. from the Late Miocene of Perú and Chile (Domning and Aguilera, 2008), are remarkable for their small size; known caudals are much smaller than USNM 534012. The caudal series is still unknown for the other larger Western Atlantic and Caribbean dugongines such as *Dioplotherium* spp., *Corystosiren varguezi* and *Xenosiren yucateca* (Domning, 1989a,b, 1990).

Two halitheriines are well known from the eastern Pacific, *Metaxytherium crataegense* and *Metaxytherium arctodites*, the former from the Miocene of the Western Atlantic and Caribbean as well as the Early to Middle Miocene of Perú (Aranda-Manteca et al., 1994; Kellogg, 1966; de Muizon and Domning, 1985; Simpson, 1932; Varona, 1972) and the latter known from the Middle Miocene of Baja California and California (Aranda-Manteca et al., 1994). These two halitheriines are large enough to have had anterior caudal vertebrae similar in size to USNM 534012; unfortunately, the caudal series of these species remains poorly known. A third halitheriine from Early Miocene deposits of Oregon is known only from fragmentary cranial material (Domning and Ray, 1986).

The halitheriine *Metaxytherium floridanum* from Middle Miocene deposits in Florida, was similar in size to *M. crataegense* and *M. arctodites* (Aranda-Manteca et al., 1994; Domning, 1988). Comparison with the Panamanian vertebra is not possible as the caudal series of *M. floridanum* is incompletely known (Domning, 1988). In addition, *M. floridanum* is found in younger deposits than USNM 534012, and it has yet to be recorded outside of Florida (Domning, 1988).

Middle to Late Miocene hydrodamalines from California and Baja California include *Dusisiren reinharti* and *D. jordani*. The first is poorly known due to the fragmentary nature of the holotype, and the latter, as mentioned above, had anterior caudals much larger than the Panamanian vertebra (Domning, 1978). In addition, hydrodamalines seem to have been restricted to the North Pacific, possibly restricted by geographic barriers that prevented them from going further south than Baja California (Domning, 1978). The dugongine *Dioplotherium allisoni*, also from the Middle Miocene of California and Baja California, is known mainly from cranial material (Domning, 1978; Kilmer, 1965), and was nearly as large as *D. jordani* (pers. obs.) and probably also restricted to this region.

Affinities with manatees (Trichechidae) can be completely ruled out, as the spinous processes of their caudal vertebrae are very short (Buchholtz et al., 2007). In addition, the earliest trichechid

**Table 2**

Measurements of sirenian vertebra USNM 534012. All measurements are in millimeters. (e = estimate).

Breadth across transverse processes	Posterior breadth of centrum	Height of centrum in midline	Thickness of centrum in midline	Width of neural canal	Height of neural canal
220e	80	60	59	20	15

fossils from the Americas are those of *Potamosiren magdalenensis*, found in freshwater deposits from the Middle Miocene of Colombia, and it seems to have been restricted to freshwater habitats (Domning, 1997, 2001).

Of the dugongids discussed above, the halitheriine *M. crataegense* is of special interest. The Early Miocene occurrence, widespread distribution (Western Atlantic, Caribbean and Eastern Pacific regions), and size of this species make it a likely candidate for the Panamanian material. Furthermore, *M. crataegense* has been proposed as giving rise, in the Pacific, to *M. arctodites* and the hydrodamalines (Aranda-Manteca et al., 1994; Domning, 2001; de Muizon and Domning, 1985), this will imply dispersion of this taxon from the Caribbean towards the Pacific through the Central American Seaway (CAS). Alternatively, the vertebra could belong to a dugongine, which were present in the West Atlantic and Caribbean region, and must have also crossed the CAS, based on the occurrence of *D. allisoni*, at least during or prior to the Middle Miocene. Unfortunately, the lack of comparative material prevents us from designating USNM 534012 to any known taxa further than Dugongidae genus and species indeterminate.

Rib fragments from both the lower and upper Culebra Formation are consistent with identification as dugongid sirenians. Based on their size, some of the upper Culebra ribs (FLMNH 244758 and 249195) seem to correspond to a smaller sirenian species than that represented by the vertebra (USNM 534012). These ribs are small when compared with the smallest, rib 20, of *M. crataegense* (USNM 16757 (Kellogg, 1966)), which is a sirenian of comparable size to the one represented by USNM 534012 (see above). FLMNH 244758 and 249195 are actually closer in size to ribs of *Nanosiren* sp. (USNM 16630). This indicates that at least two sirenians are present in the upper Culebra Formation; the vertebra representing a sirenian in the size range of *M. crataegense* whereas the ribs representing a smaller form similar to *Nanosiren* sp. Fossils assigned to *Nanosiren* are known from Early Miocene deposits of the Western Atlantic, Caribbean and southeastern Pacific. It is possible that these upper Culebra ribs represent a member of this group. However, identification beyond the family level is not possible due to the lack of diagnostic characteristics, other than its small size.

FLMNH 249198 from the upper Culebra Formation has an open medullary cavity. Most sirenians have compact medullary cortex (de Buffrénil et al., 2010), this could indicate that FLMNH 249198 belonged to a juvenile and complete bone remodeling of this area had not been completed yet.

Little can be said of the lower Culebra Formation ribs other than they belong to a sirenian, most likely a dugongid. The most complete ribs from the lower Culebra (FLMNH 249196) seem to represent a dugongid taxon larger than the one represented by the upper Culebra ribs, however, due to the fragmentary nature of the former, it is uncertain to know if this was really the case or not.

## 5. Conclusions

The whale vertebra and partial rib described here represent the first cetacean fossils known from Panama, and only the second and third described from all of Central America. Unlike sirenians, cetacean fossils are not well known in the Caribbean region from any time period. This discovery of whale fossils, while preliminary, suggests that further exploration in the area is warranted to help understand the distribution of whale taxa, particularly exchange of cetacean taxa between the Atlantic and Pacific Oceans during the Miocene, which is as yet poorly understood.

The sirenian specimens represent the first records of dugongids from the southern part of Middle America. Fossil dugongids are well known from the Miocene to Pliocene of the northern and southeastern Caribbean region. The Panamanian dugongid offers

the earliest record of a dugongid from the southwestern Caribbean and offers some evidence of the dugongids that inhabited this region and potentially the southeastern Pacific during the Early Miocene. At least two different sirenians were present in the upper Culebra Fm., which is consistent with having multispecies communities as in other regions of the Western Atlantic and Caribbean (Domning, 2001). Future efforts should be directed towards finding additional material in this region that will help shed light on the true affinities of these dugongids. Increased knowledge about the sirenians from this region will be of great benefit to our understanding of sirenian dispersal from the Caribbean towards the Pacific, and could even clarify the origins of the sirenians (dugongines, halitheriines and hydrodamalines) that later inhabited the Eastern Pacific.

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