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Shark-cetacean trophic interactions during the late Pliocene in the Central Eastern Pacific (Panama)

Dirley Cortés, Carlos De Gracia, Jorge D. Carrillo-Briceño, Gabriel Aguirre-Fernández, Carlos Jaramillo, Aldo Benites-Palomino, and Joaquín Enrique Atencio-Araúz

ABSTRACT

We provide a description of the remains of a fossil whale from western Panama. The record consists of appendicular remains of a mysticete, which has been assigned to Balaenopteridae. These remains, found in the sediments of the late Pliocene Burica Formation, represent the first record of a marine mammal in the Neogene sedimentary succession of the Burica Peninsula. Two different types of shark bite marks, serrated and deep-unserrated, found on the radius and phalanges suggest scavenging by at least two white shark (*Carcharodon*) individuals. The deep, unserrated marks were possibly caused by continual biting by sharks. Both the morphology of the shark bite marks and their relative location on the whale limb bones constitute evidence of shark-cetacean trophic interaction. Although the specimen lacks diagnostic features that would allow a species-level identification, it does provide new information on the vertebrate fauna of a very poorly prospected Central Eastern Pacific exposure, thus opening an opportunity for exploring the marine fauna during a critical episode in Earth history, the Plio-Pleistocene transition.

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INTRODUCTION

Baleen whales (Mysticeti) are a diverse group of filter-feeding cetaceans that includes the largest extant marine mammals (e.g., Tsai and Kohno, 2016; Marx and Kohno, 2016; Slater et al., 2017; Fordyce and Marx, 2018). As already highlighted elsewhere (Aguirre-Fernández et al., 2017), except for the Pisco Formation in Peru (e.g., Bianucci et al., 2016a, 2016b; Di Celma et al., 2017), the fossil record of cetaceans from the Neotropics is poorly studied compared to that from higher latitudes. Balaenopterid mysticetes have been reported in Neogene and Quaternary sequences worldwide from the early late Miocene to the late Pleistocene (Bisconti, 2010). The earliest fossil balaenopterid comes from the early late Miocene (~7–10 Ma) of the North Pacific Ocean (Deméré et al., 2005). Pliocene balaenopterid records include several occurrences from the early Pliocene (Zanclean) of Antwerp, Belgium (van Beneden, 1882) and the late Pliocene (Piacenzian) of California, USA (Deméré, 1986), Italy (Deméré et al., 2005), northern Chile (Dathe, 1983; Bisconti, 2010), and southern Nicaragua (Lucas et al., 2009). Although some Pliocene remains have been reported for the Pisco Formation of northwestern Peru (e.g., de Muizon and DeVries, 1985; DeVries, 1988), the Pliocene strata of the Pisco Formation are now generally regarded as late Miocene, e.g., Ehret et al. (2012). Pleistocene records have been reported mainly from Peru (Martínez and Jacay, 2000), Ecuador (Bianucci et al., 2006), and North America (Miller, 1971; Barnes and Mitchell, 1975; Tsai and Boessenecker, 2017), including the Champlain Sea, Canada (Harington, 1977), Florida (Morgan, 1994), California (Barnes and Mitchell, 1975), and Georgia, USA (Noakes et al., 2013).

Shark-cetacean trophic interactions have been widely reported from the fossil record (e.g., Deméré and Cerutti, 1982; Bianucci et al., 2000, 2010; Ehret et al., 2009; Godfrey et al., 2018, and references therein) including traces deriving both from active predation and scavenging (e.g., Ehret et al., 2009; Govender and Chinsamy, 2013; Collareta et al., 2017; Bianucci et al., 2018; Godfrey et al., 2018). For instance, Aguilera et al. (2008) described a cetacean lumbar vertebra pierced by a tooth of *Carcharocles megalodon* from the Miocene of Venezuela (Carrillo-Briceño et al., 2016), and Ehret et al. (2009) described a scavenging event by a *Carcharodon* sp. on a mysticete whale from the Pliocene of the Pisco Formation in Peru. Postmortem tooth marks by sharks on cetacean bones have been reported from the early Pliocene western coast of South Africa where *Carcharodon* sp. was identified as a potential predator (Govender and Chinsamy, 2013; Govender, 2015). Likewise, shark tooth marks found on both the ulna and the radius of a balaenopterid cetacean from the Miocene of Argentina were indicative of scavenging or predation (Noriega et al., 2007).

Herein, we report the first record of a balaenopterid mysticete from the late Pliocene (Piacenzian-Zanclean) sediments of the Charco Azul Group in the Burica Peninsula, western Panama, and discuss the ecological implications of several shark bite marks found on the specimen.

STUDY AREA AND GEOLOGICAL SETTING

The Burica Peninsula straddles the border between Panama and Costa Rica along the Tropical Eastern Pacific (Figure 1.1). This region was uplifted recently following the subduction of the Cocos ridge underneath the Panama microplate (Baumgartner et al., 1989; Mora et al., 1989; Corrigan et al., 1990). The collision, which began in the late Pleistocene (uplift rates of 1–8 m ka^{-1}) (Leon-Rodriguez, 2007) and continues today (2–3 m ka^{-1}) (Davidson, 2010), produced a rapid uplift, elevating the Talamanca Range to 4000 m (Coates and Obando, 1996; Coates, 1997). That allowed

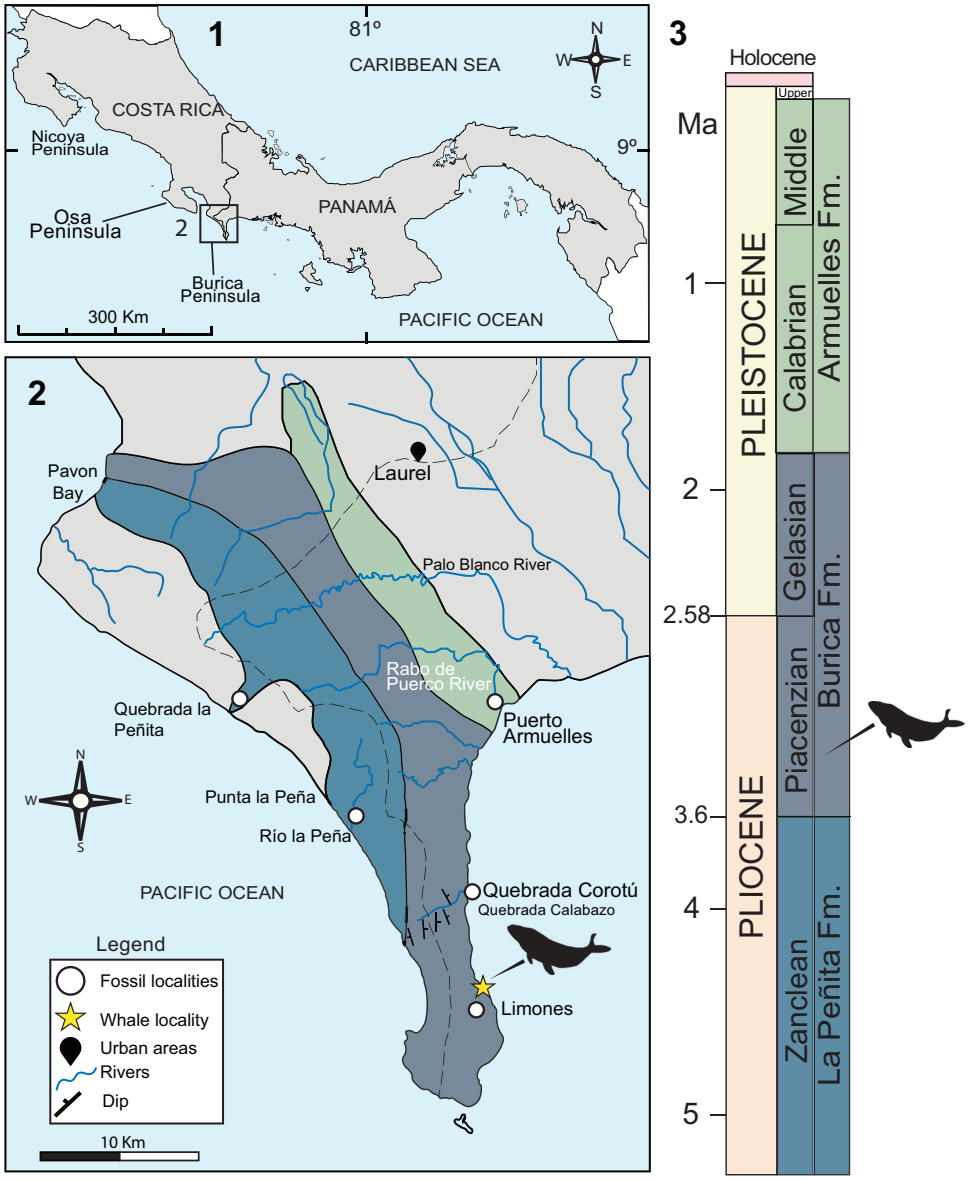

FIGURE 1. Geological setting of the find. **1,** Map of Central America, showing the Burica Peninsula. **2,** Geological map of the Burica Peninsula, indicating the fossil locality. **3,** Schematic chronostratigraphic section, showing the approximate position of the whale remains. Map modified from Coates et al. (1992); ages from Corrigan et al. (1990) and Schwarzhans and Aguilera (2013). Ma: million years; Fm., Formation.

the Charco Azul Group to become exposed subaerially in the Burica Peninsula (Figure 1.2) (Corrigan et al., 1990; O'Dea et al., 2012). The Charco Azul Group is a 4500 m thick succession of marine sediments (Olsson, 1942; Coates et al., 1992; O'Dea et al., 2007) comprising the Peñita, Burica, and Armuelles Formations (Leon-Rodriguez, 2007; De Gracia et al., 2012) (Figure 1.3).

The fossil material described herein was found in a coastal outcrop near Quebrada Calabazo creek in Playa Limones (geographic coordinates: 8°08'53.6"N, 82°52'27.4"W) (Figure 1.2). The strata containing the fossil belong to the Burica Formation, which is 2800 m thick and dominated by volcaniclastic turbidites. Dated as late Pliocene to middle Pleistocene (Corrigan et al., 1990; Coates et al., 1992; Leon-Rodriguez, 2007) (Figure 1.3), the Burica Formation is divided into two members (Coates et al., 1992; O'Dea et al., 2012; De Gracia, 2015). The balaenopterid specimen (Figure 2) was found in the late Pliocene lower member, which was deposited at water depths around

2000 m and consists of coarse-grained proximal turbidites (Corrigan et al., 1990; Collins et al., 1995; Leon-Rodriguez, 2007; O'Dea et al., 2007). Based on the stratigraphic column of Leon-Rodriguez (2007) and the geographic location of the site, the approximate stratigraphic position of the fossil is in the lower part of the lower member of the Burica Formation (~700 m above the base of the 2800 m thick formation).

The specimen was collected in a poorly consolidated, fine-grained green glauconitic siltstone with abundant mollusks, echinoids, and crustacean remains.

METHODS AND REPOSITORIES

The balaenopterid remains are represented by a partial right forelimb belonging to a single individual, consisting of the ulna, radius, five carpals, two metacarpals, three phalanges, and one indeterminate bone fragment (Figures 2-3). This specimen was recovered in 2016 under low-tide conditions by Joaquín Atencio and members of the local community (Félix Orocú and Joel Orocú). An isolated white shark tooth (*Carcharodon carcharias*, Figure 3.5) was found near the cetacean remains. The specimens are housed in the Universidad de Panamá, Panama, in two different collections. The balaenopterid specimen is housed in the Colección Nacional de Referencia de Mastozoología del Museo de Vertebrados, under collection number MNUP-1795. The white shark tooth (*C. charcarias*) is housed in the Museo de Biología Marina y Limnología, under collection number MBML-CF01. We followed the terminology of Deméré et al. (2005), Cicimurri and Knight (2009), Ehret et al. (2009), Bianucci et al. (2010), Bisconti (2010), and Marx et al. (2016) to describe the balaenopterid bones and the shark bite marks.

SYSTEMATIC PALEONTOLOGY

Order CETACEA Brisson, 1762
Suborder MYSTICETI Flower, 1864
Family BALAENOPTERIDAE Gray, 1864
Balaenopteridae gen. et sp. indet.
Figures 2-3, Table 1

Referred Material

MNUP-1795 consists of a partial right forelimb measuring 184 cm in length. A very incomplete fragment found near the radius cannot be identified but may be what remains of the humerus. The ulna and radius were not articulated in their anatomical position. Part of the carpals are also preserved, including five oval-shaped bones. Only two metacarpals and three phalanges are preserved, the latter being strongly eroded. The bones are highly porous on their surfaces, and several shark bites are recognizable on some of them (Figure 3).

Age and Type Locality

Sediments collected by Corrigan et al. (1990), where the whale was found, have been dated as late Pliocene by planktic foraminifera zones N18/N19, by the presence of *Globorotalia margaritae* Bolli and Bermúdez, 1965, and contain the calcareous nannofossil *Reticulofenestra pseudoumbilica* Gartner, 1969, Zanclean–Piacenzian in age. Dating follows the Neogene biostratigraphy provided in Hilgen et al. 2012 (figure 29.8 and 29.10).

Taphonomy

The specimen was found in the tidal zone of the Limones beach and was partially exposed by wave erosion; no other cranial or postcranial elements have been found yet. All elements have a light brown color, and on the radius and two phalanges, clear shark bite marks are recognizable. The presence of this isolated and partially preserved forelimb suggests that the carcass was consumed by scavengers, including sharks. Scavengers could have disarticulated the forelimb from the skeleton; it would then have sunk and been buried by sediments. Before the elements were buried, however, they remained exposed on the seafloor, as indicated by the presence of bryozoans and serpulids covering the exposed areas and bite marks (Figure 3.1-4).

Description

Ulna. The ulna is elongated but shorter than the radius. The proximal end of the ulna is broken. The posterior margin is more concave than the anterior. The olecranon process is present, but broken in dorsal view. The dorsal surface of the ulna is more convex than the ventral one. The ulna is as wide in the mid part of the diaphysis as it is at the proximal epiphysis. The proximal epiphysis of the ulna is circular in cross section, whereas the distal epiphysis is very oval in shape (flattened and wider than the proximal end). There is a process on the anterodistal margin of the ulna. A small anterior process begins on the proximal metaphysis of the ulna. On the distal end, a deep and very rough surface forms the articulation facet for the carpal (Figure 2.2).

Radius. The radius is elongated, with a straight anterior border and a slightly concave posterior

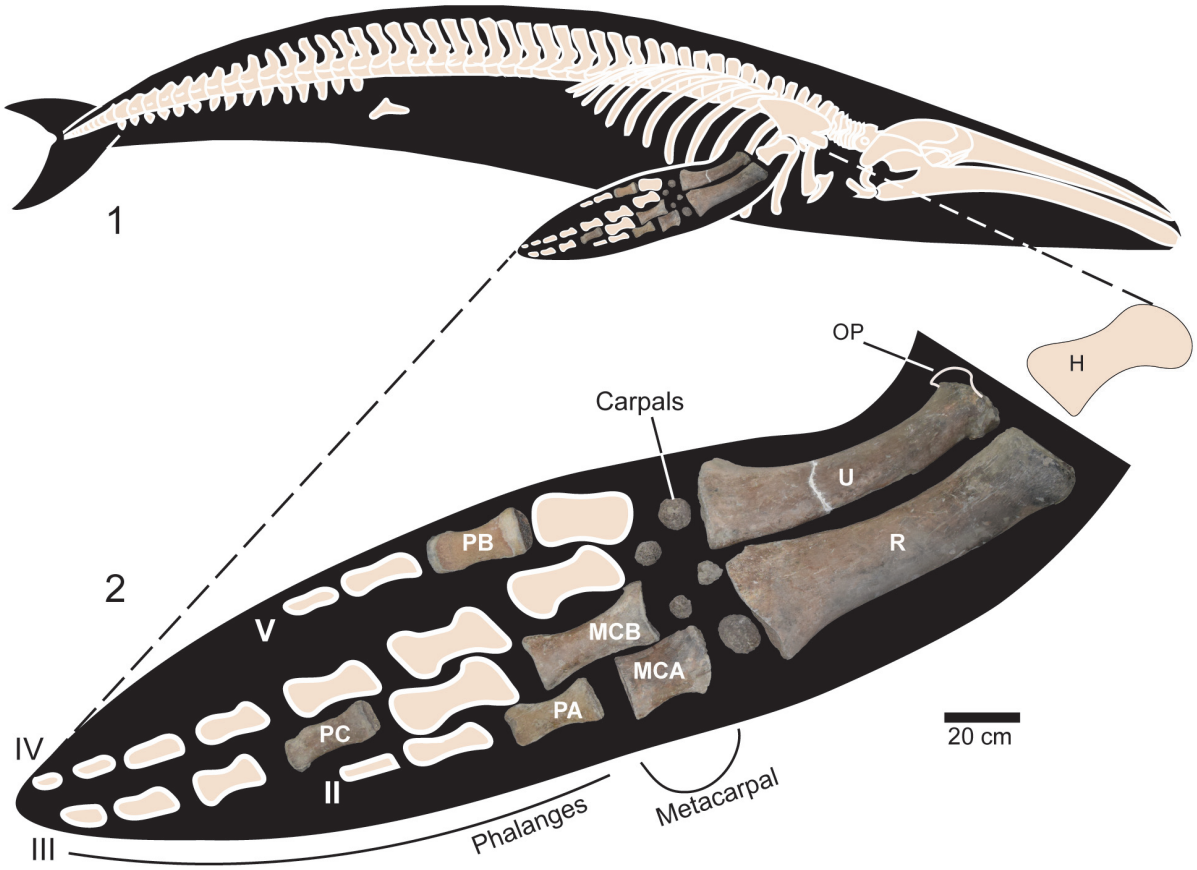

FIGURE 2. 1, Right lateral view of the skeleton of a generalized mysticete whale (modified from Marx and Fordyce, 2015; Marx et al., 2016). **2,** Dorsal view of the reconstructed forelimb of specimen MNUP-1795 from the late Pliocene of Panama. Abbreviations: H, humerus; MCA, metacarpal A; MCB, metacarpal B; OP, olecranon process; PA, phalanx A; PB, phalanx B; PC, phalanx C; R, radius; U, ulna. Roman numerals indicate the digits of the right forelimb.

border. The distal end is wider than the proximal one (Table 1). The proximal facet for the carpals is very straight. Because the distal end is broken, the features of the distal facets cannot be assessed. In distal view, the epiphysis of the radius is less oval than that of the ulna. The proximal end of the radius is significantly more robust than the proximal end of the ulna. The posterodorsal surface of the radius displays several shark bites traces. The dorsal surface of the radius is more convex than the dorsal surface of the ulna (Figure 2.2).

Carpals. Five elements are identified as carpal bones based on their oval shape. The diameter of the carpals varies between 6 and 9 cm (Figure 2.2).

Metacarpals. Because of the highly disarticulated condition of the bones, the natural position of the metacarpals cannot be assessed with confidence. However, given the small size and the anterior curvature along the shaft of metacarpal A (Figure 2.2), it might be metacarpal 2 or metacarpal 5. The proximal facets of the metacarpals are very deep. Metacarpal B is eroded on the distal end but some features can be identified: metacarpal B is longer but thinner than metacarpal A (Figure 2.2); the proximal facet for articulation with the corresponding carpal is very deep and rough; a flat process is present on the proximal dorsal border of metacarpal B; the posterior margin of metacarpal B is as curved as the anterior one and has a cleavage along its shaft.

Phalanges. Three bony elements were identified as phalanges (Figure 2.2). Phalanx A is flat and long with a large process on the distal anterior ramus. Phalanx B is the most massive. Phalanx C is equally curved on its anterior and posterior margins. The position of the phalanges in the diagram was based on the relative sizes of the preserved elements. However, neither natural position nor distance between elements can be assigned with

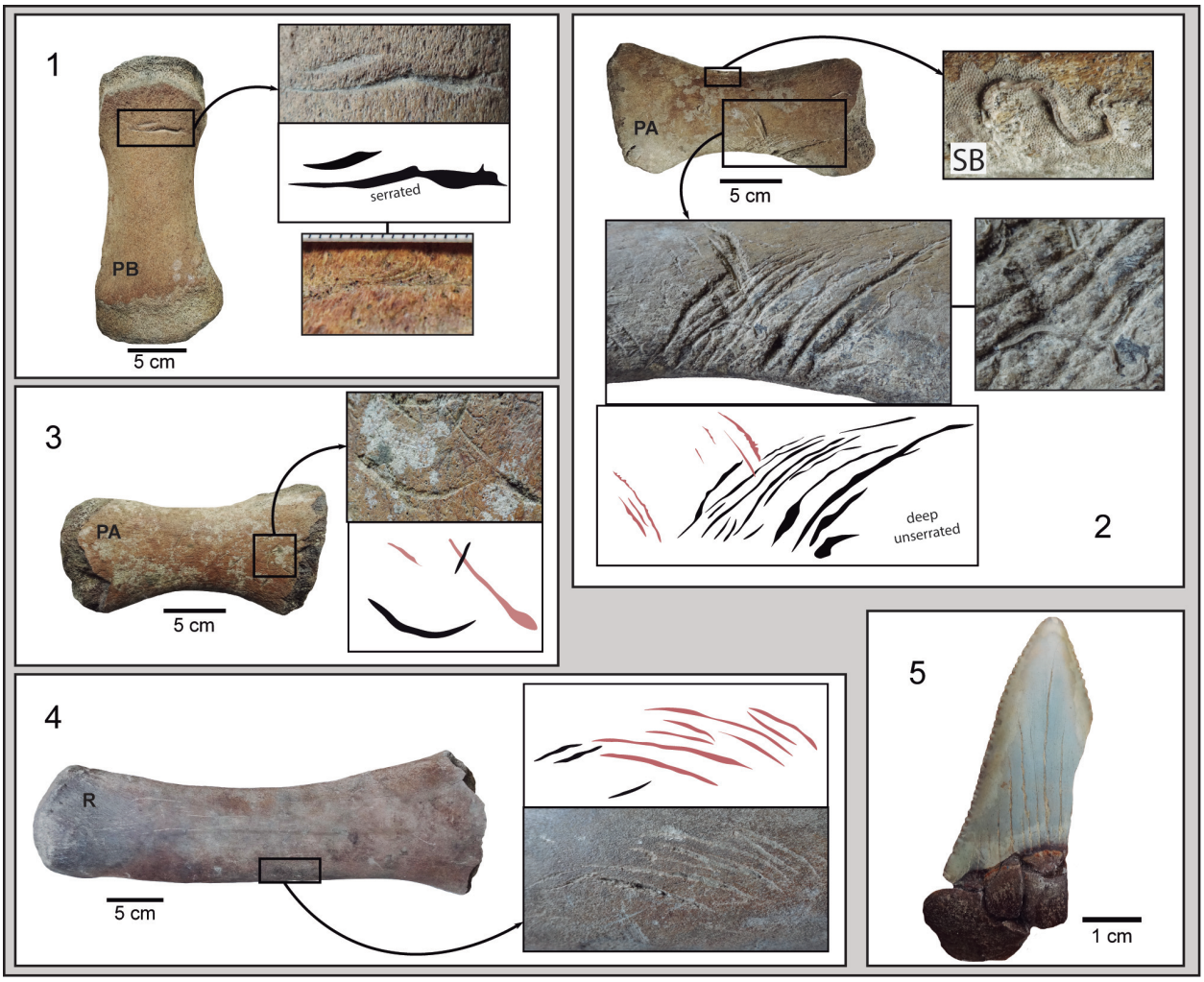

FIGURE 3. Balaenopterid and shark remains from the late Pliocene of Panama. **1-4,** Bones affected by shark bite marks, with close-up photographs and line drawings of the incisions (**1-3**: phalanges; **4**: radius). SB = Serpulids and bryozoans covering the surface of the fossil bones and partly draping the underlying bite marks. **5,** *Carcharodon carcharias* tooth (MBML-CF01) found near the cetacean remains. Abbreviations: PA, phalanx A; PB, phalanx B; R, radius. Colors on bite marks line drawings indicate the differentiation of the bite damages by two potential and different-sized conspecific shark individuals.

confidence because the bones lack diagnostic features and clues about articulation.

Remarks

The specimen MNUP-1795 is identified as belonging to Balaenopteridae based on a number of characters of the forelimb bones, including a radius and ulna remarkably elongated and flattened (Bisconti, 2010) and hourglass shaped; proximal epiphyses on both ulna and radius; and lack of metacarpal I and digit I (following the proposed interpretation of the original position of the bones).

Shark bite marks are recognizable on the radius and on two of the phalanges, i.e., phalanx A and phalanx B (Figure 3.1-4). There are two types of bite marks preserved, unserrated, and serrated. Unserrated marks are found on both phalanx A and the radius (Figure 3.2-4). Phalanx A reveals 26 bite marks on both its medial and lateral faces, the longest being 70 mm long; the marks are deep (~3–5 mm) and wide (~2–4 mm) with parallel and cross-hatched patterns, mostly clustered at the margin of the bone (Figure 3.2). Besides these, eight shallow marks can be discerned in the anterior margin of the diaphysis almost at the midpoint of the radius (Figure 3.4). The marks are oriented roughly parallel to each other, the longest being 140 mm long.

A second type of bite mark is present on the distal section of phalanx B (Figure 3.1). In phalanx B, two short but deep marks are seen running par-

TABLE 1. Measurements of the balaenopterid fin elements, specimen MNUP-1795, lower Burica Formation, Panama.

Measurements	cm
Maximum length of the radius	84
Maximum width of the radius	23
Anteroposterior width of the proximal end of the radius	23
Anteroposterior width of the distal end of the radius	33
Dorsoventral height of the proximal end of the radius	19
Dorsoventral height of the distal end of the radius	15
Length of the ulna	79
Maximum width of the ulna	31
Anteroposterior width of the proximal end of the ulna	20
Anteroposterior width of the distal end of the ulna	28
Dorsoventral width of the proximal end of the ulna	14
Dorsoventral width of the distal end of the ulna	9
Minimum diameter of metacarpal A	9
Minimum width of metacarpal A	15
Minimum diameter of metacarpal B	6
Minimum width of metacarpal B	11
Length of metacarpal A	29
Length of metacarpal B	23
Length of phalanx A	24
Length of phalanx B	24
Length of phalanx C	22

allel to each other; the longer of these two marks is 50 mm long, and it shows several millimeter-long serrations.

DISCUSSION

The fossil record of the Burica Formation includes foraminifera, mollusks, crustaceans, fish otoliths, and shark teeth (Olsson, 1942; Corrigan et al., 1990; Collins et al., 1995; De Gracia et al., 2012; De Gracia, 2015; Carrillo-Briceño et al., 2018, table S6). The record presented here represents the first occurrence of mammal remains from this succession.

Prior to this work, the only record of a mysticete for the Neogene of Central America consisted of 14 vertebral centra, one humerus, and 10 incomplete ribs from a single individual from the El Santo Formation (Pliocene) in southern Nicaragua (Lucas et al., 2009). Here we add a second record. Although the size of a whale's skull can provide a good estimate of body size (Pyenson and Sponberg, 2011; Lambert et al., 2010), forelimb measurements, in contrast, are unreliable measures of body size. For example, the fin of a humpback whale (~89 cm) is somewhat longer than that of a blue whale (~81 cm), but its body length is considerably shorter than a blue whale's (~16 m vs. 27 m) (Johnson and Wolman, 1984; Aguilar, 2009). Thus, we cannot estimate the body size of our specimen.

The shark bite marks indicate either active predation or scavenging. Neogene cetacean remains have been found with the bite marks of top predator sharks such as *Carcharocles* spp. and *Carcharodon* (e.g., Bianucci et al., 2000; Aguilera et al., 2008; Ehret et al., 2009; Bianucci et al., 2010; Godfrey et al., 2018, and references therein). Shark predation on mysticete whales is rarely reported, but it may occur more often than previously thought. Dicken et al. (2015) reported the first direct observation of dusky sharks (*Carcharhinus obscurus*) attacking a humpback whale calf during the annual sardine run off South Africa.

However, sharks often scavenge large mysticete whales while hunting smaller odontocetes (Govender and Chinsamy, 2013; Govender, 2015), and the balaenopterid whale from the Burica Formation of Panama was probably not killed by active predation. Cetacean carcasses are an energy-rich food source for sharks (Long and Jones, 1996; Bornatowski et al., 2012; Anderson and Bell, 2014). *Carcharodon carcharias* is known to feed on a floating carcass over several days, with observations of scavenging by lone individuals (Fallows et al., 2013; Dicken et al., 2015) or by two individuals simultaneously (Curtis et al., 2006). Considering the similarity of the two types (serrated and unserrated) of shark-bite marks preserved, it is possible that they were made by two different-sized conspecific shark individuals (e.g., *C. carcharias*), who scavenged on the same mysticete carcass. Serrated traces with a similar morphology, produced by *Carcharodon carcharias*, have been described on dolphin remains from both the Pliocene and the Holocene (Cigala-Fulgosi, 1990; Schouten, 2017), suggesting that marks in MNUP-1795 are those of a white shark *(C. carcharias).* A similar incident of scavenging on a balaenopterid-whale skeleton from the late Miocene Pisco Formation (Peru) was reported as having been produced by two different-sized individuals of *Cosmopolitodus hastalis* (Takakuwa, 2014). Several clues support the conclusion of scavenging (e.g., Cigala-Fulgosi, 1990; Govender and Chinsamy, 2013; Govender, 2015): 1) the combination of both superficial and deep marks (Figure 3.3-4 vs. 3.1-2), which are probably the

result of the whale and sharks being moved by currents and wave activity; 2) the presence of lateral-medial bite marks on the bones; 3) the presence of very deep unserrated marks, suggesting the shark was biting repeatedly over the same area. Overall, the marks in the whale bones of MNUP-1795 are more likely an event of scavenging by sharks on the whale from Panama rather than an event of active predation.

The fossil record of marine mammals in the Burica Formation of Panama has been improving over the past 10 years. Recent discoveries include a cetacean thoracic vertebra (Tobabe Fm.) (Uhen et al., 2010), a partial cetacean rib (Miocene Gatun Fm.) (Uhen et al., 2010), a sirenian caudal vertebra and rib fragments (Miocene Culebra Fm.) (Uhen et al., 2010), dental remains of a sperm whale (Vigil and Laurito, 2014), skull and post-cranial elements from a new inioid odontocete, *Isthminia panamensis* (Mio-Pliocene Chagres Fm.) (Pyenson et al., 2015), a new kogiid odontocete, *Nanokogia isthmia* from the Caribbean side of the isthmus (Mio-Pliocene Chagres Fm.) (Vélez-Juarbe et al., 2015), and a dugongine *Culebratherium alemani* (Miocene Culebra Fm.) (Vélez-Juarbe and Wood, 2019). This new study of a Pliocene cetacean adds to the understanding of marine mammals of the tropical Americas.

The generic diversity of cetaceans, and especially mysticetes, declined around the Pliocene-Pleistocene boundary (Marx et al., 2016), an example of a global turnover event in the marine megafauna (Valenzuela-Toro et al., 2013). This turnover may have been driven by a global reduction of neritic areas (Pimiento et al., 2017), although additional marine megafaunal turnovers may have occurred well into the Pleistocene (e.g., Boessenecker, 2013; Tsai et al., 2017). Fossil marine mammals, like the one preserved here, will be useful for understanding the dynamics of the marine fauna in one of the most critical periods of Earth history, the Plio-Pleistocene transition.

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