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RESEARCH ARTICLE

Cold-water diving in the tropics? External auditory exostoses among the pre-Columbian inhabitants of Panama

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Abstract

Objectives: The appearance of external auditory exostoses archaeologically has been attributed to aquatic activities in middle latitudes. However, recent clinical research implicates low sea surface temperatures, especially below a threshold of 19°C, as a stronger predictor of ear exostosis development than latitude. Here, we examine the frequency of external auditory exostoses in human remains from nine pre-Columbian archaeological sites in Panama, representing individuals from a warm, tropical region.

Materials and methods: External auditory exostoses were recorded as present when an abnormal bony growth was observed macroscopically within the ear canal. The presence of exostoses was compared by right and left side, geographical region, sex, and degree of stenosis.

Results: A total of 125 adult individuals made up the observable sample analyzed in this study. Exostoses were observed in seven males and one female. All individuals affected by this pathology were excavated from mortuary contexts along the Gulf of Panama—a region characterized by intense cold water upwelling in the dry season.

Discussion: This study suggests that external auditory exostoses in pre-Columbian Panama affected individuals involved in habitual aquatic activities in the cold, upwelled waters of the Gulf of Panama. These activities appear to be almost exclusively dominated by male individuals. Ethnohistorical and archaeological records point to marine shell resource acquisition by deep-water diving as the activity driving exostosis development in pre-Columbian Panama.

KEYWORDS

activity markers, auditory exostosis, diving, Panama, upwelling

1 | INTRODUCTION

External auditory exostoses (EAE) have affected populations of humans and their ancient hominin relatives dating back to the late Pleistocene (Boule, 1911; Trinkaus & Villotte, 2017). The exact pathophysiology leading to the formation of these abnormal bony outgrowths of the ear canal has never been proven conclusively (Ito & Ikeda, 1998; Ortner, 2003). Nevertheless, a consensus exists among the medical community that there is a relationship between EAE development and cold-water activities—a relationship observed repeatedly in clinical and archaeological contexts. The so-called "thermal aquatic hypothesis" of EAE formation (*sensu* DiBartolomeo, 1979) implicates increased vascular tension of the periosteum within the ear canal provoked by thermal irritation—by either cold water or the evaporative cooling effect of combined water and wind (Kennedy, 1986; King et al., 2010; Okumura, Boyadjian, & Eggers, 2007b). Such repetitive inflammation of the periosteum is thought to stimulate a chronic osteogenic reaction, resulting in a lamellated periosteal reaction of the canal lumen, such as that shown to form in experiments involving repeated cold-water irrigation in the auditory meati of guinea pigs (Fowler & Osman, 1942; Harrison, 1962). Further, anecdotal support for this hypothesis comes from modern aquatic sportspeople reporting prevention of EAE development or progression through the use of earplugs (DiBartolomeo, 1979; Moore et al., 2010; Timofeev, Notkina, & Smith, 2004).

In clinical contexts, EAE are prevalent in individuals who participate in aquatic activities (Alexander, Lau, Beaumont, & Hope, 2015; Moore et al., 2010). Similarly, many reports of this pathology in the archaeological record come from coastal geographical areas characterized by cold temperatures (Kennedy, 1986; Standen, Arriaza, & Santoro, 1997). However, recent analyses of modern clinical data have shown that water surface temperature predicts EAE development more strongly than latitude in current populations (Fabiani, Barbara, & Filipo, 1984; Ito & Ikeda, 1998; Sheard, 2002; Sheard & Doherty, 2008).

Nonetheless, it is important to consider that EAE can also result from general otitis externa—an inflammation or infection of the ear canal not always caused by exposure to water (Godde, 2010; Hutchinson, Denise, Daniel, & Kalmus, 1997). Yet infectious causation of EAE, when present, likely comprises only a small proportion of the overall sample (Villotte & Knüsel, 2016). Archaeologically, occasional references to exostoses in the ear canals of the ancient inhabitants of tropical and subtropical regions underline the observation that cold atmospheric temperatures are not required in the formation of these extra bony accretions (Kennedy, 1986; Okumura, Boyadjian, & Eggers, 2006; Okumura, Boyadjian, & Eggers, 2007a; Okumura et al., 2007b; Velasco-Vazquez, Betancor-Rodriguez, Arnay-De-La Rosa, & Gonzalez-Reimers, 2000).

As demonstrated previously by several authors, the analysis of sex differences in individuals affected by EAE permits a view into cultural activities that exposed specific individuals to environmental conditions favorable for its development. Often, these aquatic activities were dominated by male individuals, as is the case with modern-day surfers, kayakers, and free divers. Only in a few sites has EAE been found to be roughly equal between the sexes or more common in females (Pietrusewsky, 1984; Standen et al., 1997; Velasco-Vazquez, Betancor-Rodriguez, Arnay-De-La Rosa, & Gonzalez-Reimers, 2000).

Here, we provide the first report of EAE in several individuals from coastal pre-Columbian archaeological sites in Panama, located at latitudes between 10 and 7 degrees North of the equator, and characterized by tropical climates according to the Köppen climate classification system (Peel, Finlayson, & McMahon, 2007). Since the formation of EAE depends at least in part upon the temperature of the water and air, the presence of this pathology among the ancient inhabitants of the lowland tropics is somewhat surprising. Nevertheless, low seasonal sea surface temperatures in the Gulf of Panama caused by seasonal, wind-induced upwelling might have influenced the prevalence of EAE within these populations (D'Croz & O'Dea, 2007; O'Dea, Hoyos, Rodríguez, Degracia, & De Gracia, 2012; Robertson et al., 2009). A similar trade-wind-driven seasonal upwelling and cold-water current exist along the Pacific coast of South America (Montecino & Lange, 2009), where according to Kennedy's (1986) meta-analysis, the highest frequency of EAE in sites within 10 degrees of the equator were reported. These environmental factors are considered in this study, as well as potential contributing cultural factors such as diving for marine shells, and biological factors such as bacterial and fungal infections.

2 | MATERIALS AND METHODS

The samples used in this study consist of human remains excavated from mortuary precincts at pre-Columbian archaeological sites in Panama. Three sites were located between 5 and 16 km from the active shore of Parita Bay, which is a small northwesterly arm of the Gulf of Panama on the central Pacific coast of Panama. These sites are Cerro Mangote (CO-40), Sitio Sierra (AG-3), and Cerro Juan Díaz (LS-3). The mortuary activities at each of these sites occurred at different times during the Holocene (Cooke, Sánchez Herrera, Isaza Aizpurúa, & Pérez Yancky, 1998; Cooke, 1972; McGimsey, 1956; McGimsey, Collins, & McKern, 1966). Two sites—Playa Venado and Panama Viejo—lie near the active shoreline of Panama Bay, at the north-central edge of the Gulf of Panama (Smith-Guzmán et al., in press; Mendizábal, 2004; Martín, Rivera Sandoval, & Rojas Sepúlveda, 2009). Four sites located in western Panama provided one to two samples each for the present study. On the Pacific side, in the Gulf of Chiriquí, one sample comes from a site (JI-1) on the small island of Jicarita at the far southern end of the Coiba Archipelago (Isaza Aizpurúa, in press), and the other two samples were recovered from the site of La Pitahaya (IS-3) on the estuarine island of Palenque, Boca Chica (Linares, 1980b). Two samples come from the Bocas del Toro Archipelago on the northwest Caribbean coast of Panama. One, Cerro Brujo (CA-3), was a settlement located on a small island peninsula that separates the Almirante Bay from the Chiriquí Lagoon (Linares, 1980a; Linares de Sapir, 1971). The other, Sitio Drago (BT-IC-1), was located on the northwestern tip of Isla Colon (Wake, Doughty, & Kay, 2013). Figure 1 shows the location of each of these sites, as well as geographic features mentioned in the text. Table 1 lists the associated dates and locations of the human remains recovered from these sites, as well as the number of individuals and demographical characteristics of the observable sample used in this study.

2.1 | Climate and environmental conditions

Differences in topography, hydrology, and seasonal upwelling due to the flow of trade winds from the North to the South across the isthmus create four very different marine environments along and beyond the Caribbean, Gulf of Chiriquí, and Gulf of Panama coasts. Ecologists refer to the Isthmus of Panama as the "land of the four oceans" (Robertson et al., 2009), emphasizing the ecological differences between coastal areas bordering the Caribbean Sea and Pacific Ocean on the eastern and western sides of the country. The Caribbean coast along the eastern half of Panama offers warm, virtually tide-less and nutrient-poor conditions, whereas the western side of the same coast (i.e., the Bocas del Toro Archipelago) comprises similarly warm waters that are more turbid. On the Pacific side, the easterly waters of the Gulf of Panama are characterized by intense coastal upwelling in the dry season that brings cold water right up to the surface, whereas the (western) Gulf of Chiriquí contains a mild and deep upwelling zone. The Smithsonian Tropical Research Institute has been logging water temperature data at several places along Panama's coasts and islands since 1995. The data loggers record the striking difference in temperatures between these four marine environments, with temperatures in the Gulf of Panama standing in stark contrast to those in the Caribbean and Western Pacific (Figure 2). The lowest water temperatures recorded in the Caribbean Bocas del Toro and the Pacific Gulf of Chiriquí rarely sink below 24°C, whereas temperatures logged in the Gulf of Panama consistently drop to 15°C (Steve Paton, personal communication, May 23, 2018). The monthly average of daily minimum temperatures logged at Pacheca and Taboguilla Islands in the Gulf of

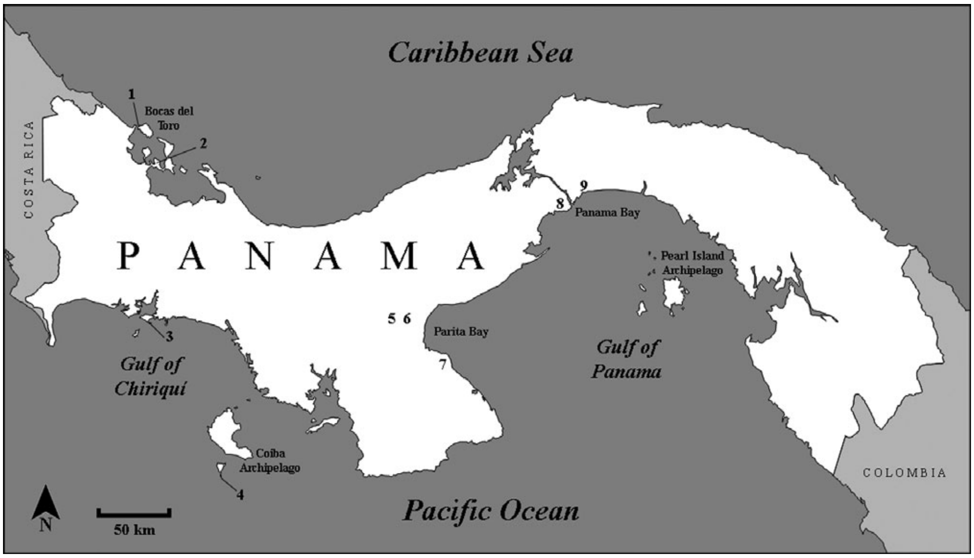

FIGURE 1 Map of Panama showing the location of archaeological sites from which the human remains used in this study were recovered. Sites are numbered as they appear on the map from west to east: 1: Sitio Drago; 2: Cerro Brujo; 3: La Pitahaya; 4: Jicarita; 5: Sitio Sierra; 6: Cerro Mangote; 7: Cerro Juan Díaz; 8: Playa Venado; and 9: Panama Viejo. Note that populations inhabiting sites along the eastern portion of the map (numbered 5–9) would have exploited the cold, upwelled waters of the Gulf of Panama, unlike the warm waters near the Western sites (1–4)

Panama hover below 19°C in the dry season months of February and March.

2.2 | Osteological analysis

The first author carried out a basic osteological assessment of the aforementioned skeletal samples used in this study. The age and sex of each skeleton was estimated preferably based on pelvic indicators for adults (Brooks & Suchey, 1990; Buikstra & Ubelaker, 1994; Lovejoy, Meindl, Pryzbeck, & Mensforth, 1985; Phenice, 1969). In the case that the pelvis was unobservable, cranial suture closure was used (Meindl & Lovejoy, 1985). For adolescents, dental development and epiphyseal fusion stages were used to determine age (AlQahtani, Hector, & Liversidge, 2010; Schaefer, Black, & Scheuer, 2009).

The first author recorded the presence or absence of EAE in adolescent and adult individuals within each site sample. Nonadults under 15 years of age were excluded from the study samples due to the low likelihood that these growths would form during childhood (Hrdlička, 1935; Paddock, Lau, Raghavan, & Dritsoula, 2018; Villotte & Knüsel, 2016). The clinically observed tendency for EAE to form principally after the first and before the seventh decades of life (Hrdlička, 1935, pp. 25–26) likely relates to the relatively higher participation in activity patterns for these age groups, as well as the time it takes from onset of repeated exposure (to the external ear canal irritant) to the formation of a macroscopically visible protuberance. The latter hypothesis is supported by lower rates of EAE formation in modern clinical cases of aquatic sportspeople practicing for less than 10 years (Alexander et al., 2015; Ito & Ikeda, 1998; Moore et al., 2010; Timofeev et al., 2004). Each individual was examined for visible protuberances within the external auditory meatus of each temporal bone separately. If an external auditory meatus was incomplete (i.e., at least partially fragmented) or absent, the bone was considered unobservable for the purposes of this study.

TABLE 1 Skeletal samples used in this study[a]

Site	Date[b]	Location	Female (%)	Male (%)	Indeterminate (%)	Total
Cerro Mangote	2475 BCE-317 CE	Gulf of Panama	12 (41)	17 (59)	0 (0)	29
Sitio Sierra (early)	41 BCE-379 CE	Gulf of Panama	7 (54)	6 (46)	0 (0)	13
Cerro Juan Díaz (early)	53–643 CE	Gulf of Panama	8 (42)	11 (58)	0 (0)	19
Playa Venado	138–556 CE	Gulf of Panama	11 (44)	12 (48)	2 (8)	25
Jicarita	670–800 CE	Gulf of Chiriquí	0 (0)	1 (100)	0 (0)	1
La Pitahaya	895–1021 CE	Gulf of Chiriquí	0 (0)	2 (100)	0 (0)	2
Sitio Sierra (late)	980–1155 CE	Gulf of Panama	4 (50)	4 (50)	0 (0)	8
Sitio Drago	892–1258 CE	Caribbean coast	0 (0)	0 (0)	1 (100)	1
Cerro Brujo	1265–1380 CE	Caribbean coast	0 (0)	0 (0)	1 (100)	1
Panama Viejo	435–1476 CE	Gulf of Panama	3 (12)	16 (62)	7 (27)	26
Total			45 (36)	69 (55)	11 (9)	125

[a] The sample sizes listed here include only individuals deemed observable for the purpose of this study (i.e., individuals over the age of 14 with at least one intact external auditory meatus).
[b] The dates listed are total 2σ ranges of radiocarbon dates from human collagen samples, calibrated with IntCal13.

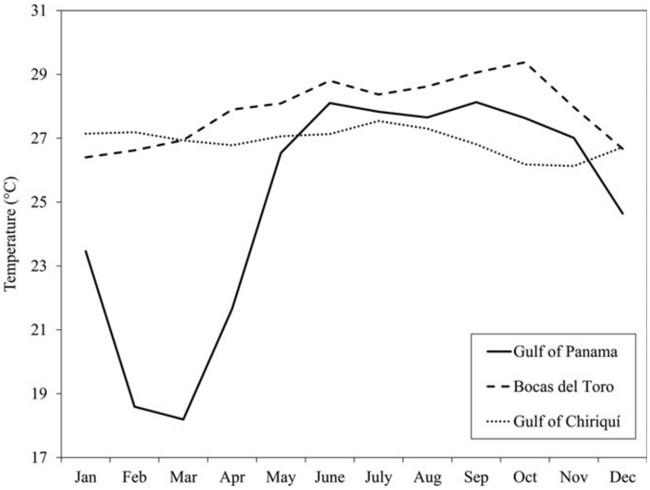

FIGURE 2 Monthly averages of daily minimum sea surface temperatures logged by underwater temperature sensors in the Gulf of Panama (Isla Taboguilla, 12 m, 1995–2017), Bocas del Toro (Isla colon, 9.1 m, 1999–2017), and the Gulf of Chiriquí (Isla Jicarita, 3 m, 2005–2014). Unpublished data sets provided by the physical monitoring program of the Smithsonian Tropical Research Institute. Used with permission of Steve Paton, director

3 | RESULTS

In total, 102 left and 109 right temporal bones made up the observable sample, which pertained to 125 individuals: 69 males, 45 females, and 11 individuals of indeterminate sex (see Table 1 and Table 2). The presence of EAE was observed in six left and six right temporal bones, comprising 5.9% of the observable sample for the left side and 5.5% for the right side, and pertaining to seven male individuals and one female (see Table 3). There was no statistical difference between EAE presence and side of the temporal bone affected. All the individuals affected by EAE pertain to archaeological sites in the Gulf of Panama. When considering the sample by sex, a clear predilection for male individuals emerged. The frequency of EAE for male individuals was 8.8% for the left side and 9.8% for the right. For females, EAE was much less frequent, affecting only 2.8% of left and no right temporal bones. None of the individuals of indeterminate sex showed signs of EAE development. The total prevalence of EAE was estimated for the 86 individuals in the total sample with both left and right auditory canals present and observable. This approach provides a more accurate estimation of prevalence as it eliminates the potential for false negatives (i.e., individuals marked as absent for EAE who could have had the lesion in a temporal bone that was damaged postmortem). Within this subsample, EAE was present in 3.3% of females, 12.2% of males, and 8.1% of all individuals from all sites combined (see Table 4). There were no significant differences between EAE presence and sex at any of the sites.

Analyzing a subset of individuals only from the coastal sites along the Gulf of Panama is warranted due to the likelihood that these individuals would have been exposed to seasonally lower oceanic water temperatures (see Figure 2). Furthermore, differences in preservation from these sites have resulted in a much larger sample size of individuals with at least one observable auditory canal from the Gulf of Panama (N = 120) as compared with combined samples from sites in Western Panama (N = 5). Within this subset, the six left and six right temporal bones affected by EAE represent 6.2% and 5.7% of the sample, respectively (see Table 2). Within male individuals from Gulf of Panama coastal sites, five left (9.3%) and six right (10.2%) were affected, whereas only one left female temporal bone was affected (2.8%). In individuals with both left and right ear canals observable from the Gulf of Panama sites (N = 82), EAE was present in 3.3% of females, 12.8% of males, and 8.5% in total (see Table 4).

In terms of the degree of stenosis, 50% of individuals with at least one ear affected by EAE had less than one-third of the auditory canal occluded (see Table 3). Three individuals had between one- and two-thirds of the canal occluded, and one individual had more than two-thirds occlusion (see Figure 3). In each of these occurrences of moderate to severe stenosis, the right side was affected. It is also notable that the sole female individual affected by EAE had the

TABLE 2 Frequencies of EAE per side within pre-Columbian sites in Panama

	Male		Female		Indeterminate		Total	
Site	Left	Right	Left	Right	Left	Right	Left	Right
Cerro Mangote	1/15 (6.7)[a]	1/12 (8.3)	0/9 (0.0)	0/11 (0.0)	0/0 (0.0)	0/0 (0.0)	1/24 (4.2)	1/23 (4.3)
Sitio Sierra (early)	0/6 (0.0)	1/6 (16.7)	0/5 (0.0)	0/4 (0.0)	0/0 (0.0)	0/0 (0.0)	0/11 (0.0)	1/10 (10.0)
Cerro Juan Díaz (early)	2/8 (25.0)	3/10 (30.0)	1/6 (16.7)	0/8 (0.0)	0/0 (0.0)	0/0 (0.0)	3/14 (21.4)	3/18 (16.7)
Playa Venado	1/8 (12.5)	0/12 (0.0)	0/9 (0.0)	0/11 (0.0)	0/1 (0.0)	0/1 (0.0)	1/18 (5.6)	0/24 (0.0)
Sitio Sierra (late)	0/3 (0.0)	0/4 (0.0)	0/4 (0.0)	0/3 (0.0)	0/0 (0.0)	0/0 (0.0)	0/7 (0.0)	0/7 (0.0)
Panama Viejo	1/14 (7.1)	1/15 (6.7)	0/3 (0.0)	0/2 (0.0)	0/6 (0.0)	0/6 (0.0)	1/23 (4.3)	1/23 (4.3)
Total (Gulf of Panama)	**5/54 (9.3)**	**6/59 (10.2)**	**1/36 (2.8)**	**0/39 (0.0)**	**0/7 (0.0)**	**0/7 (0.0)**	**6/97 (6.2)**	**6/105 (5.7)**
Jicarita	0/1 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/1 (0.0)	0/0 (0.0)
La Pitahaya	0/2 (0.0)	0/2 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/2 (0.0)	0/2 (0.0)
Sitio Drago	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)
Cerro Brujo	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)
Total (Gulf of Chiriquí & Caribbean)	**0/3 (0.0)**	**0/2 (0.0)**	**0/0 (0.0)**	**0/0 (0.0)**	**0/2 (0.0)**	**0/2 (0.0)**	**0/5 (0.0)**	**0/4 (0.0)**
Total	**5/57 (8.8)**	**6/61 (9.8)**	**1/36 (2.8)**	**0/39 (0.0)**	**0/9 (0.0)**	**0/9 (0.0)**	**6/102 (5.9)**	**6/109 (5.5)**

[a] Data given as "n/N (%)," in which "n" represents the number of ear canals with EAE present, "N" represents the total observable sample, and "%" represents the frequency of "n" per "N."
Bolded values represent regional and overall totals.

TABLE 3 Degree of stenosis in EAE affected individuals from Panama

				Left EAE[a]					Right EAE				
Site	**Individual**	**Age**	**Sex**	**0**	**1**	**2**	**3**	**9**	**0**	**1**	**2**	**3**	**9**
Cerro Mangote	Individual 1E	35–50	Male		+						+		
Sitio sierra (early)	Individual B-7	50+	Male	+						+			
Cerro Juan Díaz (early)	Burial 3.2, bundle 7, cranium 1	35+	Male		+						+		
	Burial 3.2, bundle 10	50+	Probably male		+							+	
	Burial 3.2, bundle 11	50+	Probably male					+			+		
	Burial 3.16, cranium 18	45+	Female		+				+				
Playa Venado	Trench A6, skeleton 4	35+	Probably male		+				+				
Panama Viejo	Plaza mayor, burial 1, individual 9	35–45	Probably male		+					+			

[a] Degree of stenosis is coded as follows: 0: EAE absent; 1: mild stenosis (less than 1/3 of the acoustic canal occluded); 2: moderate stenosis (between 1/3 and 2/3 of the acoustic canal occluded); 3: severe stenosis (more than 2/3 of the acoustic canal occluded); and 9: unobservable (external auditory meatus is fragmented or absent).

mildest expression of the growth. Although sample sizes are low, the fact that all affected individuals were older than 35 years at death suggests that the development of the lesion was protracted.

4 | DISCUSSION

In considering potential causes leading to the development of the observed EAE in pre-Columbian Panama, we first address the potential role of biological factors. Bacterial and fungal infections of the skin are pervasive in the warm and moist conditions of the tropics, and their ability to contribute to the irritation of the external auditory canal, and thus, potentially to the development of EAE, cannot be disregarded. Fungal infections of the external ear canal (i.e., otomycosis) often coinfect with bacteria in cases of chronic otitis externa, particularly in the tropics (Conley, 1948; Reeh, 1942). Nevertheless, fungal infections rarely spread to affect bone tissue and in such cases cause a destructive rather than proliferative reaction in bone tissue (Conley, 1948; Hsu, Chen, & Wang, 2011; Reeh, 1942; Varghese, Nair, & Kavalakkat, 2014). Further, both males and females are at equal risk for developing otitis exerna (U.S. Centers for Disease Control and Prevention, 2011).

Since the results of the present study suggest that males were at a higher risk for developing EAE than females, we would argue that infectious factors alone (i.e., in the absence of a behavioral component) could not account fully for the development of this lesion among the prehispanic Panamanian populations. Instead, the tendency for this abnormal bony growth to affect male individuals almost exclusively in the sample studied follows patterns of EAE prevalence in other areas of the world, in which social norms delegated certain aquatic resource procurement activities to male individuals (Crowe et al., 2010; Standen et al., 1997). To understand the type of aquatic activities to which EAE among pre-Columbian populations of Panama are attributable, we turn to archaeological, ecological, and ethnohistorical literature.

4.1 | Pre-Columbian fishing and other aquatic subsistence practices

Identifying the nature of freshwater and marine resource exploitation by pre-Columbian peoples has been a subject of intense research over many decades in Panama. For most of the Holocene, the subsistence patterns of human groups that settled along the Isthmus of Panama were diverse, and agriculture, tree fruit collection, fishing, coastal

TABLE 4 Frequencies of EAE per individual within pre-Columbian sites in Panama

Site	Male	Female	Indeterminate	Total
Cerro Mangote	1/10 (10.0)[a]	0/8 (0.0)	0/0 (0.0)	1/18 (5.6)
Sitio Sierra (early)	1/6 (16.7)	0/2 (0.0)	0/0 (0.0)	1/8 (12.5)
Cerro Juan Díaz (early)	2/7 (28.6)	1/6 (16.7)	0/0 (0.0)	3/13 (23.1)
Playa Venado	1/8 (12.5)	0/9 (0.0)	0/0 (0.0)	1/17 (5.9)
Sitio Sierra (late)	0/3 (0.0)	0/3 (0.0)	0/0 (0.0)	0/6 (0.0)
Panama Viejo	1/13 (7.7)	0/2 (0.0)	0/5 (0.0)	1/20 (5.0)
Total (Gulf of Panama)	**6/47 (12.8)**	**1/30 (3.3)**	**0/5 (0.0)**	**7/82 (8.5)**
Jicarita	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)
La Pitahaya	0/2 (0.0)	0/0 (0.0)	0/0 (0.0)	0/2 (0.0)
Sitio Drago	0/0 (0.0)	0/0 (0.0)	0/1 (0.0)	0/1 (0.0)
Cerro Brujo	0/0 (0.0)	0/0 (0.0)	0/1 (0.0)	0/1 (0.0)
Total (Gulf of Chiriquí & Caribbean)	**0/2 (0.0)**	**0/0 (0.0)**	**0/2 (0.0)**	**0/4 (0.0)**
Total	**6/49 (12.2)**	**1/30 (3.3)**	**0/7 (0.0)**	**7/86 (8.1)**

[a] Data given as "n/N (%)," in which "n" represents the number of individuals with EAE present, "N" represents the total number of individuals with both ear canals observable, and "%" represents the frequency of "n" per "N."
Bolded values represent regional and overall totals.

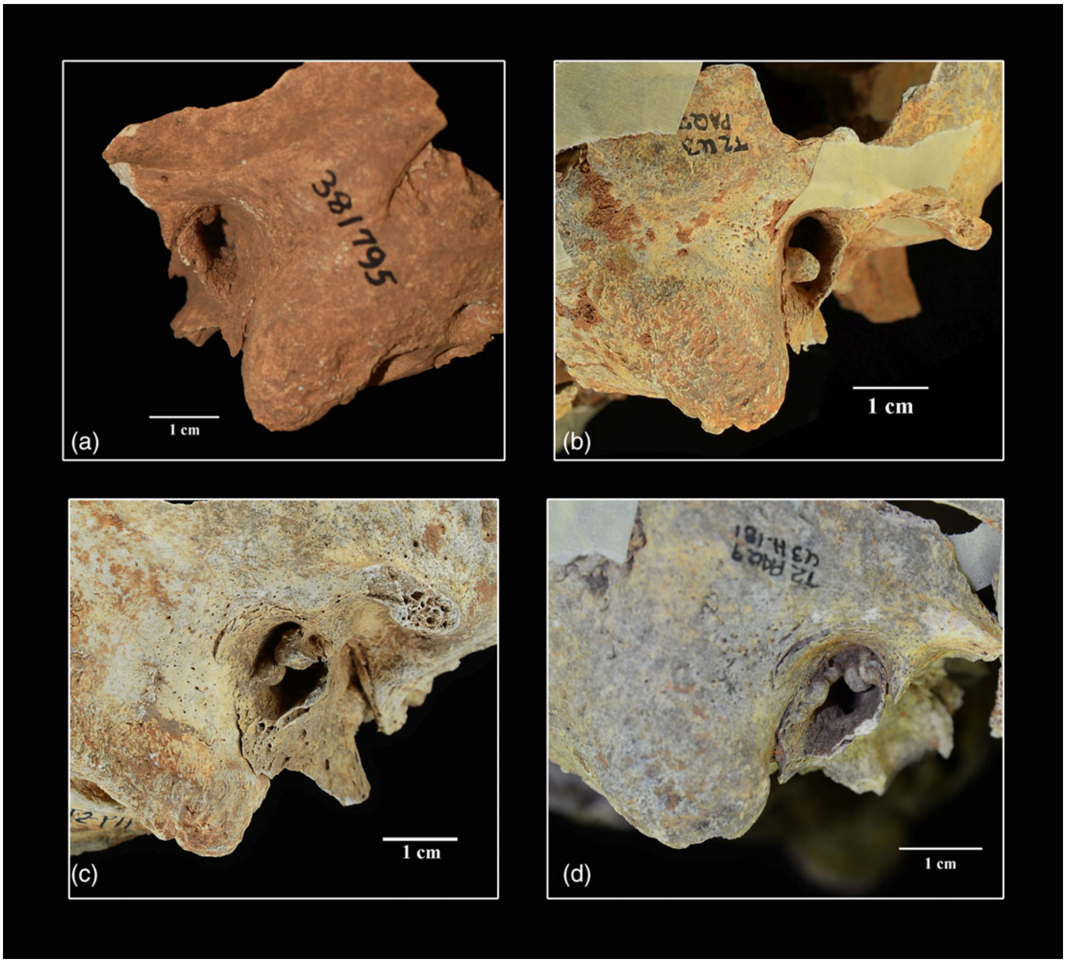

FIGURE 3 Photographs of external auditory exostoses showing variation in degree of stenosis across four individuals from pre-Columbian sites in Panama. (a) Mild EAE in Playa Venado trench A6, skeleton 4; (b) Moderate EAE in Cerro Juan Díaz, burial 3.2, bundle 7, cranium 1; (c) Moderate EAE in Cerro Juan Díaz, burial 3.2, bundle 11; (d) Severe EAE in Cerro Juan Díaz, burial 3.2, bundle 10. Photos by Nicole Smith-Guzmán (a) and Raiza Segundo (b-d)

resource collection, and hunting practices varied across time and space (Cooke & Jiménez, 2008; Cooke, Norr, & Piperno, 1996; Cooke & Ranere, 1989; Cooke, Ranere, Pearson, & Dickau, 2013). Agriculture involving early varieties of mostly exogenous plant domesticates (e.g., maize [*Zea mays*], manioc [*Manihot esculenta*], squash [*Cucurbita moschata*], sweet potatoes [*Ipomoea batatas*], and American yams [*Dioscorea* spp.]) began as soon as the late stage of the final glaciation gave way to warmer atmospheric temperatures (Dickau, Ranere, & Cooke, 2007; Dickau, 2010; Piperno, 2011b; Piperno, Ranere, Holst, & Hansell, 2000).

As agriculture intensified and human populations grew—especially on the Pacific side of the Isthmus—settlements nucleated increasingly along major rivers and near mangrove estuary systems (Carvajal Contreras & Hansell, 2008; Clary, Hansell, Ranere, & Buggey, 1984; Cooke & Ranere, 1999). These locations were favorable in terms of human subsistence, allowing exploitation of both terrestrial and aquatic resources. Expanses of fertile riverine soils were propitious for planting field crops. Gallery forests and wooded savannahs were home to abundant iguanas (Iguanidae spp.) and white-tailed deer (*Odocoileus virginianus*; Cooke, Jiménez, & Ranere, 2007, 2008). Lower river valleys had large populations of freshwater turtles (*Trachemys scripta*, *Kinosternon* spp.). The high tidal ranges of the Pacific-side mangrove estuaries created extensive mud flats, in which aquatic and avian resources were abundant. Fish diversity both in coastal and riverine waters of the Parita Bay area was prodigious (Cooke & Jiménez, 2004, 2008). Fish that daily entered estuaries and inlets in large shoals were extracted with ease using nets in tide pools, mangrove weirs, and stone-and-pole tidal traps (Cooke & Tapia, 1994).

The postglacial ocean was still rising at the beginning of the Holocene, explaining the lack of evidence for extensive subsistence practices in Pacific coastal biomes until sea level rise began to level off about 6000 BCE. Cerro Mangote, located between 1.5 and 5.5 km from the active coastline at the time of its occupation (but now at a 10.5 km distance due to the continuous coastal progradation), documents fishing and coastal collecting for shellfish for about 3,000 years (Cooke & Ranere, 1999; Ranere & Hansell, 1978). The fact that the community consumed maize at this time underlines the importance of ecotones for subsistence diversity (Piperno, 2011a). Fishing between about 6000 and 2000 BCE around Parita Bay focused heavily on oligohaline and mesohaline waters in tidal river mouths and in mangrove channels. In these habitats, individual fish of large (>500 g) size were regularly taken, such as marine catfish (e.g., *Ariopsis seemanni*, *Sciades dowii*, and *Notarius* spp.), toadfish (*Batrachoides* spp.), and snooks (*Centropomus* spp.). A concurrent strategy at Cerro Mangote focused on small fish that congregate in tidal pools and oxbow channels, such as Pacific fat sleepers (*Dormitator latifrons*; Cooke & Ranere, 1999).

A very different kind of fishing is evidenced, however, at Playa Don Bernardo on Pedro González Island (part of the Pearl Island Archipelago in the Gulf of Panama) between 4200 and 3600 BCE. This is the only mid-Holocene human settlement yet identified in the Gulf of Panama, and its initial settlers made the sea crossing from the mainland by canoe when the postglacial sea levels had nearly reached those of today (Martín et al., 2016). They hunted a dwarf deer (Cervidae sp.) to extinction on this island (Buckley et al., 2017; Martínez-Polanco, Jiménez, Buckley, & Cooke, 2015), and trapped many snakes, iguanas, and rodents (agoutis [*Dasyprocta* sp.], rufous soft-furred spiny-rat [*Diplomys labilis*], and spiny rat [*Proechimys semispinosus*]). They also fished intensively over reefs and in clear currents for fast swimming, shoaling epipelagic fish species like black skipjack (*Euthynnus lineatus*) and green jack (*Caranx caballus*; Cooke & Jiménez, 2009). The large numbers of dolphin remains (*Delphinus* and *Tursiops*) in the Playa Don Bernardo middens was either acquired at sea or by scavenging recently stranded dolphins (Cooke et al., 2016). Phytoliths and starch grains found on grinding stones at the site evidence that its occupants also consumed maize (Martín et al., 2016).

In Parita Bay, fishing practices changed by about 2000 BCE when populations began consuming small shoaling fish (under 300 g) more frequently. Taxon biomass took precedence over the earlier emphasis on large individual fish size. Small inshore shoaling taxa, such as thread-herrings (*Opisthonema libertate*), brassy grunts (*Orthopristis chalceus*), and Pacific lookdowns (*Selene peruviana*) began to be caught in large numbers (Cooke, 1992; Cooke & Ranere, 1999; Peres, 2001). The remains of these fish appear frequently 16 km inland at Sitio Sierra between 1 and 500 CE, and their transport inland is recorded at other sites by at least 1800 BCE (Cooke, 1995; Cooke, 2001). These fish eschew turbid water currents, preferring to seek out clear water currents in the lower estuary (Day, Hall, Kemp, & Yáñez-Arancibia, 1989). To fish these three species, canoers would likely have focused on sand banks in the bay. Subsequently, the small fish were probably transported from the coastline to inland sites, after being smoked or sundried or both (Carvajal-Contreras, Cooke, & Jiménez, 2008; Zohar & Cooke, 1997).

Along the western Pacific coast of Panama, in the nonupwelling inshore waters of the Gulf of Chiriquí, pre-Columbian fishing strategies were distinct to those in vogue further east. At the site of La Pitahaya, fishing remained rather similar to that of Cerro Mangote until Spanish contact (Wing, 1980). A very different pattern was observed at Jicarita Island at the Southern tip of the Coiba Archipelago in the Gulf of Chiriquí. The archaeo-ichthyological sample from this site is the most open water oriented in Panama. Fast-swimming pelagic species of fish are common, including mackerel scad (*Decapterus macarellus*) and black skipjack (*Euthynnus lineatus*; Isaza Aizpurúa, in press). Other species recorded here that are absent or unusual in other samples analyzed to date include yellowfin tuna (*Katsuwonus pelamis*), rainbow runner (*Elagatis bipinnulata*), and blue jack (*Caranx melampygus*). That pre-Columbian inhabitants of the island were consuming these marine fish as a large part of their diet is evidenced by the comparatively high nitrogen (δ15N) isotope value of a dentin sample from the only human burial recovered from the site (15.4‰, Beta-419311, 1,260 ± 30 BP, cal 670–800 CE). The Jicarita fisher folk would not necessarily have needed to venture into deep oceanic water to capture these fish. Rather, they could have used opportunistic strategies such as long and weighted nets to predate on these kinds of species as they travelled through the deep and clear strait between Jicarita and the large Coiba Island just to the North.

The Caribbean archaeo-ichthyological sample from Cerro Brujo typifies fishing mostly in two environments, which lack high tidal ranges (i.e., shallow lagoons with mangrove roots and sea grass beds and around rocky and coralline reefs). In these habitats, the top-ranked taxa by minimum numbers of individuals (MNI) between about 900 and 1100 CE were snook (*Centropomus* spp.), snappers (*Lutjanus* spp.), groupers (*Epinephelus* spp. and *Mycteroperca* sp.), jacks (*Caranx* spp.), and toadfish (*Opsanus* sp.; Wing, 1980, pp. 204–205). This suite of fish taxa points toward hook-and-line and spearing techniques, although nets along the lagoon edges, and pole or basketry traps may have been effective. However, the heaviest input of meat by far came from manatee (*Trichechus manatus*) and four genera of marine turtles (Wing, 1980). Individual capture would have been more practical than mass capture techniques such as nets, which would have snagged on rocks and coral. A similar but more diverse pattern was noted at the nearby and contemporary site of Sitio Drago on Isla Colon, concurring with the wider range of marine environments available to inhabitants of this island (Wake, Doughty, & Kay, 2013).

4.2 | Nonsubsistence based marine shell collection

It is quite evident from the archaeological record that certain marine shells amounted to a sumptuary good for the pre-Columbian inhabitants of Pacific Panama and adjoining areas of the Isthmo-Columbian Area. These included not only pearl oysters (*Pinctada mazatlanica*), but perhaps more importantly, thorny oysters (*Spondylus* spp.) and the Eastern Pacific giant conch (*Lobatus galeatus*). Inhabitants of the region manufactured the shells into white and brightly-colored ornaments that often comprised mortuary regalia for human burials. The earliest known use of *Spondylus* for this purpose goes back as far as 400 BCE at Cerro Mangote (AMS-standard ^{14}C date for a rib from Individual 31E: AA-4942, 2,260 ± 50 BP, 401–203 cal BCE), but marine shell ornament manufacture increased greatly in intensity after the BCE/CE boundary.

The preferred marine shell genera eschew the mixing zone of estuaries and require clearer water columns (Mayo & Cooke, 2005). Some islets around Parita and Panama Bays provide these habitats (e.g., Otoque, Farallón de Chirú, Isla Villa, and Isla Iguana). Species of the two oyster genera cement themselves to the rocky substrate, which exists from the rocky intertidal zone to 15 m below sea level in the Gulf of Panama (Harilaos Lessios, personal communication, May 11, 2018). To harvest these mollusks, pre-Columbian artisans could have simply collected dislodged shells from nearby beaches after a storm. However, contact-period accounts suggest that the prized large shells were almost exclusively obtainable by diving to great depths (Martyr D'Anghera, 1912, p. 295). Divers would have used prying tools, perhaps made out of wood, to separate the shells from their substrate (Blower, 1995). Storms blow up quickly during the rainy season, and thus, shell diving may have been an activity performed during the dry season when winds are high and cold, upwelled water filled the Gulf of Panama.

Upon initial arrival to the Pacific Ocean in 1513 CE, Spanish explorer and *conquistador* Vasco Núñez de Balboa described finding teams of expert divers in the Eastern region of Panama who had trained from infancy, diving to depths of up to four fathoms for pearl oysters (Irving, 1831, p. 197; Martyr D'Anghera, 1912, p. 295). The tradition of using trained indigenous divers to procure these marine resources in the Gulf of Panama continued in the early years after the conquest up until the mid-sixteenth century when the Spanish settlers began replacing native divers with African slaves (Camargo, 1983). Pearl oysters in Panama remained an important commodity for export up until a collapse of the industry for the exploitation for natural pearls between the 1930s and 1940s due to overfishing of these mollusks as well as the production of synthetic and cultured pearl oysters (Camargo, 1983; Jackson et al., 2001).

The pre-Columbian practice of using *Spondylus* shells for rituals and personal ornamentation extended to Mesoamerican and Andean cultures to the North and South of the Isthmo-Columbian Area (Lodeiros et al., 2016; Moore, 1987). Diving for *Spondylus* and other marine shells comprised an intense industrial activity in Ecuador and Northern Peru, which was driven by long-distance commodity trade in the Andean region (Bauer, 2007; Blower, 1995; Cordy-Collins, 1990). Such long-distance trade is evidenced by worked *Spondylus* shells in archaeological contexts as far south as Northern Chile—over 1,500 km south of the mollusk's natural range (Moore, 1987; Reinhard, 2002). Divers in these coastal areas would have been exposed similarly to very low sea surface temperatures driven by the Humboldt Current that jets northward along the western coast of South America (Montecino & Lange, 2009), likely contributing to high rates of EAE (Hrdlička, 1935; Kennedy, 1986; Tattersall, 1985; Ubelaker, 1981).

4.3 | Implications for the development of EAE in Panama

Thus, based on the wide exploitation of aquatic resources by pre-Columbian peoples, it seems unlikely that the frequencies of EAE among the human remains reported here are attributable simply to the widespread fishing or shoreline collecting activities. If this were the case, we would expect more of the population to have been affected. Instead, it is more reasonable to envision that the small group of individuals affected by EAE was participating in subsurface marine resource acquisition, which involved the complete submersion of the head in water. Such activities involving a select group of specialized divers, as described by the Spanish chroniclers upon initial contact with populations on the Pacific coast, could explain the general low prevalence of EAE in the population, as well as the higher prevalence of EAE within the male-specific subsample as compared with the female-specific subsample.

These implications, although speculative, would appear to stand in contrast to Timofeev et al.' (2004) observation that severe EAE form more rapidly in modern individuals participating in above water activities (e.g., surfing and sailing) than below water activities like diving. However, we would suggest that the findings of the aforementioned study are dependent largely on the low atmospheric temperatures of the region in which the study took place (i.e., Cornwall, United Kingdom). In a region such as Panama with year-round high atmospheric temperatures, the irritant role of wind-blown sea spray in the development of EAE would be diminished or nonexistent.

Half of the individuals affected came from the early mortuary contexts (cf. "sub-oven" burials; Cooke & Sánchez Herrera, 1997; Cooke et al., 1998; Cooke, Sánchez, & Udagawa, 2000, pp. 160–164) at the site of Cerro Juan Díaz in Los Santos, Panama, including three male individuals recovered from within the same multiple burial (Burial 3.2). At other sites along the Gulf of Panama, EAE appeared rarely, pertaining to only one individual from each site: Cerro Mangote, Sitio Sierra, Playa Venado, and Panama Viejo. The four sites outside the Gulf of Panama contained no examples of EAE, but these correspond to a miniscule sample of only five individuals in total. For similar issues of preservation, no human osseous remains have been recovered and made available for study from highland archaeological sites in Panama. Thus, no clear association with geographical area within Panama can be estimated at present. However, following Sheard's (2002) and Sheard and Doherty (2008) observation that sea surface temperature below a threshold of 19°C is the strongest predictor of EAE formation in modern populations, the seasonal upwelling in the Gulf of Panama might provide a more suitable environment for increased EAE development than the warm waters of the Gulf of Chiriquí and the Caribbean. More samples are needed, however, to confirm this hypothesis.

Importantly, the situation in Panama brings up an important issue in the interpretation of the presence and absence of EAE at archaeological sites. Panama is a relatively small strip of land, comprising just 650 km in total length from East to West and separating Atlantic and Pacific Oceans by as little as 50 km at its narrowest point. With ample coastline and plentiful aquatic resources, there were likely people diving at most if not all pre-Columbian sites. However, oceanographic conditions within the different marine zones along Panama's coastline suggest the absence of EAE at sites along the Caribbean and Western Pacific coasts of Panama would not have formed as readily as at those along the Central and Eastern Pacific Gulf of Panama. Thus, an understanding of local environmental conditions influencing biocultural markers such as EAE is crucial in picking apart differences in activity patterns of ancient groups.

5 | CONCLUSION

This study surveyed the prevalence of EAE at nine archaeological sites in Panama corresponding to 10 different precontact periods. All these sites are located within 16 km of the present active shoreline, where populations were highly engaged in aquatic activities for food procurement, as well as nonsubsistence based sumptuary marine shell acquisition. A conservative prevalence estimation of EAE found the lesion to be present in 8.1% of individuals, including 12.2% of males and 3.3% of females. Low sea surface temperatures and high constant winds during the dry season months likely contributed to the increased development of EAE in individuals diving for precious marine shells in the Gulf of Panama. Based on the results of this study and in light of ethnohistorical accounts at the time of Spanish contact, it is likely that diving activities in this region were restricted to a select group of male specialists.

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