

Evaluation of Putative Hybrid Hatchlings between Hawksbill Sea Turtle (*Eretmochelys imbricata*) and Green Sea Turtle (*Chelonia mydas*) in Tortuguero, Costa Rica

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ABSTRACT.—Although hybridization processes in the Cheloniidae family have been documented since the 19th century, detailed reports of these occurrences are scarce. Therefore, the record of a hybridization between Green Sea Turtles (*Chelonia mydas*) and Hawksbill Sea Turtles (*Eretmochelys imbricata*) signifies an important event. In this study, we report the third known record of hybridization between *C. mydas* and *E. imbricata* in the Caribbean Sea. In Tortuguero, Costa Rica, we marked and monitored several nests from both species during the 2020 nesting season. Offspring from two *E. imbricata* clutches showed morphological characteristics corresponding to both species. We compared 20 individuals from each of these nests to large groups of pure *C. mydas* and *E. imbricata* individuals. We measured carapace length and mass of each hatchling and documented other morphological properties such as scale patterns on the head to better identify the species. Because these hatchlings presented different combinations of representative characteristics of each species, we concluded that they are hybrid individuals. Our findings provide a new record of a *C. mydas* × *E. imbricata* hybridization event.

Hybridization occurs when individuals from different species mate (Karl et al., 1995; Proietti et al., 2014; Kelez et al., 2016) but natural hybridization is rarely detected in wild populations. Nevertheless, numerous species have effectively hybridized at the population level, influencing their evolutionary trajectory. Close to a quarter of all known plants and 10% of animal species have been susceptible to hybridization that can result in the generation of recently diverged taxa (Mallet, 2005; Genovart, 2008). Natural hybridization represents a potential threat of extinction for a substantial number of plant and animal species (Wolf et al., 2001). If hybridization becomes common among wildlife, even low rates of individual hybridization can have important evolutionary consequences in a large number of species (Mallet, 2005).

Hybridization may contribute to decline of a species when hybrid fitness is reduced relative to the parental species causing lowered reproductive success for one or both parental lineages, a phenomenon known as outbreeding depression (Wolf et al., 2001; Todesco et al., 2016; Arantes et al., 2020a). Hybridization events can be especially problematic for rare species that interact with more abundant populations (Allendorf et al., 2001). Continued hybridization events can lead to a reduction in the population growth rate, bringing less abundant species to a level below that required for replacement and eventual demographic swamping. On the other hand, if hybrids are fertile and their fitness is affected very little or not at all, populations may succumb to genetic assimilation where emerging hybrid individuals could displace pure conspecifics of the hybridizing taxa (Wolf et al., 2001; Soares et al., 2018; Arantes et al., 2020a).

Among sea turtles, specifically the Cheloniidae, hybridization reports have been historically scarce. The first record of interspecific hybridization within the Cheloniidae dates back to the end of the 19th century, when fishermen in the Cayman Islands described the merged characteristics of Loggerhead Sea Turtles (*Caretta caretta*) and Hawksbill Sea Turtles (*Eretmochelys imbricata*) in a few captured individuals (Garman, 1888). More recently, hybridization events between different sea turtle

species have been reported in almost every region around the globe (Kamezaki, 1983; Conceição et al., 1990; Karl et al., 1995; Seminoff et al., 2003; James et al., 2004; Garofalo et al., 2012; Witzell and Schmid, 2003; Koo et al., 2014; Kelez et al., 2016; Hart et al., 2019) and between multiple species (Bowen and Karl, 2007; Naro-Maciel et al., 2008; Vilaça et al., 2012). Reports of sea turtle hybridizations have had an especially high incidence along the northeastern coast of Brazil (Arantes et al., 2020a), whereas reports elsewhere have been anecdotal or circumstantial (Karl et al., 1995). The frequency of hybrid sea turtles found on the northeastern Atlantic coast of Brazil is much higher than in any other region worldwide, with hybrids comprising up to 42% of the nesting population in some beaches (Lara-Ruiz et al., 2006; Vilaça et al., 2012; Proietti et al., 2014; Soares et al., 2017, 2018; Arantes et al., 2020a,b).

It is still unclear why hybridization events occur among sea turtle species, whether as a survival strategy to compensate for fluctuations in population size or as a natural mechanism of evolution inherent to these species (Kelez et al., 2016). Sea turtle hybrids are believed to arise from a disproportional abundance of multiple species relying on the same resources, occupying similar spatial ranges and occurring simultaneously in specific niches during their respective reproductive seasons (Arantes et al., 2020b). Similarly, a biased sex ratio within co-occurring populations may also be a factor that contributes to mating encounters between individuals of different species (Proietti et al., 2014); having a larger number of males from another species available during courtship and mating seasons may potentiate the chances of cross-breeding among different populations.

Globally, populations of *E. imbricata* have faced many threats over past decades leading to a drastic decline in their populations around the Caribbean and elsewhere. During the second half of the last century, estimated numbers dropped by 95% in the region, including at the well-monitored nesting population at Tortuguero (Carr and Stancyk, 1975; Bjørndal et al., 1993; Meylan, 1999; Bjørndal and Jackson, 2003). Nevertheless, the Tortuguero rookery presents a predominant genetic stock for *E. imbricata* that can be traced throughout several foraging areas and other nesting beaches around the Caribbean (Troëng et al., 2005; Leroux et al., 2012). Similarly, Green Sea Turtles (*Chelonia mydas*) at Tortuguero possess a predominant

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haplotype present in roughly 90% of the nesting population that is distinct from others found around the Greater Caribbean (Peare and Parker, 1996; Bjorndal et al., 2005).

Despite the fact that hybridization in *E. imbricata* has received little attention and the frequency of hybridization under natural conditions is not well understood, its frequency is likely to be very low. Hybridization events have been reported for populations of *E. imbricata* nesting in Brazil but with no apparent negative effects of hybridization on hatchling viability (Lara-Ruiz et al., 2006; Reis et al., 2010; Soares et al., 2017, 2018; Arantes et al., 2020b). Moreover, offspring from hybrid individuals were found to be fertile and capable of producing viable progeny. There are also reports on the fitness and viability of hybrid individuals of *C. mydas* (Wood et al., 1983; Karl et al., 1995; Kamezaki et al., 1996; Seminoff et al., 2003; James et al., 2004; Koo et al., 2014; Kelez et al., 2016; Hart et al., 2019).

Information on hybridization events is fundamental for understanding its prevalence and consequences, particularly among sea turtle species (Kelez et al., 2016). Loss of rare species due to genetic or demographic swamping, changes in mating dynamics, and decreases in hatchling fitness and viability, as well as offspring fertility are some possible major effects of hybridization (Soares et al., 2018). Given the ecological importance of hybrid individuals, monitoring and documenting them is of great value to defining long-term conservation strategies (Proietti et al., 2014). Therefore, long-term conservation programs should consider documenting hybridization in sea turtle populations (Soares et al., 2018). Our study evaluated some putative hybrid offspring in clutches laid by an *E. imbricata* female in Tortuguero during the 2020 nesting season that showed characteristics of a cross between *E. imbricata* and *C. mydas*. We report the morphological characteristics of these putative hybrid individuals and compare them with the parental species descriptions.

MATERIALS AND METHODS

Study Site.—Tortuguero National Park (TNP) is located on the northern Caribbean coast of Costa Rica (10°32.319N, 83°30.016W; WGS 84) and hosts the most important nesting beach for *C. mydas* in the western hemisphere, with between 37,395 and 149,569 clutches laid every year (Bjorndal et al., 1999; Solow et al., 2002; Troëng and Rankin, 2005; Saragoça Bruno et al., 2020). Populations of critically endangered *E. imbricata*, endangered Leatherbacks (*Dermochelys coriacea*), and vulnerable *C. caretta* also use the 30-km stretch of beach for nesting purposes. The Sea Turtle Conservancy (STC) has monitored and studied nesting populations of sea turtles at TNP for over 60 years. As part of the monitoring protocol each season, we mark and monitor over 200 nests for *C. mydas* and as many *E. imbricata* nests as possible (up to 40 clutches in one nesting season) in order to estimate average hatching and emerging success, as well as average reproductive output.

Marking of Nests.—Sea turtle nests are marked during night patrols, after encountering a female digging an egg chamber. To mark a nest, we record clutch size by counting the eggs as they are laid, and we triangulate the precise site of the chamber to be monitored thereafter. Encountering *E. imbricata* females while nesting at Tortuguero beach is not common, due to the great length of beach monitored and the relatively short time females take to complete the nesting process. Nevertheless, nesting events by *E. imbricata* can be identified by their very distinctive

asymmetrical track, small body pit, and shallow egg chamber (Bjorndal et al., 1985; Pritchard and Mortimer, 1999). At TNP, nests of *E. imbricata* are located most commonly close to or under overhanging vegetation. These distinctive nesting characteristics allowed us to identify clutches hours after female turtles returned to the sea.

During the 2020 nesting season, we identified and monitored 44 *E. imbricata* nests, during either night patrols or morning surveys. We placed metallic or plastic mesh around each clutch to protect them against mammalian predation and other disturbances. Similarly, we marked and monitored a sample of 99 *C. mydas* nests throughout the nesting season, from May through November 2020. On 9 July, we found and marked an *E. imbricata* nest during night patrol. On 25 July, during a morning census, we detected and triangulated another *E. imbricata* nest less than 2 km from the first but were unable to see the laying female on either occasion. After 55 days of incubation, we collected 20 live hatchlings from each marked nest and brought them into the laboratory to assess diagnostic features of each individual that would allow identification of hybrids.

Hatchling Analysis.—We categorized hatchlings by species according to the female that laid the clutch, which generated two large groups of individuals that presented typical features of either *C. mydas* or *E. imbricata*. A third, smaller group contained the 44 hatchlings collected from the two peculiar clutches (20 live ones from each, plus an additional four from the second clutch that did not emerge successfully and perished under the heat) that presented characteristics corresponding to both species. We refer to this group as the analyzed hatchlings (AH).

We recorded hatchling weight using an electronic scale with a graduated precision to the nearest 0.01 g. We measured carapace length as both notch-to-notch minimum curved length (CCLmin) and maximum straight carapace length (SCLmax) from the anterior edge of the carapace to the posterior tip of the supracaudal scutes. We measured CCLmin using a flexible measuring tape with 0.1 cm accuracy. For SCLmax, we used plastic 15 cm calipers with 0.05 mm accuracy. We took each measurement three times to ensure accuracy within 0.1 cm. We also conducted a general examination to detect potential abnormalities by recording the number of scutes present on the carapace and plastron. We checked the head composition for any alterations of the scale pattern corresponding to each species (Pritchard and Mortimer, 1999; Wyneken, 2001). Finally, we conducted a thorough examination to detect congenital malformations (Bárcenas-Ibarra et al., 2015). We then released hatchlings on the beach at night while ensuring they were able to move to the ocean.

Statistical Analysis.—We ran ANOVA tests in R (version 3.6.0) to test for differences in mass and size measurements (measured as SCL and CCL) amongst the hatchling groups. We applied post hoc pairwise Tukey honest significant difference tests to ask which groups were different. We report all means \pm SD.

RESULTS

Based on physical characteristics such as coloration, mass, and size measurements, 1,295 hatchlings were classified as either *C. mydas*, *E. imbricata*, or hybrid (Fig. 1A). Most *C. mydas* hatchlings (96.7%) presented a regular scale composition of one pair of prefrontal and four postocular scales, in accordance with the species description (Fig. 1B). Similarly, 95.9% of *E. imbricata* hatchlings fit the species description, presenting two pairs of

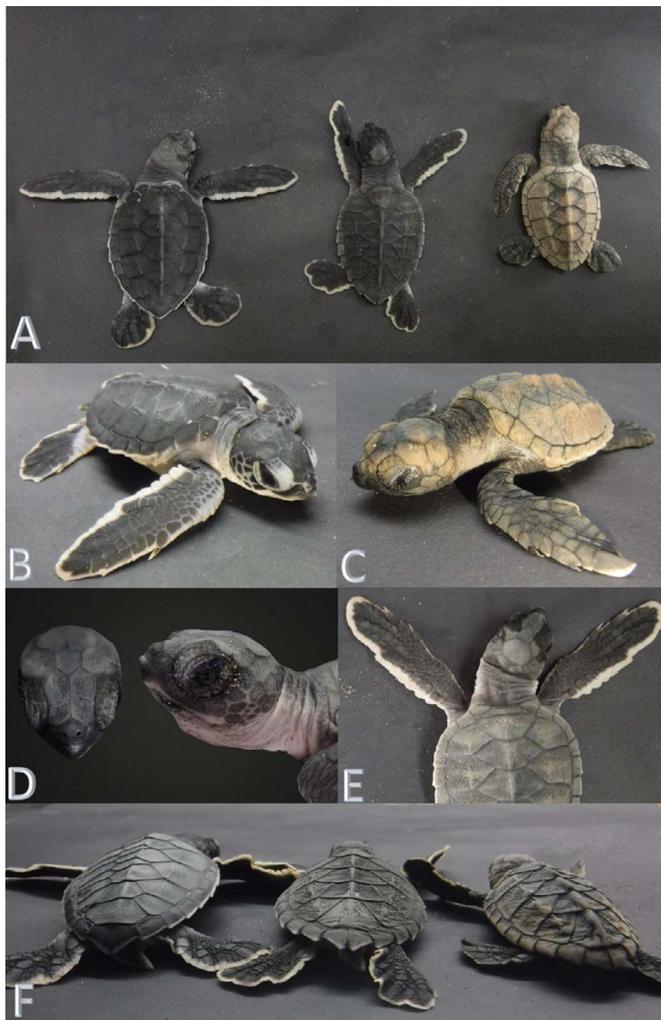


FIG. 1. Comparison of morphological characteristics in hatchling *Chelonia mydas* (Cm), *Eretmochelys imbricata* (Ei), and putative hybrids (AH). (A) Coloration and size comparison between sampled hatchlings (left to right: *C. mydas*, putative hybrid, *E. imbricata*). (B) *C. mydas* hatchling presenting typical head scale composition and absence of a second claw on anterior limbs. (C) *E. imbricata* hatchling showing typical head scale composition and presence of a second claw on anterior limbs. (D) Putative hybrid hatchling showing the typical *E. imbricata* head scale composition. (E) Putative hybrid hatchling with second pair of claws on anterior limbs. (F) Carapace scute comparison (left to right: Cm with smooth carapace; AH with thick scute edges slightly overlapped; Ei with overlapping carapace scutes).

prefrontal scales, three postocular scales, and a second set of claws on the anterior flippers (Fig. 1C).

The putative hybrid nests were found relatively close together temporally (14 days apart), perhaps indicating that they were laid by the same *E. imbricata* female. We evaluated these separately from others due to the peculiar characteristics presented by eggs and hatchlings. Eggs appeared viable, slightly larger than a typical *E. imbricata* egg, with an average diameter of $37.3 \text{ cm} \pm 1.3 \text{ SD}$. Both nests incubated successfully, and hatching success was relatively high, at 78.1% and 90.4%, resulting in a total of 263 hatchlings.

The putative hybrid hatchlings (AH) from these two clutches presented a dorsal dark blue coloration and a pale white underside (Fig. 1D) (characteristic of *C. mydas*), and a mixture of diagnostic characteristics from *C. mydas* and *E. imbricata*. Of the 44 individuals, 22.7% had typical *E. imbricata* head scale

TABLE 1. Mean differences in mass (g) amongst three groups of hatchlings from Tukey multiple comparison tests (95% confidence intervals represented by lower and upper bounds). Cm, *Chelonia mydas*; AH, putative hybrid hatchlings; Ei, *Eretmochelys imbricata*.

Contrast	Difference	Lower	Upper	P
Cm-AH	-9.9796	9.3444	10.6148	0.0000
Ei-AH	-0.0604	-0.6970	0.5762	0.9731
Ei-Cm	-10.0400	-10.2707	-9.8092	0.0000

composition with two pairs of prefrontal and three postocular scales (Fig. 1D). Only 4.5% presented a typical *C. mydas* composition, with one pair of prefrontal and four postocular scales. Most individuals presented a combination of characteristics of the two species: 47.7% with one pair of prefrontal and three postocular scales and 4.5% with two pairs of prefrontal scales and four postoculars. The remainder presented a combination of head scale patterns outside regular standards. Despite showing the typical *C. mydas* coloration observed in the AH, the majority of this group presented a second pair of claws on their anterior flippers (Fig. 1E) and exhibited overlapping vertebral scutes (Fig. 1F), both morphological features characteristic of *E. imbricata*.

Mean mass for *C. mydas* hatchlings was $24.44 \text{ g} \pm 1.99$, ranging from 16.30 to 29.29 g. For *E. imbricata*, the mean mass was $14.40 \text{ g} \pm 1.48$, with a range from 9.22 to 18.59 g (Fig. 2). The mass of *Chelonia mydas* hatchlings was significantly greater than the other two groups ($F_{2,1291} = 5397$, $P < 0.0001$), but the mass of the AH and *E. imbricata* hatchlings were not significantly different from each other (Table 1, Fig. 2). Measurements for SCL differed significantly between the three groups ($F_{2,1289} = 4296$, $P < 0.0001$) (Fig. 3), and pairwise comparisons indicated that all hatchling groups were different in SCL (Table 2). Similarly, CCL was significantly different amongst the three groups of hatchlings ($F_{2,1292} = 4233$, $P < 0.0001$) (Fig. 4), and all were different from one another (Table 3).

DISCUSSION

Standard morphological traits for species identification of sea turtles have been defined (Pritchard and Mortimer, 1999; Wyneken et al., 2001). We analyzed eggs and offspring from two presumed *E. imbricata* nests laid at TNP, but they did not fit into one defined species category. Some of their characteristics were atypical for either species. For instance, egg diameter was larger than previously reported for *E. imbricata* (Hirth, 1980; Limpus et al., 1983; Pritchard and Mortimer, 1999), and a dark blue dorsal coloration and mixed scale pattern suggested that they were putative hybrid hatchlings (Wood et al., 1983; James et al., 2004; Anyembe and Van de Geer, 2015; Hart et al., 2019). Thus, based on color pattern, carapace length, and scale composition, we identified these as hybrid offspring of *C. mydas* and *E. imbricata* (Wood et al., 1983; Seminoff et al., 2003; Kelez et al., 2016).

The peculiar coloration of these hatchlings may be attributed to the genetic contribution of at least one male *C. mydas*. Tortuguero harbors the largest aggregation of *C. mydas* in the Caribbean basin, with mating occurring just hundreds of meters offshore between May and August each season (Miller, 1996; Bevan et al., 2016). Far fewer individuals from the decimated *E. imbricata* population occur simultaneously in the Caribbean Basin (Meylan, 1999; Bjorndal and Jackson, 2003). They may be

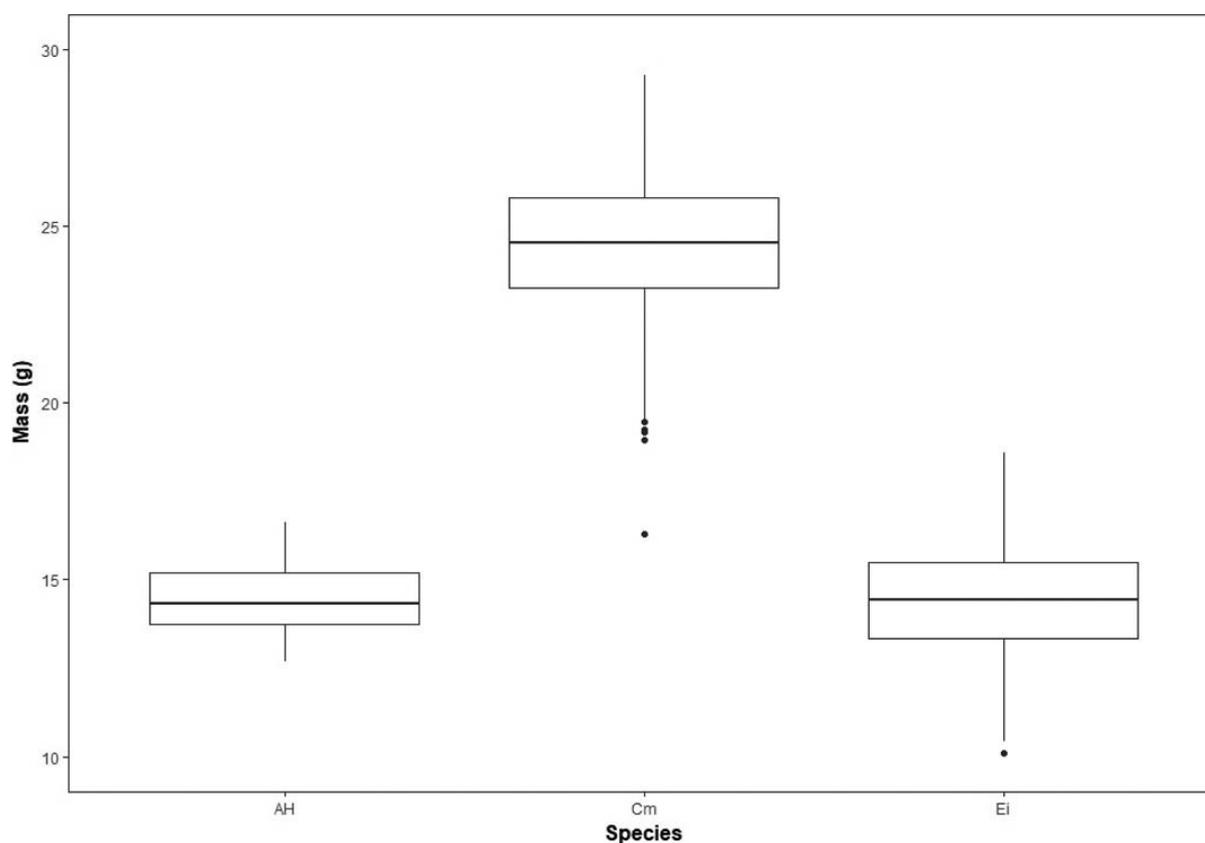


FIG. 2. Hatchling mass in three groups: putative hybrids (AH, $n = 44$), *Chelonia mydas* (Cm, $n = 646$), *Eretmochelys imbricata* (Ei, $n = 605$). Standard boxplots showing interquartile ranges (box edges), medians (solid thick lines), standard deviations (whiskers), and individual outliers (black points). Cm was significantly greater than the other two groups, which were not different from one another.

unable to find conspecific mates which could have led to cross-fertilization between these two species (Karl et al., 1995; Proietti et al., 2014; Kelez et al., 2016; Arantes et al., 2020b).

Crossbreeding between *C. mydas* and other cheloniids has been previously reported with *C. caretta* (Kamezaki et al., 1996; James et al., 2004; Garofalo et al., 2012; Koo et al., 2014) and *E. imbricata* (Wood et al., 1983; Karl et al., 1995; Seminoff et al., 2003; Kelez et al., 2016). Hart et al. (2019) presented the only case of hybridization between *C. mydas* and *Lepidochelys olivacea*. So far, no evidence of hybridization involving *L. kempii* or Flatback Sea Turtles (*Natator depressus*) has been documented. On the other hand, hybridization between *C. caretta* and *E. imbricata* has been seen more often and may be common in some regions. The reported frequency of *C. caretta* \times *E. imbricata* hybrid females along the Brazilian coast is as high as 42% at some sites (Lara-Ruiz et al., 2006; Reis et al., 2010).

Hybrids between *C. mydas* and *E. imbricata* are rare with only a few instances reported in the literature. Two of them involved

the East Pacific *C. mydas*, one in the Gulf of California, Mexico (Seminoff et al., 2003), and the other in northern Peru (Kelez et al., 2016). Both were immature individuals captured in the waters of known foraging grounds. Due to the presence of obvious intermediate species-specific morphological characteristics, these individuals were classified as *C. mydas* \times *E. imbricata* hybrids. A third report is the only documented case of this phenomenon in the Indian Ocean, where an individual with combined characteristics was recaptured by fishermen several times during the same season (Anyembe and van de Geer, 2015). The last report corresponds to a group of hatchlings from Green Sea Turtle eggs collected in Surinam in 1977 that differed from their cohort in appearance and behavior. After a year reared in captivity, based on their morphological characteristics, 37 turtles were identified as hybrids (Wood et al., 1983; Karl et al., 1995). In addition, two other reports of *C. mydas* \times *E. imbricata* hybrid turtles have been revealed recently in a press release article from Australia and another from Florida

TABLE 2. Mean differences in straight carapace length (mm) amongst three groups of hatchlings from Tukey multiple comparison tests (95% confidence intervals represented by lower and upper bounds). Cm, *Chelonia mydas*; AH, putative hybrid hatchlings; Ei, *Eretmochelys imbricata*.

Contrast	Difference	Lower	Upper	P
Cm-AH	6.3066	5.5924	7.008	0.0000
Ei-AH	-3.9369	-4.6525	-3.2212	0.0000
Ei-Cm	-10.2435	-10.5030	-9.9839	0.0000

TABLE 3. Mean differences in curved carapace length (cm) amongst three groups of hatchlings from Tukey multiple comparison tests (95% confidence intervals represented by lower and upper bounds). Cm, *Chelonia mydas*; AH, putative hybrid hatchlings; Ei, *Eretmochelys imbricata*.

Contrast	Difference	Lower	Upper	P
Cm-AH	0.7721	0.6964	0.8477	0.0000
Ei-AH	-0.3007	-0.3765	-0.2249	0.0000
Ei-Cm	-1.0728	-1.1003	-1.0454	0.0000

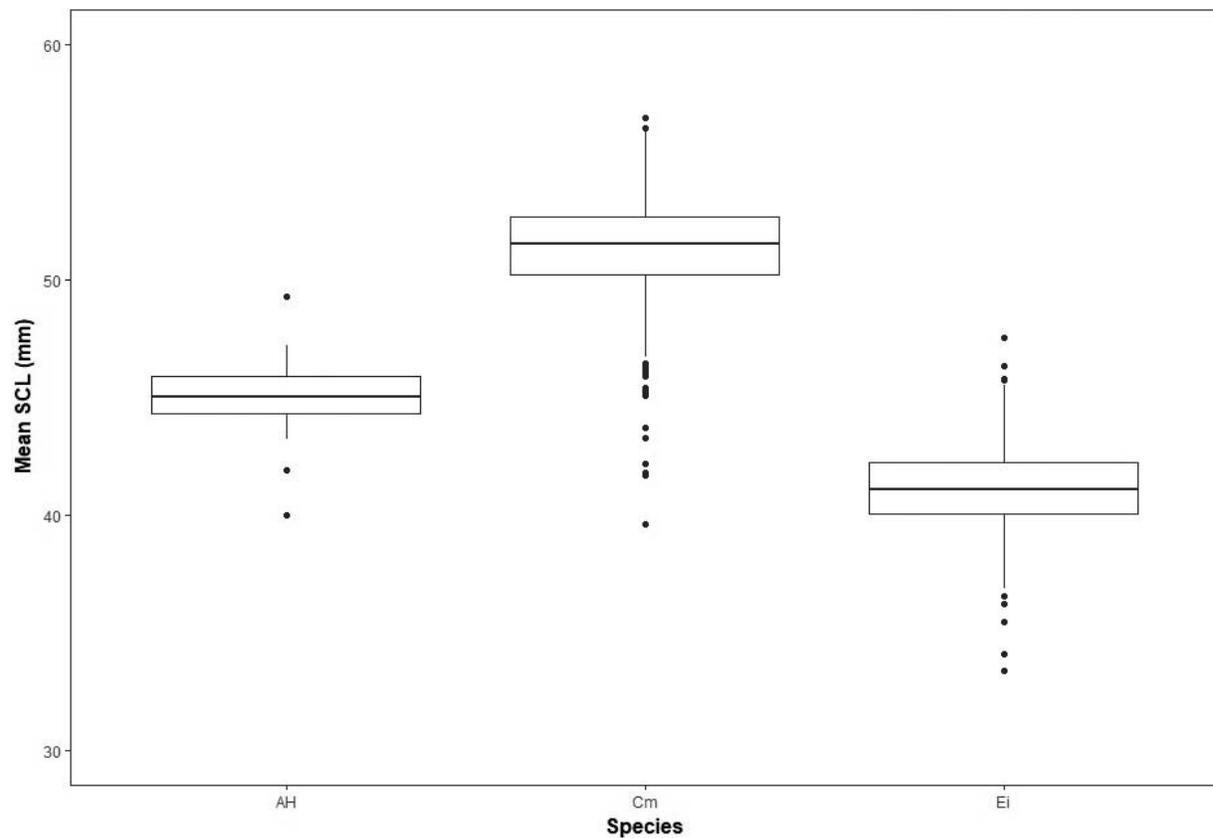


FIG. 3. Hatching straight carapace length (SCL) in three groups: putative hybrids (AH, $n = 44$), *Chelonia mydas* (Cm, $n = 643$), *Eretmochelys imbricata* (Ei, $n = 605$). Standard boxplots showing interquartile ranges (box edges), medians (solid thick lines), standard deviations (whiskers), and individual outliers (black points). All groups were significantly different from one another.

reporting on the work of sea turtle organizations (Verhagen, 2016; Helgason, 2020). Thus, our study represents the third record of hybridization between these two species in the Caribbean, and the second one evaluating hybrid hatchlings.

Globally, very few confirmed reports exist of hybrid hatchlings, and the most extensively studied cases are from Brazil. Soares et al. (2018) found that hatching success and hatchling viability of hybrid clutches were indistinguishable from nonhybrid clutches, for almost every combination of crossbreeding species. Furthermore, Soares et al. (2017) found that hybridization between *C. caretta* and *E. imbricata* presented no reproductive advantage or disadvantage, and reproductive output was not different from that of the parental species. On the other hand, *C. mydas* hybrid hatchlings appeared to be larger, stronger, and faster than nonhybrid turtles from the same cohort, and they were characterized as aggressive. Moreover, they were susceptible to infections and prone to diseases, suggesting that hybrid matings can reduce progeny fitness (Wood et al., 1983; Karl et al., 1995; Hart et al., 2019).

Interspecific hybridization poses a number of challenges for conservation (Soares et al., 2018; Arantes et al., 2020b), and we still do not understand completely its role in conservation, ecology, and evolution (Soares et al., 2018). Furthermore, crossbreeding between close species raises interesting questions about evolutionary relationship (Seminoff et al., 2003). Hybridization events within populations could lead to fewer reproductively viable individuals in subsequent generations (Wood et al., 1983; Soares et al., 2018), contributing to further decline of nesting populations. At Tortuguero, both *E. imbricata* and *C. mydas* nesting trends have fluctuated over recent decades

(Bjorndal et al., 1999; Meylan, 1999; Troëng and Rankin 2005; Troëng et al., 2005). Temporal and spatial overlap among *E. imbricata* and *C. mydas* individuals during mating and nesting is conducive to reproductive interactions between the two species. Karl et al. (1995) detected a strong tendency for females to be members of the rarer species involved in crossbreeding, which suggests a scarcity of *E. imbricata* males at Tortuguero, contributing to increased likelihood of interspecific hybridization.

To date, the extent to which natural hybridization in sea turtles occurs has yet to be determined. Fortuitous encounters of hybrid individuals have contributed to our understanding of this phenomenon (Kamezaki et al., 1996; James et al., 2004; Garofalo et al., 2012; Koo et al., 2014; Kelez et al., 2016; Hart et al., 2019). Nevertheless, because of the high phenotypic variation inherent to species morphological traits, it is possible that hybrids go undetected in monitored populations without detailed morphological evaluations (Karl et al., 1995; James et al., 2004). An increase in hybridization reports around the world could be an indication that it is more common than previously thought. Global initiatives and sea turtle monitoring programs have increased population monitoring and explored new areas, so it is unclear whether hybridization is increasing recently or is now detected more often.

Hybridization events between sea turtle species is a rather rare phenomenon but further assessment of the mating dynamics in *E. imbricata* and *C. mydas* nesting populations at Tortuguero seems warranted. The presence of hybrid hatchlings can potentially affect population growth for either or both parental populations, and the findings we report may reflect

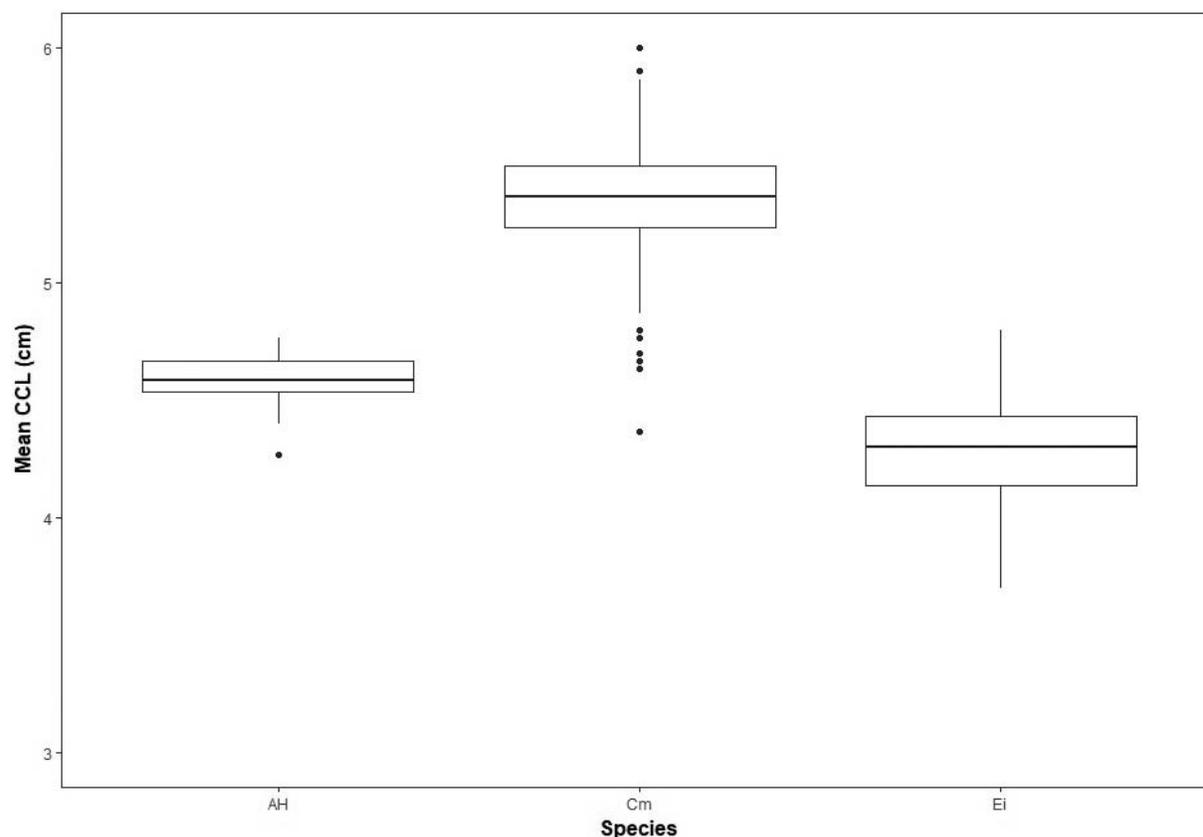


FIG. 4. Hatchling curved carapace length (CCL) in three groups: putative hybrids (AH, $n = 44$), *Chelonia mydas* (Cm, $n = 646$), *Eretmochelys imbricata* (Ei, $n = 605$). Standard boxplots showing interquartile ranges (box edges), medians (solid thick lines), standard deviations (whiskers), and individual outliers (black points). All groups were significantly different from one another.

poor condition of at least one of the populations of marine turtles nesting at Tortuguero.

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