Origins and Speciation of the Endemic Puerto Rican Coquí and Relation to Indigenous Boricuas

The Caribbean island of Puerto Rico, which is actually an archipelago of over 140 islands, is home to a colorful assortment of tropical fauna. One such animal, which makes its home in El Yunque (the island's tropical rainforest) is the coquí: the singing Puerto Rican tree frog. The presence of the coquí on the island, called Borikén by the Indigenous Taino inhabitants, predates European colonization. Pre-contact petroglyphs of the coquí dating back to the 13th century C.E. show that Indigenous Boricuas (people of Borikén) were aware of the tiny amphibian. Its image also appears on artisanal creations such as pottery, showing that the coquí had and still has significant cultural relevance. Today, it has become a national symbol of Indigenous Boricua heritage and pride, and it currently appears on necklaces, beaded artworks and other forms of adornment and art. But how long has the iconic coquí frog been present in Puerto Rico? Did it arrive via ancient migration from South and Central America, as the Taino did? Or does it predate the archipelago's human inhabitants? In this essay, we will take a look at its evolutionary history and origins to see how it came to be there.

Firstly, it is important to note that "coquí" does not refer exclusively to one species of Puerto Rican tree frog. The common Puerto Rican coquí, *Eleutherodactylus coquí*, is a member of the genus *Eleutherodactylus*, meaning "free-toed" (referring to the unique lack of webbing between their toes), which comprises about two-thirds of the more than 240 different frog species across the Caribbean Islands (Blackburn, et al., 1). Its name is a reference to a mating call that is only produced by two species in this genus: *Eleutherodactylus portoricensis* and *Eleutherodactylus coquí*. Yet, the term coquí actually describes several species within this genus and some subgenera that are native to the archipelago of Puerto Rico. Despite living in habitats all over Puerto Rico, these frogs prefer the more temperate climate of the rainforest El Yunque.

Eleutherodactylus portoricensis, or the upland coquí, occupying the higher elevations and mountainous regions above 1200 meters, and *Eleutherodactylus coquí* occupying the lower regions up to about 1200 meters (Maiorana). The "co" part of the coquís' call is a territorial warning to other males, while the "qui" part is a mating call to females; due to sexual dimorphism in the inner ear of these species, female and male coquís physically perceive these sounds differently (Narins). Thus, these essential mating functions depend on the efficacy of sending and receiving these auditory signals. Unfortunately, as global temperatures increase, the body mass of coquís decreases, and the sound of their mating call changes. If climate change continues at its current pace, coquís could look and sound different within a few generations, especially given their approximately 1 year lifespan in the wild (Maiorana). This would present major challenges both culturally and ecologically if female coquís' inner ears are not able to adapt to the new mating call since the coquís are a major link in the food chain of the Puerto Rican rainforest. In Puerto Rico their unique call and natural predation of herbivorous arthropods (plant-eating bugs) and other small critters endears them to the islanders. But outside of Puerto Rico, they are considered a nuisance and a hazard to biodiversity which also threatens their population as they are exterminated as invasive species.

Externally, coquí are morphologically distinguished from other Caribbean frog genera and species by the sticky disks on their toe pads, which assist them in climbing despite their lack of toe webbing (NBII, et al.). But, they also have skeletal features that distinguish their tiny, frail bones from the tiny, frail bones of other Caribbean frogs. These include a rounded distal humeral head (knobby elbow joint), distally projecting entepicondyle (elbow muscle socket pointed away from the shoulder), and lack of prominent medial and lateral crests in their arm bones (Blackburn, et al., 2). Despite this, geographical distribution tends to be a more accurate

indicator of cladistics for the subgenera of *Eleutherodactylus* to which coquís belong. Coquí frogs are not exclusive to the archipelago of Puerto Rico. Prior to 2012, the oldest frog fossil in the Caribbean was from a member of the *Eleutherodactylus* genus found preserved in Miocene Era amber in the Dominican Republic. Most other fossils have been dated to various times within the Pleistocene-Holocene epochs (Blackburn, et al., 2). However, the tiny and frail bones of *Eleutherodactylus* frogs coupled with the hot, humid climate of the Caribbean comprise circumstances ill-suited to fossilization and/or skeletal preservation, limiting the fossil record for Caribbean frogs to the Neogene and Quaternary Cenozoic period.

Fortunately, fossils are not the only means by which phylogenetic hypotheses can be studied. In 2005, analysis of mitochondrial DNA, tRNA (transfer RNA), and part of the nuclear c-myc gene (which regulates cell growth and rRNA transcription) between subgenera of *Eleutherodactylus* has suggested to researchers that a common ancestor for these subgenera entered Central America from South America between the late Cretaceous period and early Paleocene epoch (Crawford, et al.). A caveat for this conclusion, however, is that researchers assumed that a proto-Antillean land bridge (exposed land connecting the mainland to land that would become the Greater Antillean islands) was once available for biogeographical movement and diversification. The research conclusions especially support a common ancestor of the *Eleutherodactylus* subgenera *Eleutherodactylus*, *Euhya*, and *Syrrophus* that, itself, still belonged to the *Eleutherodactylus* genus (Crawford, et al.). Ergo, it was believed that *Eleutherodactylus* members closely related to the modern coquí were extant in the Greater Antilles by the Oligocene epoch. But the circumstances described above meant a lack of fossil evidence to support this hypothesis.

However, on November 20th, 2012, (results published in April 2020) researcher J. Vélez-Juarbe discovered a small arm bone fragment, the distal end of a left humerus, in a mudstone outcrop on the west bank of Río Guatemala, a Puerto Rican river (Blackburn, et al., 2). The bone showed a a rounded distal humeral head, distally projecting entepicondyle, and a lack of prominent medial and lateral crests, which, as previously discussed, point to it belonging to a member of the genus *Eleutherodactylus*, more specifically, being most closely related to the subgenera *Eleutherodactylus*, *Euhya*, and/or *Syrrophus* (Blackburn, et al., 2), which are thought to share a sister-group relationship with a common *Eleutherodactylus* ancestor (despite not forming a clade [Blackburn, et al., 2]). This was a promising find in light of the results of the 2005 study. Given the size of the arm bone, the animal is likely to have been about 36mm in length: well within the 11-88mm size range for *Eleutherodactylus* species (Blackburn, et al., 2). The fossil was found below shells that were strontium-dated to approximately 29-30 million years ago (early Oligocene epoch). From this, the inferred age of the fossil is early Oligocene at the latest (Blackburn, et al., 2): far before the Pleistocene-Holocene evolution of modern humans and population of the Greater Antilles by them. This direct evidence corroborated the prior phylogenetic analysis suggesting Greater Antillean presence of *Eleutherodactylus* in the Oligocene epoch, but, unlike those studies, provides no insight into the diversification of its subgenera. However, given the positively identified genus and subgenera (two of which comprise West Indian population of *Eleutherodactylus* that include coquís) as well as the locality of the discovery (recall that geography is a superior indicator of cladistics for *Eleutherodactylus*), the fossil can be positively stated to be that of a coquí.

This affirms that the oldest yet found frog fossil in the Caribbean is a fossil arm bone of a coquí. This discovery also contradicts more recent phylogenetic studies that attempted to dispute

the Oligocene establishment of *Eleutherodactylus* in the Caribbean and confirms the persistence of Oligocene-Miocene *Eleutherodactylus* species, meaning that the coquís referenced in pre-contact Indigenous art were undoubtedly similar or identical to the coquís visible on the island today (Blackburn, et al., 2-3). Furthermore, it supports alternative hypotheses for the *Eleutherodactylus* population establishment in the Greater Antilles, including overwater dispersal (Blackburn, et al., 3). Although the species from which this bone came is now extinct, its existence in the area no doubt constituted a set stage for the evolution of the extant coquí species in Puerto Rico today.

The complete story of coquí evolution is still unknown due to the rarity of Caribbean amphibian fossils and the vast diversity within species of the *Eleutherodactylus* genus. The size, skeletal structure and morphological features of this now-extinct species of *Eleutherodactylus* are speculated only by this single fossil and by the morphological features of its extant closest biogeographical relatives (van Hoose). Even recent phylogenetic studies have only focused on a fraction of the approximately 16 coquí species and approximately 400 *Eleutherodactylus* species (Crawford, et al.). As it stands, DNA and fossil evidence suggests that the diversification of the species and subgenera of *Eleutherodactylus* occurred after the establishment of the genus in the West Indies (Crawford, et al.), thus making the Puerto Rican coquí truly endemic to the archipelago. The perfect niche into which it fits in its native habitat is reflected by the vast schism between how it is treasured by Puerto Ricans and seen as an invasive pest everywhere else. This disconnect has even lead to population control measures against it, and this coupled with the deforestation, pollution, and exploitation of Puerto Rico and El Yunque, the introduction of amphibian fungus, and the typical one-or-less year long lifespan of the wild *Eleutherodactylus coquí* has resulted in a near threatened status for the species (Maiorana). Working to counteract

global climate change and prevent the escape of coquís to areas where they will be exterminated as invasive species is crucial to the survival of this beloved animal and the ecological and cultural preservation of its beloved island home.

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