# NATURAL HYBRIDIZATION BETWEEN TWO SPECIES OF GREEN ANOLES: MORPHOLOGICAL AND GENETIC EVIDENCE

## Hibridación natural entre dos especies de *Anolis* verdes: evidencia morfológica y genética

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## ABSTRACT

Anoles are a group of lizards that offer a wide range of opportunities to study different biological topics. In this work, we examined some aspects of the morphology from 139 individuals of green anoles collected in urban parks of Santo Domingo and the Distrito Nacional. We investigated evidence of hybridization between the two Hispaniola endemic species *Anolis chlorocyanus* and *A. cyanostictus* and the introduced species *A. porcatus*. We categorized the individuals in pure species and intermediates based on their phenotype. Additionally, mitochondrial 16S sequence data was generated from the collected specimens, to compare molecular and phenotypic species assignments. We consider the general congruence between both data sets in most but inconsistency in a few specimens as evidence for hybridization between the two endemic species. However, we did not find evidence of hybridization between any of these species and the introduced species *A. porcatus*. Nevertheless, the continuous expansion of the distribution of this invasive species possibly will have drastic negative consequences for the populations of the endemic species.

*Keywords*: Hispaniola, urban anoles, interspecific mating, intermediate morphology, gene introgression.

## RESUMEN

Los *Anolis* son un grupo de lagartos que ofrecen una amplia gama de oportunidades para el estudio de diversos temas biológicos. En este trabajo, examinamos algunos aspectos de la morfología de 139 individuos de *Anolis* verdes presentes en parques urbanos de Santo Domingo y el Distrito Nacional. Nosotros investigamos evidencias morfológicas y genética de hibridación entre las dos especies endémicas de La Española, *Anolis chlorocyanus* y *A. cyanostictus* y la especie introducida *A. porcatus*. Basados en su fenotipo, clasificamos a los individuos en especies puras o intermedias. Además, se recopilaron datos mitocondriales 16S para una comparación fenotípica y molecular. A partir de la asociación general entre los dos conjuntos de datos en la mayoría, pero la incongruencia en pocas muestras, concluimos sobre la presencia de hibridación entre las dos especies endémicas. Sin embargo, no se encontró evidencia de hibridación entre ninguna de estas especies y la especie introducida *A. porcatus*. A pesar de ello, la continua expansión de la distribución de esta especie invasora posiblemente tendrá consecuencias negativas drásticas para las poblaciones de las especies endémicas.

*Palabras clave*: Hispaniola, *Anolis* urbanos, apareamiento interespecífico, morfología intermedia, introgresión genética.

## INTRODUCTION

The Hispaniolan green anoles are a group of *Anolis* lizards characterized by having (among other morphological characteristics) brilliant-green body color in live, although capable of color changes to brown (Williams, 1965; Köhler & Hedges, 2016). Like all members of this genus, they can be distinguished from other lizards by the combination of having a dewlap (i.e., an extensible skin fold in the throat region, more developed in males than in females) and widened adhesive lamellae below fingers and toes (Poe *et al*., 2017).

In his revision of the green anoles from Hispaniola, Williams (1965) recognized four species in this group (*Anolis chlorocyanus*, *A. coelestinus*, *A. aliniger*) and his new species (*A. singularis*). He distinguished two groups of species based on their distribution and morphological similarities: one group composed of *A. chlorocyanus* and *A. coelestinus*, and another containing *A. aliniger* and *A. singularis*.

Fifty-one years later, Köhler and Hedges (2016) made the second revision of this group, where they described eight new species, resurrected four from synonymy, and raised three taxa from subspecies to species level. They also reorganized the species groups, and thus, currently 16 species of green anoles from Hispaniola are recognized, distributed in three groups (i.e., the *Anolis chlorocyanus* group, the *Anolis coelestinus* group, and the *Anolis aliniger* group). As a group, these species are well distributed across Hispaniola and can be found in a variety of habitats from near sea level to more than 2000 m above sea level. Two of these species *A. cyanostictus* and *A. chlorocyanus* occur in sympatry along with the introduced green anole from Cuba, *A. porcatus*, in many green areas and urban parks in the city of Santo Domingo and the Distrito Nacional. Prior to Köhler and Hedges (2016) work, *Anolis cyanostictus* was considered as a subspecies of *A. chlorocyanus* but currently both taxa are recognized as two distinct species which can be distinguished by some external characteristics such as the dewlap coloration and the presence versus absence of characteristic pale brown blotches. *Anolis cyanostictus* has a yellowish-green dewlap with little or no black pigment on the posterior portion and has pale brown blotches near the shoulder and behind the eye, whereas *A. chlorocyanus* shows black suffusion in the posterior part of the dewlap and does not have any pale brown blotches (Mertens, 1939; Cochran, 1941; Williams, 1965; Schwartz & Henderson, 1991; Köhler & Hedges, 2016). These two taxa also differ in geographic distribution. *A. chlorocyanus* can be found throughout the eastern part of Hispaniola north and east of the Cordillera Central, whereas *A. cyanostictus* is restricted to the National District and nearby towns (Köhler & Hedges, 2016) that includes its type locality, the vicinity of the Haina River in San Cristóbal province.

The introduced species *A. porcatus* can be distinguished from both species by having a pink male dewlap as well as a more robust body and a bigger size. After its introduction to Hispaniola, it used to be restricted to only a few areas of Santo Domingo (Arias, 1985; Powell *et al*., 1990). In recent years has been reported to expand its range to more localities (Stuart *et al*., 2012) but apparently, Santo Domingo is the only contact zone between these three species. Having three similar looking green anoles in sympatry raises questions about possible hybridization and competition. To address these issues, we conducted field and lab work with individuals of all three species from their area of sympatry. Here we report our results of an analysis using mtDNA sequence data combined with an evaluation of morphological characters for species identification to evaluate potential hybridization among these taxa.

## OBJECTIVES

- To evaluate whether there is evidence for hybridization among the three species of green anoles (*Anolis chlorocyanus*, *A. cyanostictus* and *A. porcatus*) occurring in sympatry in the metropolitan area of Santo Domingo, Dominican Republic.

## MATERIALS AND METHODS

*Study areas*. We collected specimens from seven study sites in Santo Domingo and the Distrito Nacional: the National Botanical Garden "Dr. Rafael M. Moscoso" (NBG), three urbans parks: Parque Mirador Norte (PMN), Parque Mirador Sur (PMS) and Parque Mirador Oeste (PMO), the Plaza de la Cultura (PC), La Feria and Los Maestros.

The NBG is located in Altos de Galá, in the northwestern part of Santo Domingo de Guzmán, between the coordinates 18.490556° N and 69.958611° W. It has an area of 1.28 km² and an elevation between 70 and 80 meters above sea level. The soil is of limey origin, shallow and of low fertility, its relief is flat and with slight undulations (Mejía & García, 1994).

The PMN is located on the northern margin of the Isabela River in the municipality of Santo Domingo Norte (Fig. 1). It is the largest protected area in the city, with an area of about 10 km². It is characterized by having extensive forests and galleries; as well as lagoons, gullies and wetlands (Consejo Nacional de Asuntos Urbanos [CONAU], 2007).

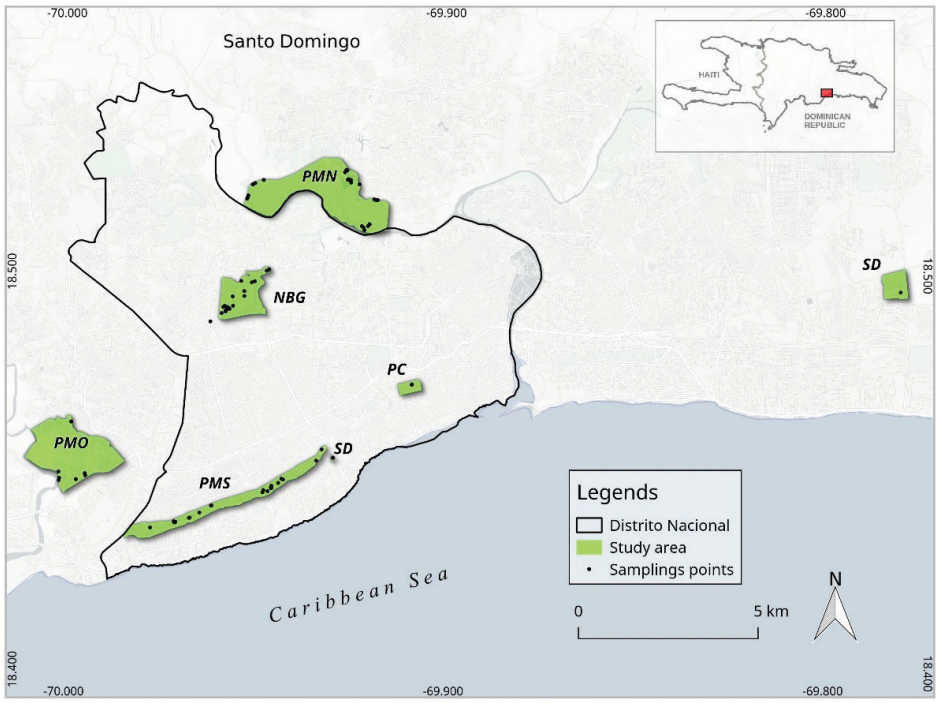



Figure 1. Sampling sites in Santo Domingo and Distrito Nacional.

The PMS, created in 1970, was the first urban park in Santo Domingo. It is located on the avenue of the same name (Parque Mirador Sur) in the Distrito Nacional. It occupies a surface of approximately 7 km$^2$ and presents, rock formations, caves, underground springs, bushes and scattered trees. (CONAU, 2007; Szabó, 2010).

The PC is located in the center of the Distrito Nacional. It covers an approximate area of 1 km$^2$. Its vegetation is composed of ornamental plants, open bushes and scattered trees (Almonte-Espinosa, 2018). Currently this area is under renovation and many of the vegetation patches where the specimens were collected has been cut.

The PMO, with an area of about 7 km$^2$, is located in the Santo Domingo Oeste municipality, near the Haina River. Together with the PMN, they are part of the so-called "Green Belt of Santo Domingo", an ecological corridor that surrounds the periphery of the city and whose function is to stop urban expansion while protecting the flora and fauna associated with each area (Ayuntamiento del Distrito Nacional [ADN], 2016).

In addition to the aforementioned areas, collections were made at two additional sites. One in the municipality of Santo Domingo Este (Los Maestros) and another in the Distrito Nacional (La Feria) near PMS. Unlike the previous ones, these points do not constitute green areas or urban parks and will be referred as Santo Domingo (SD); see Appendix A for coordinates.

*Sample collection*. A total of 141 green lizards were collected. The number of individuals per site was distributed as follows: NBG (n = 33), PMN (n = 38), PMS (n = 36), PMO (n = 20) PC (n = 8) and SD (n = 6). Additionally, 18 specimens were included as putatively pure individuals of each species from non-contact areas: *A. cyanostictus* (n = 3), *A. chlorocyanus* (11) and *A. porcatus* (4). Specimens of the two endemic species were revised and confirmed by Köhler and Hedges (2016). All the additional individuals were collected outside of Santo Domingo; see Appendix B for coordinates. Of the 159 samples (141 collected and 18 added), we only used those that could be sequenced (139), including the supposedly"pure" ones.

*Methodology*. Prior to preserving the specimens collected in the field, color photographs of each individual's extended dewlap were taken, following Köhler (2014) for dewlap extension and animal position. After euthanasia, we cut tissue samples from the tip of the tail of each individual and stored them in 98 % non-denatured ethanol. The specimens were preserved by injecting a solution of 5 mL absolute (i.e., 36 %) formalin in 1 L of 96 % ethanol into the body cavity and thighs. We deposited part of the specimens in the collection of the Museo Nacional de Historia Natural "Prof. Eugenio de Jesus Marcano" (MNHNSD), Santo Domingo, Dominican Republic, and the remaining specimens have been deposited in the Senckenberg Forschungsinstitut Frankfurt (SMF), Frankfurt, Germany.

For DNA extraction, we followed the protocol of Ivanova *et al.* (2006). To eliminate potential PCR-inhibiting contaminants, the tissue samples were incubated for 14 hrs in 200 µL low PBS buffer (20 µL PBS in 180µL of water) before overnight digestion with the vertebrate lysis buffer at 56 °C. After extraction, the DNA was eluted in 50 µL TE buffer. A fragment of the mitochondrial 16S rRNA gene was amplified in an Eppendorf Mastercycler® pro, using the following protocol: initial denaturation for 2 minutes at 94 °C followed by 40 cycles with denaturation for 35 seconds at 94 °C, hybridization for 35 s at 48.5 °C, and elongation for 60 s at 72 °C; final elongation for 10 minutes at 72 °C. The reaction mix for each sample contained 1 µL DNA template. We used the following primers: L2510 (CGCCTGTTTATCAAAAACAT) for the forward and H3066 (CCGGTCTGAACTCAGATCACGT) for the reverse strand (Köhler *et al*., 2014). For each sample, 9 µl of distilled H2O + 1 µl of DNA was used.

The cleaning and editing of the sequences for both primers was carried out with the MEGA 7 bioinformatics program package (Kumar *et al.*, 2016). Once all the sequences were edited, the alignment of the multiple sequences was performed using the MUSCLE algorithm included in MEGA 7 and following the default parameters. The generated matrix was used to perform a phylogenetic analysis based on the Neighbor-Joining (NJ) method (Saitou and Nei 1987). The support of the tree branches was evaluated by boostrap (10,000 repetitions) and for the calculation of the evolutionary distances the Kimura 2-parameter method was used (Kimura, 1980). The analysis involved 140 nucleotide sequences. The species A. rodriguezii was included in the analysis as an external group (outgroup).

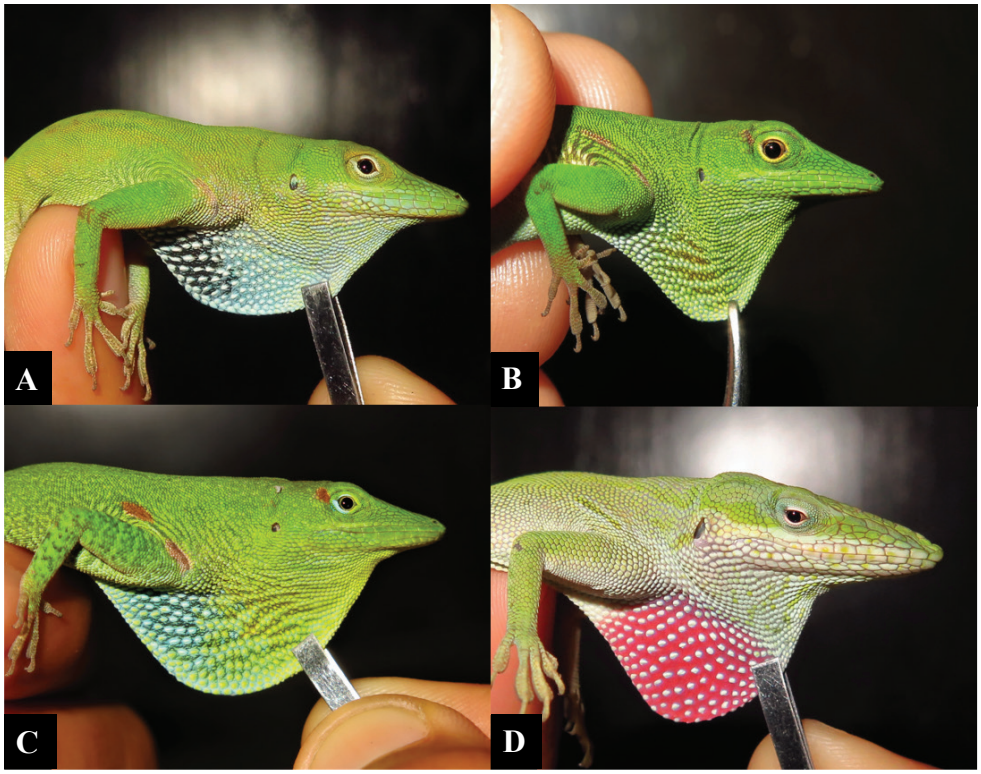



Figure 2. Representative specimens (all adult males) of the species treated in this work as well as a specimen that we considered intermediate in morphology between *A. chlorocyanus* and *A. cyanostictus*. A, *A. chlorocyanus*. B, *A. cyanostictus*. C, intermediate. D, *A. porcatus*.

For specimen's examination, the photographs were revised for two characters: (1) dewlap coloration (see below) and (2) body coloration (i.e., presence versus absence of pale brown blotches above the shoulder or near eye). For dewlap coloration, we checked if there was black suffusion on the posterior portion of the dewlap and also categorized the intensity of the black suffusion (i.e., absent, weak, strong). Based on the results of this morphological evaluation, we placed each specimen in one of five categories reflecting its phenotype: 0 = 100 % *chlorocyanus* phenotype; 0.25 = intermediate, but exhibiting more of the *chlorocyanus* characteristics than those for *cyanostictus*; 0.5 = intermediate, exhibiting equally characteristics of both *cyanostictus* and *chlorocyanus*; 0.75 = intermediate, but exhibiting more of the *cyanostictus* characteristics than those for *chlorocyanus*; and 1 = 100 % *cyanostictus* phenotype. This category number was later translated into the species ID (Table I).

To test the null hypothesis of no association between phenotypic class (pure species 1, intermediate, pure species 2) and mitochondrial cluster (clade 1, clade 2), we conducted a 3 x 2 Fisher's exact test.

Table I. Specimen's assignation and identification

| **Black suffusion on dewlap** | **Brown spot** | **Assignation** | **Species ID** |
|---|---|---|---|
| strong | absent | 0.0 | *A*. chlorocyanus |
| weak | absent | 0.0 | *A*. chlorocyanus |
| strong | present | 0.5 | intermediate |
| weak | present | 0.75 | intermediate |
| absent | present | 1 | *A*. cyanostictus |
| absent | absent | 2 | *A*. porcatus |

## RESULTS

*Morphology*. We collected 41 individuals (33.9 %) with phenotypic characteristics for *Anolis chlorocyanus* (our category 0) and 17 (14.0 %) with characteristics typical for *A. cyanostictus* (our category 1). However, we found 36 individuals (29.8 %) with characteristics of both species (our categories 0.5 and 0.75, but none with our category 0.25). 10.8 % of these 36 individuals were categorized as 0.5, that is, they exhibited equally characteristics of both species (black suffusion on dewlap and brown blotches present); 15.1 % were allocated to our category 0.75, showing more characteristics of one species than of the other (Fig. 3). In the case of *A. porcatus*, the 27 individuals reviewed (22.3 % of total samples), corresponded well to the characteristics described for this species (Fig. 2d).

Individuals of all categories and phenotypically pure species were only found at NBG (Fig. 3). At PMO, PMS and PC we found *A. porcatus*, and intermediates individuals along with just one of the native species. Phenotypically pure *A. chlorocyanus* and *A. porcatu*s were obtained at SD. The PMN was the only locality were all the individuals, had the characteristics of the species *A. chlorocyanus* (Fig. 3).

The phylogenetic tree reconstructed with the 16S sequences placed all the individuals in three clades: in one clade, *chlorocyanus* phenotypes were in the majority, the second clade consisted mainly of *cyanostictus* phenotypes, and in the third clade all individuals have phenotypic characteristics of the species *A. porcatus*. For the *chlorocyanus* clade, 51 of 71 individuals possess the *A. chlorocyanus* phenotype; 12 are individuals with an intermediate phenotype

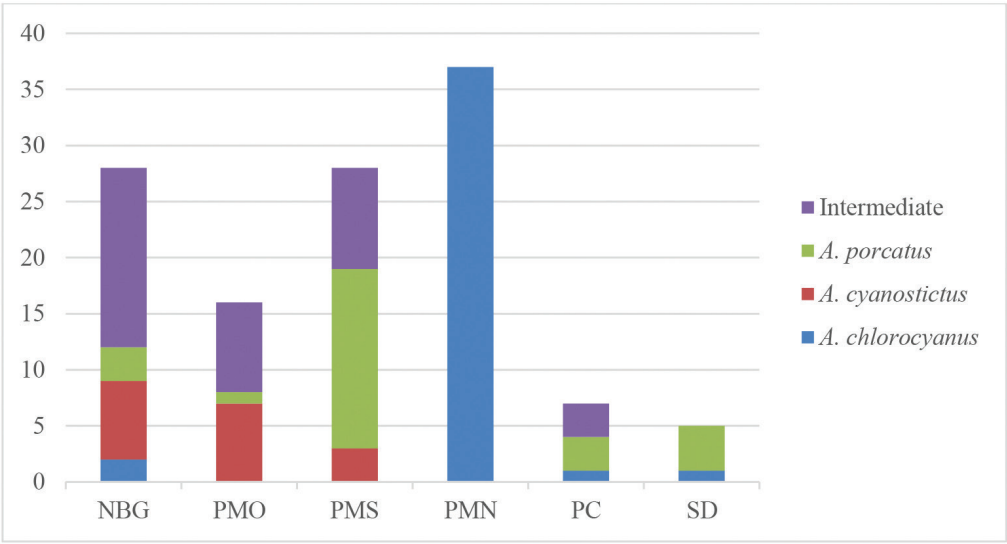



Figure 3. Distribution of specimens collected based on phenotypic characteristics.

between this species and *A. cyanostictus*, of which six were placed in the phenotypic category of 0.5 (black suffusion strong and pale brown blotches) and six specimens were categorized as 0.75 (characteristics more typical for one species than the other). In addition to these intermediates, this clade includes eight individuals with *A. cyanostictus* phenotype (Category 1).

The *cyanostictus* clade contained 37 individuals, of which 12 have the typical phenotype of *A. cyanostictus* (Category 1) and 24 have an intermediate phenotype between *A. cyanostictus* and *A. chlorocyanus*. Of the latter group, nine were in the phenotypic category of 0.5, while 15 were placed in 0.75. This clade includes only a single individual with the *A. chlorocyanus* phenotype (Category 0). We tested for a genotype/phenotype association between *A. cyanostictus* and *A. chlorocyanus* only, because of the complete association between mitochondrial clade 3 and the *A. porcatus* phenotypes. The test rejected the null hypothesis and showed a clear association of the *A. chlorocyanus* phenotype with clade 1 and *A. cyanostictus* with clade 2 (Table II).

Table II. Association of phenotypic class with mitochondrial clade. Given is the contingency table with the observed values followed by the expected values in brackets. The association was highly significant ($X^2 = 46.81$, $p < 0.0001$).

| | ***A. chlorocyanus* phenotype** | **intermediate** | ***A. cyanostictus* phenotype** |
|---|---|---|---|
| Mitochondrial clade 1 | 51 (34.19) | 12 (23.67) | 8 (13.15) |
| Mitochondrial clade 2 | 1 (17.81) | 24 (12.33) | 12 (6.85) |

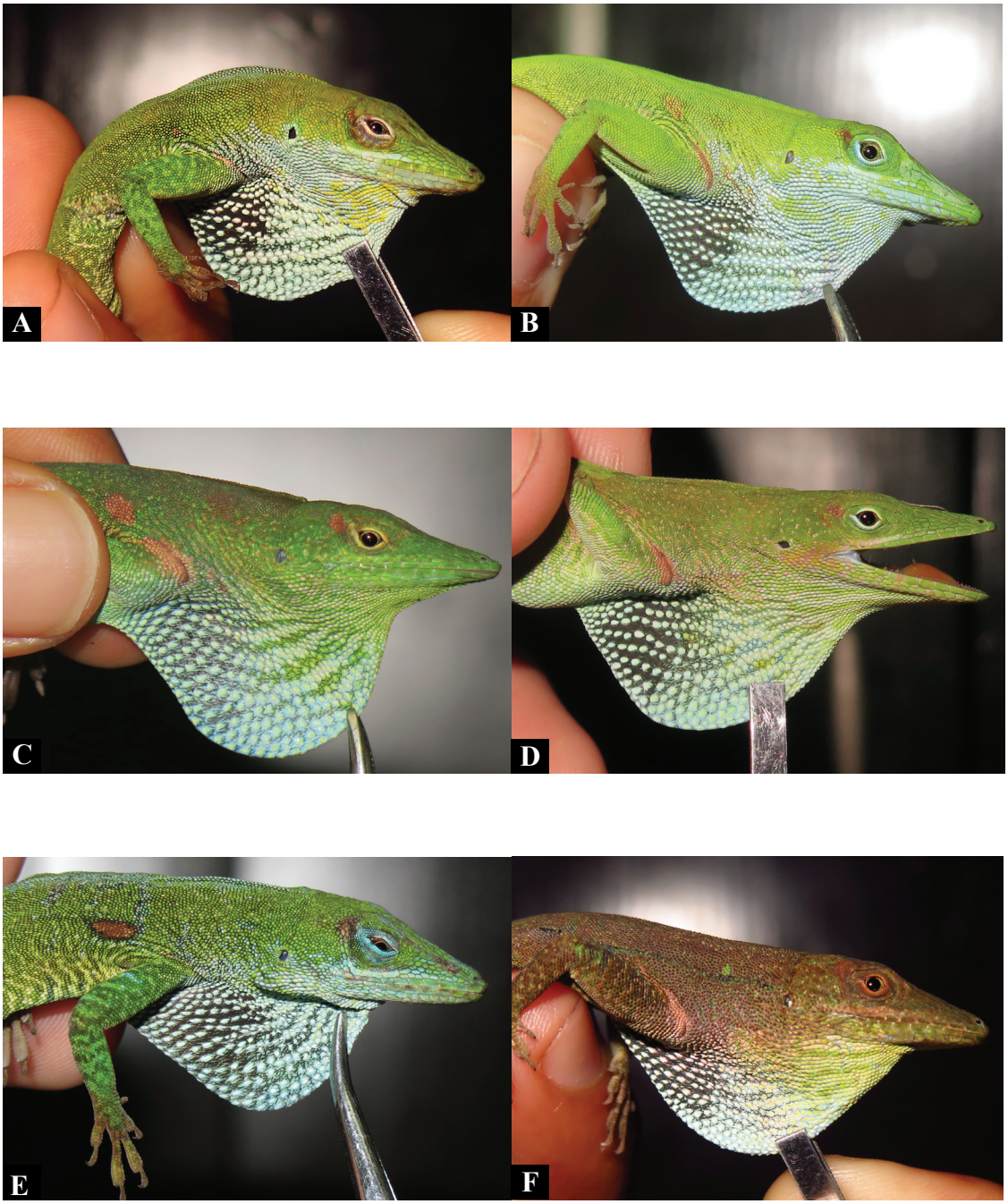



Figure 4. Intermediate individuals assigned to category 0.5. All these specimens had a strong black suffusion on dewlap and had pale brown blotches above shoulder and near eye present. A, MNHNSD 23.3767. B, MNHNSD 23.3765. C, SMF 105326. D, SMF 105319. E, MNHNSD 23.3762. F, MNHNSD 23.3766.

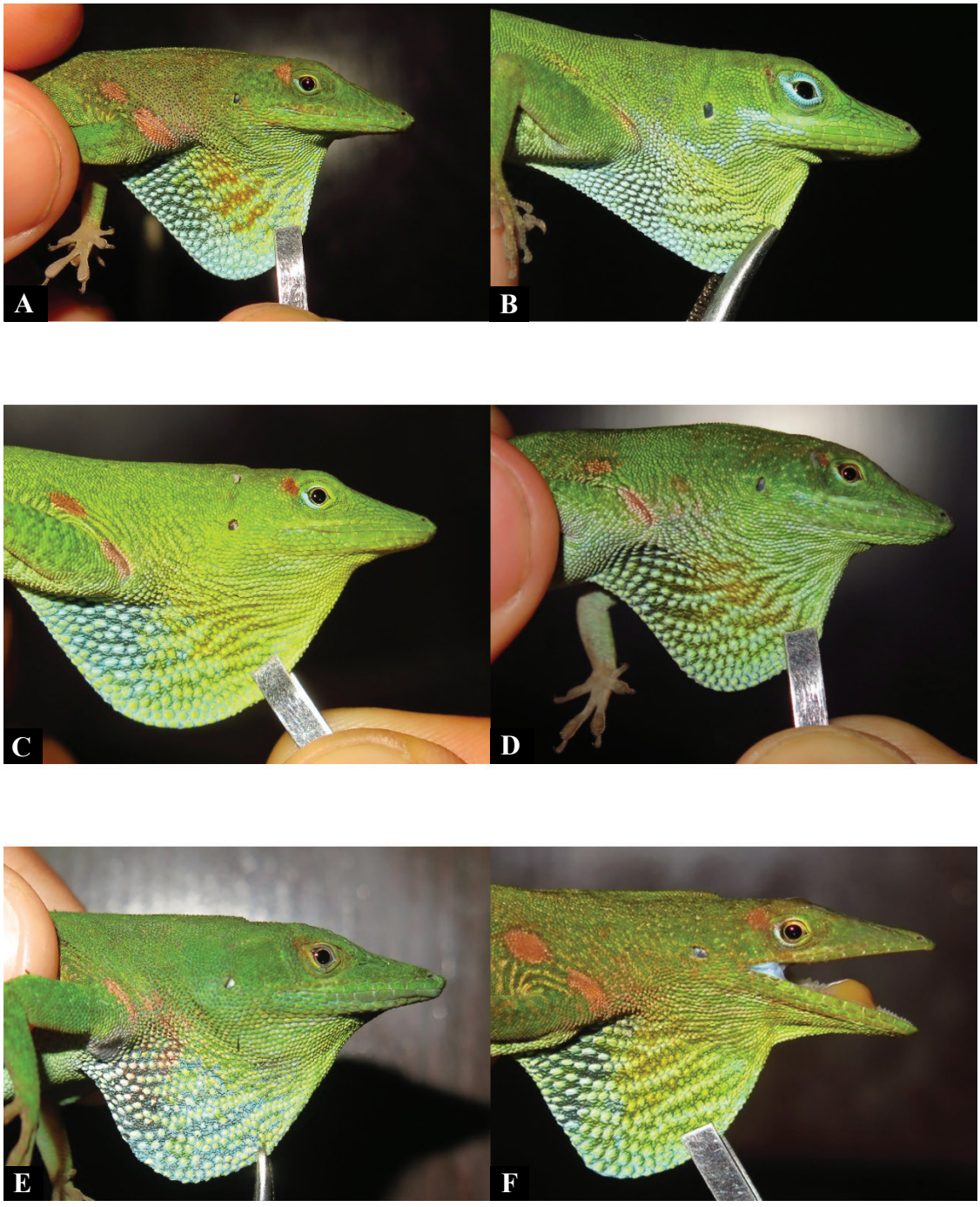
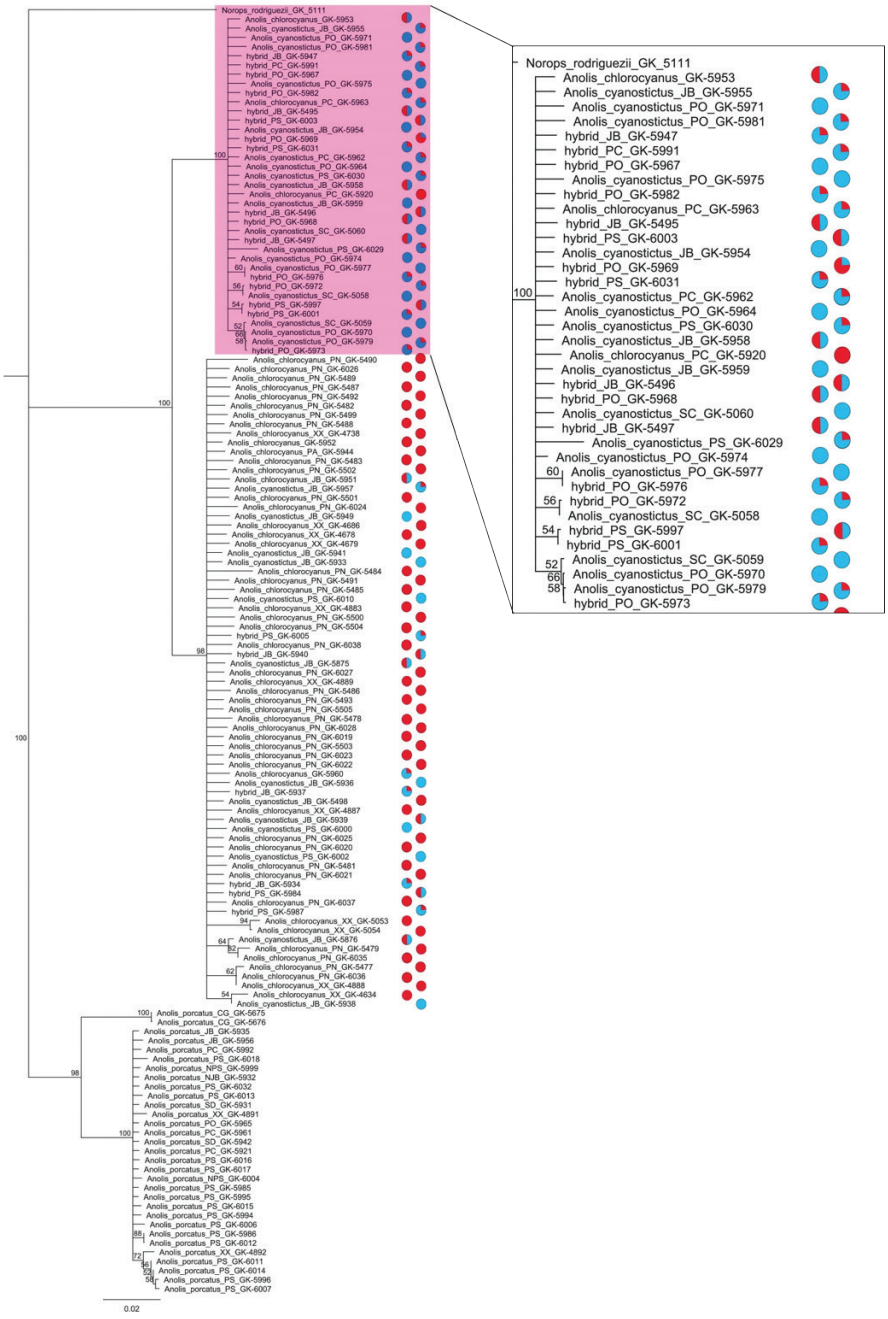


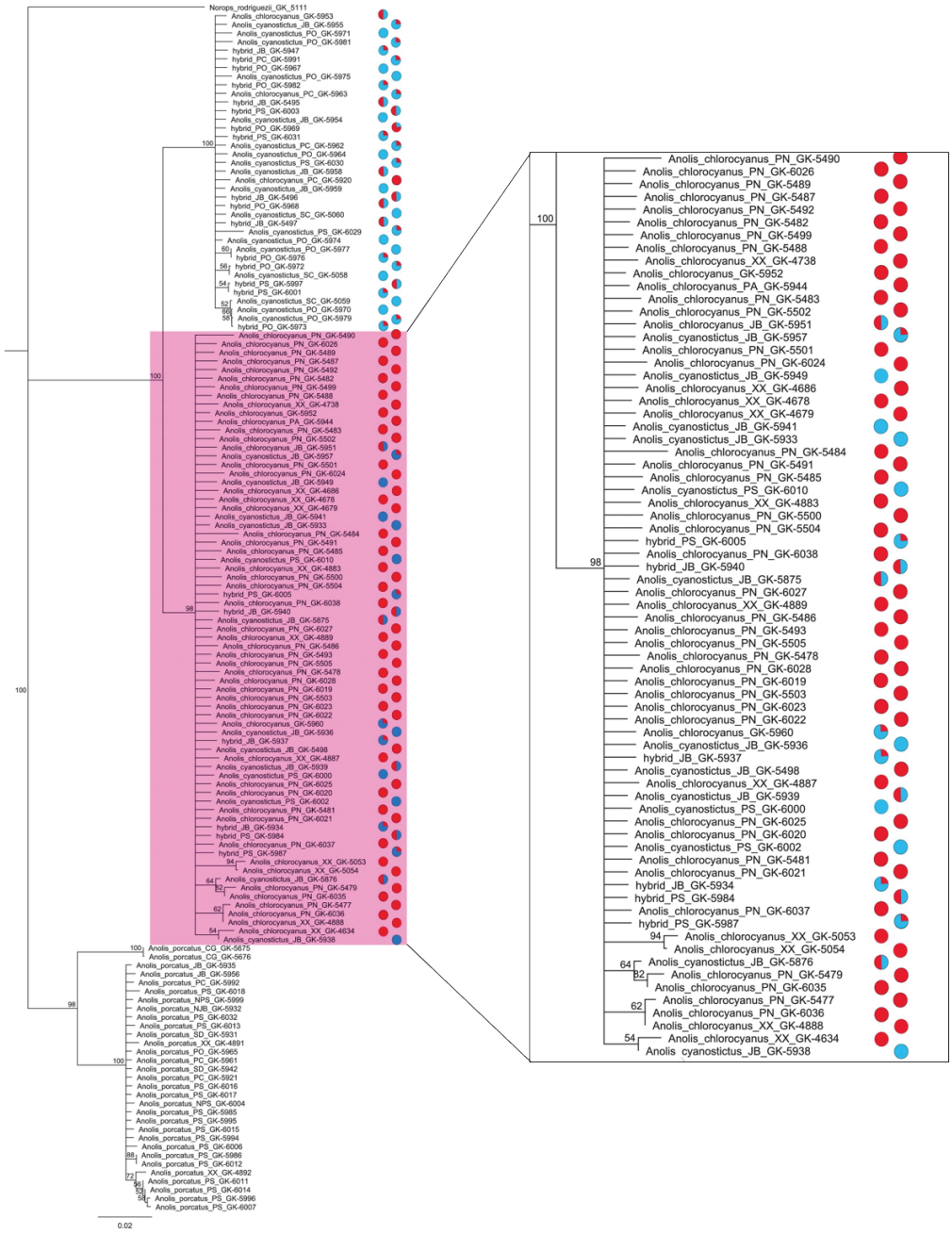

Figure 5. Intermediate individuals assigned to category 0.75. All these specimens had the black suffusion weak and the brown spot above shoulder and near eye present. A, MNHNSD 23.3793. B, GK-5937. C, MNHNSD 23.3783. D, MNHNSD 23.3792. E, SMF 105344. F, MNHNSD 23.3746.

FIGURE 6

(a) ***Anolis cyanostictus*** **clade**



(b) ***Anolis chlorocyanus*** **clade**



## (c) ***Anolis porcatus*** **clade**

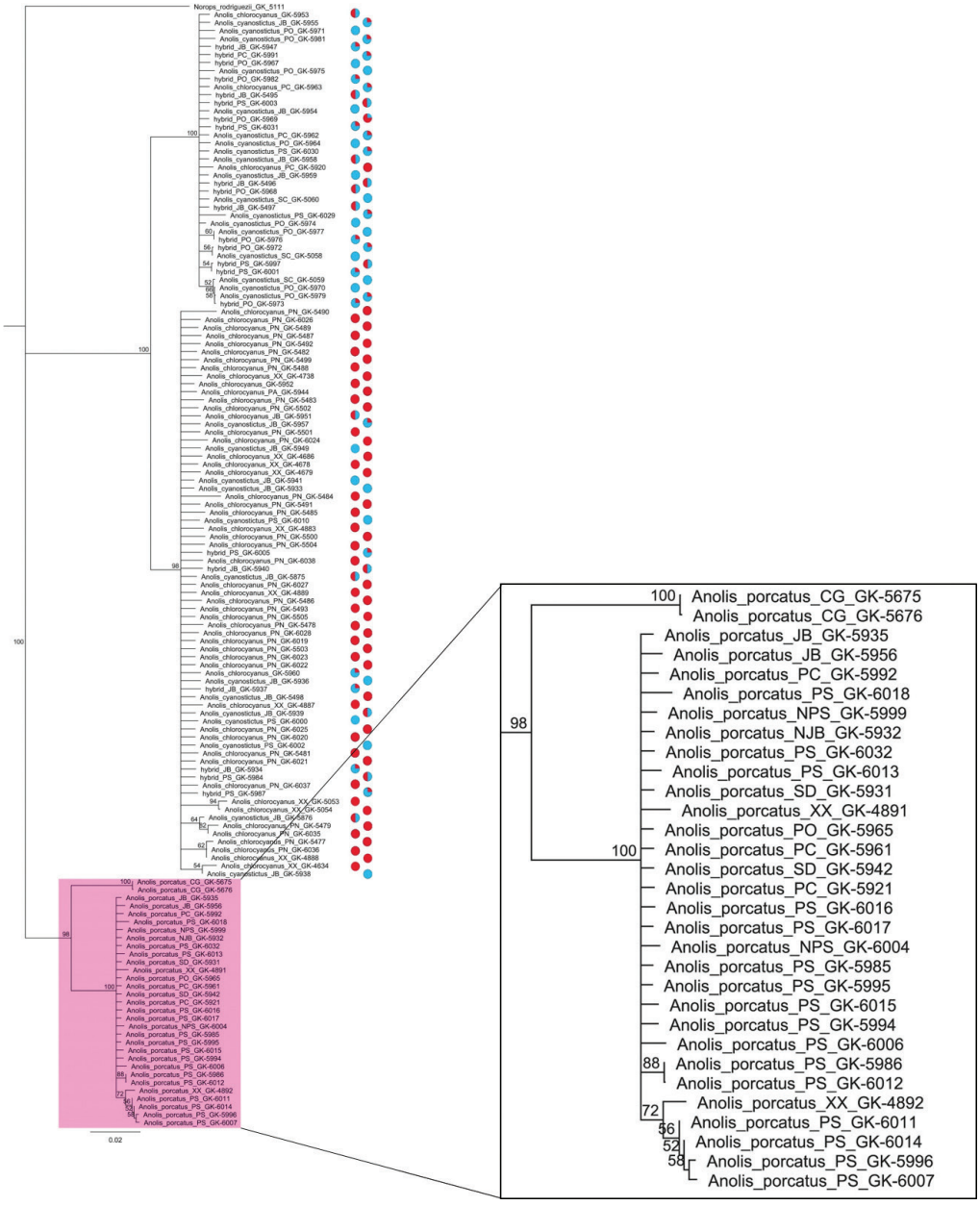



Figure 6. Phylogenetic tree obtained by analyzing Neighbors Union (Neighbor Joining, NJ) of the 16S gene sequences. The numbers at the nodes represent the bootstrap values. (a) *chlorocyanus* clade, (b) *cyanostictus* clade, (c) *porcatu*s clade. The pie diagram shows the morphological assignment, *A.chlorocyanus* (red), *A. cyanostictus* (blue).

## DISCUSSION

According to Köhler and Hedges (2016), the evidence presented in Garcia *et al*. (1994) does not constitute reliable evidence for hybridization between *Anolis peynadoi* (formerly *A. chlorocyanus*) and *A. viridius* (formerly *A. coelestinus*). Therefore, our work constitutes the first report of hybridization between two species of green anoles from Hispaniola.

A general cyto-nuclear association between morphological (as a proxy for nuclear loci) and mitochondrial data, accompanied by incongruence in some individuals constitutes strong indication for hybridization between species (e.g., Pfenninger *et al*., 2002; Dépraz *et al*., 2009), as found between the two endemic species *A. chlorocyanus* and *A. cyanostictus*. Based on their intermediate morphology, hybrids can be placed in two groups: those showing equally characteristics of both parental species and those that are distinctly more similar in their phenotype to one of the parental species. These findings indicate the presence of backcrosses of hybrids with one of the parental species. Some hybrids were found in places where one of the species (*A. cyanostictus* or *A. chlorocyanus*, respectively) was apparently absent, or its existence at least not documented by us, suggesting (1) a small population of the species not found by us or instead, (2) that these intermediate individuals are the result of a historical hybridization event and that one of the two parental species had become locally extinct since, perhaps even by this introgression (Rhymer & Simberloff, 1996).

In both clades of these species we found individuals with intermediate phenotypic characteristics and individuals whose phenotypic characteristics are typical for one species but genetically they clustered with the other. Accordingly, the lack of intermediate morphological traits is not a reliable criterion to distinguish between hybrid and non-hybrid individuals; this is similar to what was found by Cedeño-Vázquez *et al*. (2008), in crocodiles. In some cases, hybridization can occur due to a shortage of conspecific mating partners, especially when a rare species and a common species are found in sympatry (Wirtz, 1999). In the case of the hybrids collected in the NBG, more phenotypically pure individuals of *A. cyanostictus* than of *A. chlorocyanus* were found, suggesting that at this site *A. cyanostictus* is the much more common species and *A. chlorocyanus* is a relatively rare species. Assuming a female mate choice, it is likely that hybridization occurs mostly between females of *A. chlorocyanus* (rare species) with males of *A. cyanostictus* (common species).

The fact that only a few reports on anoles hybridization exist (e.g., Gorman & Atkins, 1968; Glor *et al*., 2004; Köhler *et al*., 2010; Jezcova *et al*., 2013; Wegener *et al*., 2019) and even fewer reports on interspecific mating (e.g., Arias, 1985), might be interpreted as evidence of the existence of good reproductive isolating mechanisms, but could also be interpreted as a lack of combined genetic and morphologic investigations. (Schenk *et al*., 2008).

In the particular case of PMN, given the congruence of the morphological and the genetic results, all individuals collected were assigned to the species *A. chlorocyanus*, i.e., no specimens of the other species were caught, nor specimens with an intermediate morphology. This may be due to the fact that the Isabela River separates this park from the rest of the areas studied, possibly acting as a geographical barrier, favoring the isolation of this species and preventing the dispersal of these anoles across the river.

Interestingly, sympatry of *A. cyanostictus* and *A. chlorocyanus* along with evidence of hybridization was only documented in areas that are historically known as the range of distribution of *A. cyanostictus*, but not in the original range of *A. chlorocyanus*. We assume that the latter species is translocated with human aid, most likely by bringing decorative plants into the metropolitan area. Flower pots with substrate containing anole eggs are a likely source of anoles when brought to a new place.

We did not find evidence of hybridization between either of the endemic species with the introduced species *A. porcatus*. However, Arias (1985) observed males of *A. cyanostictus* trying to copulate with females of *A. porcatus*, unsuccessfully due to rejection by the latter.

## CONCLUSIONS

Our study revealed evidence for hybridization between *Anolis chlorocyanus* and *A. cyanostictus* in the metropolitan area of Santo Domingo, Dominican Republic. The hybrids between these two species were grouped into three categories: (1) individuals that exhibit equally characteristics of both species, (2) individuals that exhibit more characteristics of one species than of the other, and (3) individuals that phenotypically represent one of the two species but that cluster genetically with the other species. Therefore, in areas of sympatry identification at the species level based on morphology is not reliable.

## ACKNOWLEDGMENT

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## APPENDIX A

Specimens examined with their phenotypic category assignment (Phenot), genetic clade (0 = *chlorocyanus* clade; 1 = *cyanostictus* clade), identification (ID), locality, GPS coordinate and their corresponded genbank accession numbers.

| Specimen ID | Museum Number | Phenot | Clade | ID | Locality | Latitude | Longitude | GenBank Number |
|---|---|---|---|---|---|---|---|---|
| GK-5933 | SMF 105301 | 1 | 0 | hybrid | NBG | 18.49534 | -69.95293 | MN514321 |
| GK-5936 | SMF 105302 | 1 | 0 | hybrid | NBG | 18.49133 | -69.95732 | MN514322 |
| GK-5938 | MNHNSD 23.3740 | 1 | 0 | hybrid | NBG | 18.49133 | -69.95845 | MN514323 |
| GK-5941 | MNHNSD 23.3741 | 1 | 0 | hybrid | NBG | 18.49165 | -69.95587 | MN514325 |
| GK-5954 | SMF 105304 | 1 | 1 | *A. cyanostictus* | NBG | 18.49785 | -69.95015 | MN514327 |
| GK-5959 | MNHNSD 23.3743 | 1 | 1 | *A. cyanostictus* | NBG | 18.49410 | -69.95291 | MN514331 |
| GK-5964 | SMF 105305 | 1 | 1 | *A. cyanostictus* | PMO | 18.44759 | -70.00159 | MN514333 |
| GK-5967 | SMF 105306 | 1 | 1 | *A. cyanostictus* | PMO | 18.44935 | -69.99472 | MN514388 |
| GK-5970 | SMF 105307 | 1 | 1 | *A. cyanostictus* | PMO | 18.44935 | -69.99472 | MN514334 |
| GK-5971 | MNHNSD 23.3744 | 1 | 1 | *A. cyanostictus* | PMO | 18.44935 | -69.99472 | MN514335 |
| GK-5974 | MNHNSD 23.3745 | 1 | 1 | *A. cyanostictus* | PMO | 18.44787 | -69.99706 | MN514336 |
| GK-5975 | MNHNSD 23.3746 | 1 | 1 | *A. cyanostictus* | PMO | 18.44787 | -69.99706 | MN514337 |
| GK-5977 | MNHNSD 23.3747 | 1 | 1 | *A. cyanostictus* | PMO | 18.44817 | -70.00147 | MN514338 |
| GK-6000 | SMF 105309 | 1 | 0 | hybrid | PMS | 18.44632 | -69.94556 | MN514341 |
| GK-6002 | SMF 105310 | 1 | 0 | hybrid | PMS | 18.44632 | -69.94556 | MN514342 |
| GK-6010 | MNHNSD 23.3749 | 1 | 0 | hybrid | PMS | 18.43738 | -69.97121 | MN514343 |
| GK-5949 | MNHNSD 23.3750 | 1 | 0 | hybrid | NBG | 18.49534 | -69.95293 | MN514326 |
| GK-5478 | SMF 105313 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52222 | -69.95071 | MN514272 |
| GK-5479 | SMF 105314 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52231 | -69.92271 | MN514273 |
| GK-5481 | SMF 105315 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51841 | -69.91827 | MN514274 |
| GK-5483 | SMF 105316 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51875 | -69.95221 | MN514276 |
| GK-5484 | SMF 105317 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51841 | -69.91827 | MN514277 |

Appendix A. Continuation

| Specimen ID | Museum Number | Phenot | Clade | ID | Locality | Latitude | Longitude | GenBank Number |
|---|---|---|---|---|---|---|---|---|
| GK-5485 | SMF 105318 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51853 | -69.91879 | MN514278 |
| GK-5487 | MNHNSD 23.3752 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51844 | -69.91846 | MN514280 |
| GK-5488 | MNHNSD 23.3753 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51838 | -69.91791 | MN514281 |
| GK-5489 | MNHNSD 23.3754 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51881 | -69.95222 | MN514282 |
| GK-5490 | MNHNSD 23.3755 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51838 | -69.91791 | MN514283 |
| GK-5491 | MNHNSD 23.3756 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52219 | -69.95084 | MN514284 |
| GK-5493 | MNHNSD 23.3757 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52222 | -69.95071 | MN514286 |
| GK-5495 | SMF 105319 | 0.5 | 1 | hybrid | NBG | 18.49790 | -69.95375 | MN514380 |
| GK-5496 | MNHNSD 23.3758 | 0.5 | 1 | hybrid | NBG | 18.50081 | -69.94642 | MN514381 |
| GK-5497 | MNHNSD 23.3759 | 0.5 | 1 | hybrid | NBG | 18.50081 | -69.94642 | MN514382 |
| GK-5500 | SMF 105320 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51182 | -69.92204 | MN514288 |
| GK-5501 | SMF 105321 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51232 | -69.92000 | MN514289 |
| GK-5502 | SMF 105322 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51185 | -69.92040 | MN514290 |
| GK-5503 | MNHNSD 23.3760 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51185 | -69.92040 | MN514291 |
| GK-5505 | MNHNSD 23.3761 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51148 | -69.92157 | MN514293 |
| GK-5875 | SMF 105323 | 0.5 | 0 | hybrid | NBG | -- | -- | MN514319 |
| GK-5876 | SMF 105324 | 0.5 | 0 | hybrid | NBG | -- | -- | MN514320 |
| GK-5939 | MNHNSD 23.3762 | 0.5 | 0 | hybrid | NBG | 18.49020 | -69.95783 | MN514324 |
| GK-5940 | MNHNSD 23.3763 | 0.5 | 0 | hybrid | NBG | 18.49088 | -69.95679 | MN514385 |
| GK-5944 | MNHNSD 23.3764 | 0 | 0 | *A. chlorocyanus* | SD | -- | -- | MN514269 |
| GK-5951 | SMF 105326 | 0.5 | 1 | hybrid | NBG | 18.49161 | -69.95811 | MN514266 |
| GK-5953 | SMF 105327 | 0.5 | 1 | hybrid | NBG | 18.49789 | -69.95008 | MN514264 |
| GK-5958 | MNHNSD 23.3765 | 0.5 | 1 | hybrid | NBG | 18.49399 | -69.95598 | MN514330 |
| GK-5968 | SMF 105328 | 0.5 | 1 | hybrid | PMO | 18.44935 | -69.99472 | MN514389 |

| Specimen ID | Museum Number | Phenot | Clade | ID | Locality | Latitude | Longitude | GenBank Number |
|---|---|---|---|---|---|---|---|---|
| GK-5984 | SMF 105329 | 0.5 | 0 | hybrid | PMS | 18.44604 | -69.94566 | MN514395 |
| GK-5997 | MNHNSD 23.3766 | 0.5 | 1 | hybrid | PMS | 18.44632 | -69.94556 | MN514397 |
| GK-6003 | MNHNSD 23.3767 | 0.5 | 0 | hybrid | PMS | 18.44632 | -69.94556 | MN514399 |
| GK-6019 | SMF 105330 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52581 | -69.92589 | MN514294 |
| GK-6020 | SMF 105331 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52534 | -69.92652 | MN514295 |
| GK-6021 | SMF 105332 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52345 | -69.92583 | MN514296 |
| GK-6022 | SMF 105333 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52359 | -69.92567 | MN514297 |
| GK-6023 | SMF 105334 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52534 | -69.92652 | MN514298 |
| GK-6024 | SMF 105335 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52352 | -69.92547 | MN514299 |
| GK-6025 | SMF 105336 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52276 | -69.92490 | MN514300 |
| GK-6026 | SMF 105337 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52593 | -69.92618 | MN514301 |
| GK-6027 | SMF 105328 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52341 | -69.92500 | MN514302 |
| GK-6035 | MNHNSD 23.3768 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51836 | -69.91804 | MN514304 |
| GK-6036 | MNHNSD 23.3769 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52330 | -69.94794 | MN514305 |
| GK-6037 | MNHNSD 23.3770 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52330 | -69.94794 | MN514306 |
| GK-6038 | MNHNSD 23.3771 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51938 | -69.95202 | MN514307 |
| GK-5477 | MNHNSD 23.3772 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51938 | -69.95202 | MN514271 |
| GK-5482 | MNHNSD 23.3773 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51855 | -69.95230 | MN514275 |
| GK-5486 | MNHNSD 23.3774 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52252 | -69.95018 | MN514279 |
| GK-5498 | SMF 105339 | 0 | 0 | *A. chlorocyanus* | NBG | 18.50049 | -69.94707 | MN514318 |
| GK-5499 | MNHNSD 23.3775 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51083 | -69.92132 | MN514287 |
| GK-5504 | MNHNSD 23.3776 | 0 | 0 | *A. chlorocyanus* | PMN | 18.51228 | -69.91997 | MN514292 |
| GK-5952 | MNHNSD 23.3778 | 0 | 0 | *A. chlorocyanus* | NBG | 18.49071 | -69.95873 | MN514263 |
| GK-6028 | MNHNSD 23.3779 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52534 | -69.92652 | MN514303 |
| GK-5934 | SMF 105341 | 0.75 | 0 | hybrid | NBG | 18.49040 | -69.95785 | MN514383 |

Appendix A. Continuation

| Specimen ID | Museum Number | Phenot | Clade | ID | Locality | Latitude | Longitude | GenBank Number |
|---|---|---|---|---|---|---|---|---|
| GK-5937 | SMF 105342 | 0.75 | 0 | hybrid | NBG | 18.49096 | -69.95684 | MN514384 |
| GK-5947 | MNHNSD 23.3780 | 0.75 | 1 | hybrid | NBG | 18.49020 | -69.95781 | MN514386 |
| GK-5955 | MNHNSD 23.3781 | 0.75 | 1 | hybrid | NBG | 18.49755 | -69.95094 | MN514328 |
| GK-5957 | SMF 105343 | 0.75 | 0 | hybrid | NBG | 18.49534 | -69.95293 | MN514329 |
| GK-5960 | SMF 105344 | 0.75 | 0 | hybrid | NBG | 18.49131 | -69.95751 | MN514265 |
| GK-5962 | SMF 105345 | 0.75 | 1 | hybrid | PC | 18.47209 | -69.90864 | MN514332 |
| GK-5963 | MNHNSD 23.3782 | 0.75 | 1 | hybrid | PC | 18.47206 | -69.90868 | MN514267 |
| GK-5969 | SMF 105346 | 0.75 | 1 | hybrid | PMO | 18.44935 | -69.99472 | MN514390 |
| GK-5972 | SMF 105347 | 0.75 | 1 | hybrid | PMO | 18.44787 | -69.99706 | MN514391 |
| GK-5973 | SMF 105348 | 0.75 | 1 | hybrid | PMO | 18.44787 | -69.99706 | MN514392 |
| GK-5976 | MNHNSD 23.3783 | 0.75 | 1 | hybrid | PMO | 18.44759 | -70.00159 | MN514393 |
| GK-5979 | MNHNSD 23.3784 | 0.75 | 1 | hybrid | PMO | 18.44979 | -70.00165 | MN514339 |
| GK-5981 | MNHNSD 23.3786 | 0.75 | 1 | hybrid | PMO | 18.46233 | -69.99838 | MN514340 |
| GK-5982 | MNHNSD 23.3787 | 0.75 | 1 | hybrid | PMO | 18.46233 | -69.99838 | MN514394 |
| GK-5987 | SMF 105351 | 0.75 | 0 | hybrid | PMS | 18.44581 | -69.94562 | MN514396 |
| GK-5991 | MNHNSD 23.3789 | 0.75 | 1 | hybrid | PC | 18.47198 | -69.90866 | MN514387 |
| GK-6001 | SMF 105353 | 0.75 | 1 | hybrid | PMS | 18.44598 | -69.94550 | MN514398 |
| GK-6005 | SMF 105354 | 0.75 | 0 | hybrid | PMS | 18.44646 | -69.94558 | MN514400 |
| GK-6029 | MNHNSD 23.3791 | 0.75 | 1 | hybrid | PMS | 18.44478 | -69.94787 | MN514344 |
| GK-6030 | MNHNSD 23.3792 | 0.75 | 1 | hybrid | PMS | 18.44510 | -69.94655 | MN514345 |
| GK-6031 | MNHNSD 23.3793 | 0.75 | 1 | hybrid | PMS | 18.44537 | -69.94766 | MN514401 |
| GK-5492 | SMF 105355 | 0 | 0 | *A. chlorocyanus* | PMN | 18.52219 | -69.95084 | MN514285 |
| GK-5920 | SMF 105356 | 0 | 1 | hybrid | PC | 18.47208 | -69.90862 | MN514270 |

## APPENDIX B

*Anolis porcatus* and additional specimens examined. Abbreviations of localities: NBG = National Botanical Garden ‘‘Dr. Rafael M. Moscoso, PMS = Parque Mirador Sur, PMO = Parque Mirador Oeste, PC = Plaza de la Cultura, SD = Santo Domingo, VA = Villa Altagracia, LR = La Romana, BA = Bávaro, BC = Boca Chica, AD = Autopista Duarte and PP = Puerto Plata.

| Specimen ID | Museum Number | Species | Locality | Latitude | Longitude | GenBank Number |
|---|---|---|---|---|---|---|
| GK-5956 | MNHNSD 23.3794 | *A. porcatus* | NBG | 18.48978 | -69.95885 | MN514353 |
| GK-5932 | MNHNSD 23.3795 | *A. porcatus* | NBG | 18.48768 | -69.96184 | MN514351 |
| GK-6032 | MNHNSD 23.3796 | *A. porcatus* | PMS | 18.44141 | -69.96142 | MN514375 |
| GK-6013 | MNHNSD 23.3797 | *A. porcatus* | PMS | 18.43835 | -69.96703 | MN514369 |
| GK-5965 | MNHNSD 23.3798 | *A. porcatus* | PMO | 18.44885 | -69.99464 | MN514357 |
| GK-5961 | MNHNSD 23.3799 | *A. porcatus* | PC | 18.47205 | -69.90863 | MN514355 |
| GK-6006 | MNHNSD 23.3800 | *A. porcatus* | PMS | 18.43725 | -69.97080 | MN514365 |
| GK-5986 | MNHNSD 23.3801 | *A. porcatus* | PMS | 18.44803 | -69.94247 | MN514359 |
| GK-6012 | MNHNSD 23.3802 | *A. porcatus* | PMS | 18.43827 | -69.96722 | MN514368 |
| GK-6011 | MNHNSD 23.3803 | *A. porcatus* | PMS | 18.43725 | -69.97080 | MN514367 |
| GK-6014 | MNHNSD 23.3804 | *A. porcatus* | PMS | 18.43582 | -69.97744 | MN514370 |
| GK-5996 | MNHNSD 23.3805 | *A. porcatus* | PMS | 18.44823 | -69.94293 | MN514362 |
| GK-6007 | MNHNSD 23.3806 | *A. porcatus* | PMS | 18.43963 | -69.96449 | MN514366 |
| GK-5921 | SMF 105359 | *A. porcatus* | PC | 18.47207 | -69.90862 | MN514354 |
| GK-5931 | SMF 105360 | *A. porcatus* | SD | - | - | MN514376 |
| GK-5935 | SMF 105361 | *A. porcatus* | NBG | 18.49040 | -69.95785 | MN514352 |
| GK-5942 | SMF 105362 | *A. porcatus* | SD | 18.49575 | -69.77985 | MN514377 |
| GK-5985 | SMF 105363 | *A. porcatus* | PMS | 18.44717 | -69.94374 | MN514358 |
| GK-5992 | SMF 105364 | *A. porcatus* | PC | 18.47197 | -69.90866 | MN514356 |
| GK-5994 | SMF 105365 | *A. porcatus* | PMS | 18.45564 | -69.93234 | MN514360 |
| GK-5995 | SMF 105366 | *A. porcatus* | PMS | 18.45284 | -69.93379 | MN514361 |

Appendix B. Continuation

| Specimen ID | Museum Number | Species | Locality | Latitude | Longitude | GenBank Number |
|---|---|---|---|---|---|---|
| GK-5999 | SMF 105367 | *A. porcatus* | SD | 18.45357 | -69.92937 | MN514363 |
| GK-6004 | SMF 105368 | *A. porcatus* | SD | 18.45357 | -69.92937 | MN514364 |
| GK-6015 | SMF 105369 | *A. porcatus* | PMS | 18.43714 | -69.97083 | MN514371 |
| GK-6016 | SMF 105370 | A. porcatus | PMS | 18.43714 | -69.97111 | MN514372 |
| GK-6017 | SMF 105371 | *A. porcatus* | PMS | 18.43725 | -69.97080 | MN514373 |
| GK-6018 | SMF 105372 | *A. porcatus* | PMS | 18.44141 | -69.96128 | MN514374 |
| GK-4891 | SMF 97976 | *A. porcatus* | BC | 18.44918 | -69.60341 | MN514378 |
| GK-4892 | SMF 97977 | *A. porcatus* | BC | 18.44918 | -69.60341 | MN514379 |
| GK-5675 | SMF 105357 | *A. porcatus* | - | - | - | MN514349 |
| GK-5676 | SMF 105358 | *A. porcatus* | - | - | - | MN514350 |
| GK-5058 | SMF 99014 | *A. cyanostictus* | VA | 18.44004 | -69.99910 | MN514346 |
| GK-5059 | SMF 99015 | *A. cyanostictus* | VA | 18.44004 | -69.99910 | MN514347 |
| GK-5060 | SMF 99016 | *A. cyanostictus* | VA | 18.44004 | -69.99910 | MN514348 |
| GK-4634 | SMF 97836 | *A. chlorocyanus* | LR | 18.43476 | -69.19080 | MN514308 |
| GK-4678 | SMF 97841 | *A. chlorocyanus* | BA | 18.64256 | -68.34635 | MN514309 |
| GK-4679 | SMF 97842 | *A. chlorocyanus* | BA | 18.64821 | -68.36394 | MN514310 |
| GK-4686 | SMF 105311 | *A. chlorocyanus* | BA | 18.64735 | -68.42858 | MN514311 |
| GK-4738 | SMF 105312 | *A. chlorocyanus* | BC | 18.44780 | -69.61122 | MN514312 |
| GK-4883 | SMF 97858 | *A. chlorocyanus* | AD | 18.52900 | -70.00996 | MN514268 |
| GK-4887 | SMF 97861 | *A. chlorocyanus* | AD | 18.52900 | -70.00996 | MN514313 |
| GK-4888 | SMF 97862 | *A. chlorocyanus* | AD | 18.52900 | -70.00996 | MN514314 |
| GK-4889 | SMF 97847 | *A. chlorocyanus* | BC | 18.44918 | -69.60341 | MN514315 |
| GK-5053 | SMF 97840 | *A. chlorocyanus* | PP | 19.63135 | -70.58644 | MN514316 |
| GK-5054 | SMF 97841 | *A. chlorocyanus* | PP | 19.63135 | -70.58644 | MN514317 |

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