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The identity of the introduced green anole (Reptilia: Squamata) of Hawaii and other Pacific islands

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Abstract.—Green anoles of the *Anolis carolinensis* Voigt, 1832 species group have been become successfully established by human transport on many islands in the Pacific, from Okinawa in the west to Hawaii in the east. First recorded from Oahu in 1950, from the time of their discovery, and for decades afterwards, the green anoles of the Pacific were identified as the Cuban green anole, *Anolis porcatus*. We show that Pacific green anoles are readily distinguished from *A. porcatus* by the larger head scales of *A. porcatus* but are essentially indistinguishable from *A. carolinensis* from South Carolina, which come from within the range of the same mtDNA clade as the source of the Pacific invasion in Texas and Louisiana. Genetically distinct *A. carolinensis* from southern Florida are intermediate in scale size, differing in this respect from Pacific green anoles. These results are in harmony with recent molecular genetic studies on the phylogeny and status of green anoles from the Pacific, North America, and Cuba. The green anole of the Pacific is *A. carolinensis* sensu stricto.

Keywords: *Anolis carolinensis*, *Anolis porcatus*, biological species, Cuba, Florida, invasive species

The green anoles of the *Anolis carolinensis* group (Ruibal & Williams 1961) are widely distributed in the southeastern United States, Cuba, the Bahamas, and other West Indian islands (Williams 1969, Schwartz & Henderson 1991). Williams (1969) called them "the most successful of all anole colonists," and this is reflected not only in their extensive native range but in their establishment by human transport in other parts of North America (Jones & Lovich 2009), the West Indies (Schwartz & Henderson 1991), and the islands of the Pacific. In the latter islands they are known from Hawaii (Oahu, Hawaii, Kauai, Molokai, Lanai, Maui), the Marianas (Guam, Rota, Saipan, Tinian, Managaha), Palau (Malakal, Oreor), Yap, the Bonin Islands (Chichi-jima, Haha-jima, Ani-jima), and the Ryukyu Islands (Okinawa) (Shaw & Breese 1951, Vance 1987, Mayer & Lazell 1992, Ota et al. 1995, McKeown 1996, Crombie & Pregill 1999, Zug 2013, Sugawara et al. 2015, Michaelides et al. 2018).

At the time of their first discovery, on Oahu in 1950 (Fig. 1), Pacific green anoles were identified as *Anolis carolinensis porcatus* Gray, 1840, a Cuban form, on the authority of James A. Oliver (Shaw & Breese 1951). This identification was followed for many years thereafter (Oliver & Shaw 1953, Hunsaker & Breese 1967, Smith & Kohler 1977, McKeown 1978, Chan et al. 1987, Collins 1990, Michael 1996). Vance (1987) considered that the identification as *A. porcatus* was indeed correct, identifying specimens from the

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Fig. 1. *Anolis carolinensis* collected on 7 Mar 1950 in Kaimuki, Honolulu, Oahu, Hawaii (SDNHM 41049–41051), all males; a scale-retaining composite made from three photographs by B. D. Hollingsworth. Note the presence of dark postorbital spots, light flank spots (rather faint in SDNHM 41050) and a middorsal light stripe (only in SDNHM 41049). Scale in millimeters.

Marianas Islands as such and suggesting that the Pacific green anoles may have originated from central Cuba (Las Villas or Camagüey); he did not cite any characters in support of these identifications. However, Powell (1992; see sources cited therein, including personal communications from the present authors and Ronald I. Crombie) and McKeown (1996, citing Mayer & Lazell 1992) identified the Pacific green anoles as *A. carolinensis* Voigt, 1832, the North American form, and most authors have followed this identification since (e.g., Crombie & Pregill 1999, Zug 2013).

Recent molecular genetic studies confirmed that the genetic origins of the Pacific green anoles are from within the North American form, derived from a genetic lineage distributed from Texas to South Carolina (Michaelides et al 2018). Here, we present morphological data consonant with these genetic data, showing that the green anole of the Pacific islands is derived from the North American form, *Anolis carolinensis*.

Materials and Methods

We examined the following morphological characters in green anoles from various Pacific islands, North America, and Cuba (see Appendix): scales between supraorbital semicircles (SSC); scales between the interparietal and the supraorbital semicircles (SCIP); scales across the snout between the second canthals (SNSC); scales behind the rostral (SCBR; also called postrostrals); minimum number of loreal rows counted from the second canthal to contact with the supralabials

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(LORMIN); and number of scales in the space bounded by the canthals, supralabials, and preoculars (LORNUM). The number of loreal rows, as defined by Williams et al. (1995), is counted in a straight line below the second canthal. LORMIN differs from this in that the count may diverge from a straight line if doing so lowers the count; LORMIN must be less than or equal to the number of loreal rows as defined by Williams et al. (1995). SCIP, LORMIN, and LORNUM are bilateral characters; left and right counts were summed to give a single value for each specimen examined. For all of these head scale characters, smaller values indicate larger scales (large-scaled lizards have low values); Williams et al. (1995) provide further discussion and illustrations.

For statistical analyses, specimens were grouped into four regions: Pacific ($n = 84$), with subregions West Pacific (Chichi-jima; the Marianas, including Guam, Rota, Tinian, Saipan, Managaha; and Yap) and Hawaii (Oahu, Kauai); South Carolina ($n = 12$); South Florida ($n = 15$); and Cuba ($n = 32$), with subregions West Cuba (Pinar del Río, Isla de la Juventud, La Habana), Central Cuba (Camagüey), and East Cuba (Oriente). Within North America, South Carolina is within the range of the widespread Gulf/Atlantic mtDNA lineage, whereas South Florida is inhabited by a genetically distinct mtDNA lineage (Michaelides et al. 2018). Preliminary analyses of variance (ANOVA) indicated there were few or no significant differences among subregions within regions (see Results), so further ANOVAs were carried out with regions as the factor. Post hoc tests of pairwise differences between regions were made using the Tukey-Kramer method (Sokal & Rohlf 2012).

For discriminant analysis (Gotelli & Ellison 2013, Manly & Navarro Alberto 2017), LORNUM was not included, as this character had the smallest sample size; only the 64 specimens with data for all five of the other characters were used. These specimens with complete data were grouped into Pacific (Guam, Rota, Saipan, Managaha, Oahu), South Carolina, South Florida and Cuba (La Habana, Oriente). All statistical analyses were carried out with SYSTAT 10 (SPSS Inc., Chicago, IL).

Elements of color pattern, especially the size of the dark postorbital spot and presence of a shoulder ocellus, were noted in the specimens used for morphological study, but the variable visibility of these elements in preserved anoles limited us to qualitative assessment of these characters. We have also seen in life green anoles from Hawaii and throughout its North American range, as well as *A. porcatus* from Guantanamo, Cuba, and from the introduced population in Santo Domingo, Dominican Republic. We have included our experience with these in our assessment of color differences.

Results

Univariate analysis of morphology.— There were no significant differences among subregions within regions (F tests, all $p > 0.1$) for any characters (Table 1), except for SSC, in which there was a small but statistically significant difference between West Pacific and Hawaii ($\bar{X} = 1.4$ and $\bar{X} = 1.2$, respectively; $F_{1,81} = 5.02$, $p = 0.03$). Further analyses used regions (i.e., Pacific, South Carolina, South Florida, and Cuba) as the basis for analysis.

There were significant differences among regions for all of the morphological traits (Fig. 2). For all characters, Pacific and South Carolina had higher counts, Cuba the lowest, with South Florida in between. By post hoc tests of pairwise differences between regions (Fig. 2), the Pacific showed no significant differences from South Carolina but was significantly different from Cuba for all characters. South Carolina was significantly different from Cuba for all characters, except SCIP. South Florida was

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Table 1.—Scale counts of samples of *Anolis carolinensis* group anoles. For each region and subregion, means, ranges, and standard deviations (with sample size in parentheses) are given in successive rows.

Region	Subregion	SSC	SCIP	SNSC	SCBR	LORMIN	LORNUM
Pacific		1.3	4.4	7.2	7.0	7.8	62.3
		1–2	2–6	5–8	7–8	6–10	43–76
		0.46 (83)	0.96 (82)	0.93 (41)	0.22 (42)	0.93 (42)	10.08 (10)
	West Pacific	1.4	4.4	7.2	7.1	7.9	70
		1–2	2–6	5–8	7–8	6–10	–
		0.49 (48)	0.90 (47)	0.73 (29)	0.25 (30)	0.91 (30)	(1)
	Hawaii	1.2	4.5	7.3	7.0	7.6	61.4
		1–2	2–6	6–8	7–7	6–9	43–76
		0.38 (35)	1.03 (35)	0.62 (12)	0 (12)	1.00 (12)	10.30 (9)
South Carolina		1.4	4.1	7.5	7.2	8.3	61.7
		1–2	3–6	6–10	7–8	7–10	52–74
		0.51 (12)	0.79 (12)	1.09 (12)	0.39 (12)	0.87 (12)	6.85 (12)
South Florida		0.9	3.9	6.5	6.6	6.6	51.0
		0–1	2–6	6–7	5–8	6–8	49–55
		0.35 (15)	1.25 (15)	0.71 (2)	0.74 (15)	0.85 (14)	3.46 (3)
Cuba		0.6	3.4	5.6	6.1	6.0	37.9
		0–1	2–6	5–7	5–7	4–8	29–49
		0.50 (32)	1.21 (32)	0.63 (14)	0.86 (13)	1.30 (14)	6.20 (13)
	West Cuba	0.5	3.4	5.7	6.1	6.2	38.7
		0–1	2–6	5–7	5–7	4–8	30–49
		0.51 (22)	1.22 (22)	0.63 (13)	0.90 (12)	1.21 (13)	5.84 (12)
	Central Cuba	0.7	3.3	–	–	–	–
		0–1	3–4	–	–	–	–
		0.58 (3)	0.58 (3)	–	–	–	–
	East Cuba	0.7	3.4	5.0	6.0	4.0	29
		0–1	2–6	–	–	–	–
		0.49 (7)	1.51 (7)	(1)	(1)	(1)	(1)

not significantly different from Cuba in four characters (SSC, SCIP, SNSC, LORMIN) and not significantly different from the Pacific or South Carolina in three characters (SCIP, SNSC, LORNUM); for SCBR it differed significantly from all other regions.

Despite the pattern of the Pacific and South Carolina not differing significantly from one another, but usually differing significantly from Cuba (South Florida being intermediate), the overlap of the ranges of the characters (Table 1) means that no single character can distinguish lizards from these regions. LORNUM (Fig. 2F) comes closest, with a single Pacific anole falling within the range of Cuban ones.

Multivariate analysis of morphology.—There was a significant difference among the multivariate centroids of the regions by Wilks' lambda (lambda = 0.239, $F_{15,154} = 6.97$, $p < 0.0001$). When plotted in the space defined by the first two discriminant functions (Fig. 3), Cuba is largely separated from the Pacific and South Carolina, with the latter two regions broadly overlapping one another; the discrimination of Cuba from the latter two regions is provided by discriminant function 1. South Florida falls within Cuba on discriminant function 1 but has somewhat higher scores on discriminant function 2, so that the South Florida specimens (only two of which had complete data for the discriminant analysis) are separated in the two-dimensional space.

The classification matrix (Table 2) shows only a relatively modest 67% (43/64) correct assignment to region of the lizards used in the discriminant analysis. However, almost all of the misclassifica-

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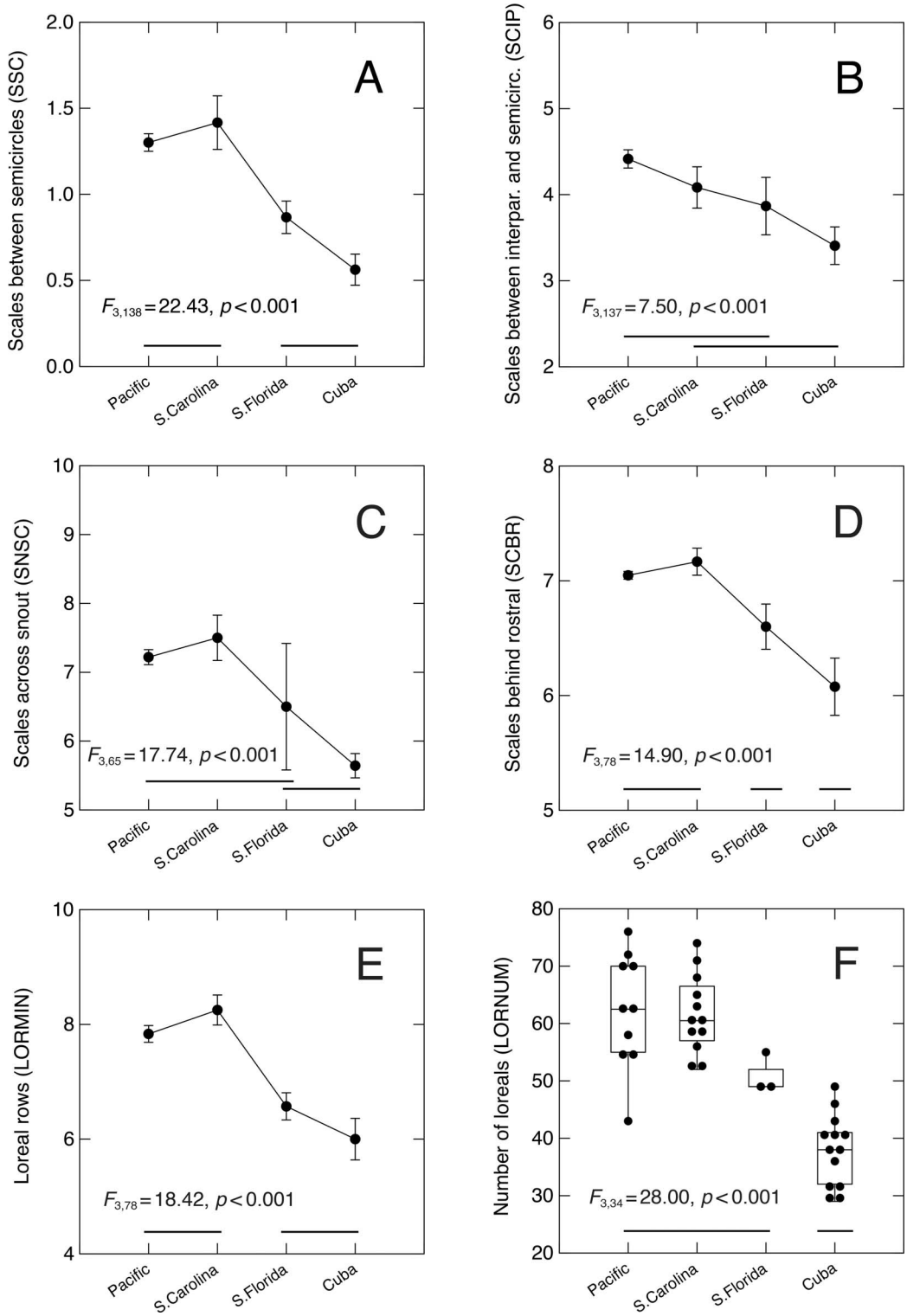


Fig. 2. A–E, ANOVA main effect plots for SSC, SCIP, SNSC, SCBR, and LORMIN, showing the mean with one standard error; the standard errors are based on each region's standard deviation, not the pooled standard deviation. The maximum and minimum of each ordinate is the observed range of the character. F, Dox plot of LORNUM. For all panels, F and p values from ANOVAs with region as the factor are given, and horizontal bars join regions not significantly different ($p > 0.05$) by the Tukey-Kramer method.

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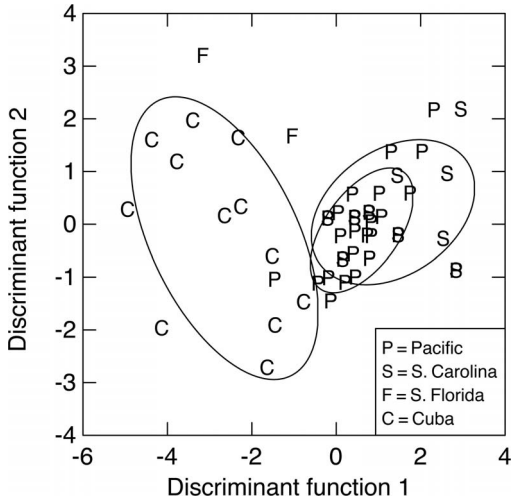


Fig. 3. Scatter plot of the first and second axes from a discriminant analysis of the regions Pacific (P, $n = 37$), South Carolina (S, $n = 12$), South Florida (F, $n = 2$), and Cuba (C, $n = 13$). One standard deviation confidence ellipses are shown for regions with $n > 2$.

tion is due to anoles from the Pacific being misclassified as being from South Carolina (9 of 37), and vice versa (6 of 12). These misclassifications are readily comprehended by reference to Fig. 3, which shows the already noted broad overlap between these two regions. If these two regions are grouped together, only 1 of 49 lizards from the joined grouping is misclassified. Similarly, if South Florida and Cuba are grouped together, only 1 of 15 lizards from the joined grouping is misclassified.

The two specimens misclassified under the joined groupings are, firstly, a Pacific anole, USNM 301052 from Guam, which is misclassified as Cuban. This individual can be seen as the only "P" within the Cuba confidence ellipse in Fig. 3. The second is a Cuban anole, USNM 194330 from Marianao, La Habana, which is misclassified as from the Pacific (in Fig. 3, this specimen is the "C" closest to the Pacific specimens). Note that this lizard is within the Cuba confidence ellipse and does not overlap Pacific or South Carolina specimens on discriminant function 1. It is

Table 2.—Classification matrix from discriminant analysis of the regions. Rows are regions from which a specimen originated; columns are the regions into which they were classified.

	Classified as:			
Origin	Pacific	South Carolina	South Florida	Cuba
Pacific	27	9	0	1
South Carolina	6	6	0	0
South Florida	0	0	2	0
Cuba	1	0	4	8

classified as Pacific because it is closer to the Pacific centroid. The loreal number (LORNUM) of this lizard was 41, outside of the range of this character for Pacific anoles (43–76). Considering this character (which was not included in the discriminant analysis due to small sample size) would allow it to be correctly identified.

Coloration.—Hawaiian lizards examined in life are typically green in the light color phase, with one or two rows of light dots along the flank, and a large, dark postorbital spot that extends over most of the temporal region when fully visible (see McKeown 1978:29). Females and some males have a light middorsal stripe that is invaded and partially obscured by darker markings from the sides (see McKeown 1978:30, 31). All of these pattern elements can also be discerned in some preserved specimens (Fig. 1). In this they resemble typical North American *A. carolinensis* from Texas to North Carolina (see, for example, Mount 1975: Fig. 174, Palmer & Braswell 1995: Pl. 27) but differ from some southern Florida individuals of *A. carolinensis* and *A. porcatus*. *Anolis porcatus*, by contrast, while mostly green, is often strongly patterned (Ruibal & Williams 1963: Figs. 7–9), including having a shoulder ocellus or scapular spot (see Schwartz & Henderson 1985: Pl. II, Fig. 2, Rodríguez Schettino 1999: Pl. 19), which is found only rarely in North American *A. carolinensis* (though more frequently in southern Florida) and has a smaller postorbital spot, not reaching as far

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dorsally in the temporal region as in *A. carolinensis*. Green anoles from other Pacific islands (Japan: Ota et al. 1995, Goris & Maeda 2005; Guam: Zug 2013) are consistent with the description of those from Hawaii.

Throat fans in Hawaiian green anoles are variable in color. The following color descriptions are from JL's field notes on males from Kauai, Oahu, and Maui: "magenta to deep lavender—all could be called purple", "rose red fans blotched w/ deep purple post-centrally", "fan blue basally, shading to magenta at edge", "all purple", "magenta", "brilliant magenta purple", "rose pink", "magenta fan becoming blotchy purple at base", "purple fans", "rose", and "magenta-purple like Gulf Coast spec[imen]s." There is an ontogenetic progression from white with rose-red blotches, becoming rose-red, which is then invaded by blotches of purple, becoming purple (ranging from magenta to lavender). Oliver & Shaw (1953) first remarked upon the strong fan color variability in Hawaiian green anoles.

Discussion

Identity of Pacific green anoles.—Garman (1887) stated that *Anolis porcatus* from Cuba was "really quite distinct" from its relative *A. principalis* (=*carolinensis*) in the southern United States. Comparing specimens of the latter from the Carolinas with the Cuban form, he cited, among other characters, "larger scales on the loreal region" in Cuban lizards, an observation with which our data are in complete accord. Green anoles from the Pacific and South Carolina have smaller head scales, and thus higher counts for all six morphological traits, than do Cuban lizards (Table 1, Fig. 2). Although there are significant differences among regions for all the characters, identification of individuals cannot be confidently made on the basis of a single character. LORNUM, the precise equivalent of Garman's (1887) character, however, comes close (Fig. 2F).

Considering multiple characters shows little ability to discriminate between Pacific and South Carolina anoles but clear separation between these regions and Cuban anoles (Fig. 3). Using a combination of characters would thus allow correct allocation of all but a few individuals; doing so on a sample from a population, given the significant differences among regions for all of the characters, would enhance the ability of researchers in the field or museum to allocate the population.

For all characters, South Florida specimens (all from Monroe County) are intermediate between Pacific/South Carolina anoles and Cuban anoles, being significantly different from one or the other for some, but not all characters (Fig. 2). The number of South Florida specimens included in the discriminant analysis ($n = 2$) is too few to say anything confidently, but they were clearly separated from Pacific/South Carolina lizards but not at all from Cuban lizards, on discriminant function 1 (Fig. 3).

In color, Hawaiian anoles are most similar to *Anolis carolinensis*, lacking the usually stronger patterning and shoulder ocelli of *A. porcatus*, but are variable in fan color. Other Pacific anoles, as far as can be seen in preserved specimens and photographs, are consistent with greater similarity to *A. carolinensis*. Green anoles from southern Florida are somewhat intermediate in color pattern as well as scale characters, more frequently having the shoulder ocelli typical of *A. porcatus*.

Relation to molecular genetic studies.—Michaelides et al. (2018) analyzed mtDNA from green anoles from the Bonin Islands, Marianas, Palau, Yap, and Hawaii and found that they originated from within a genetic lineage of *Anolis carolinensis* (Gulf Coast/Atlantic) that extends from Texas across the southeastern U.S.A. to the Atlantic coast, including South Carolina (exclusive of most of Florida). Pacific

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anoles have a dual origin from within the phylogeny of this lineage, with both sources being found in the area of Louisiana and Texas. Michaelides et al. (2018) also found that *A. carolinensis* from southern Florida were genetically distinctive. Other molecular genetic studies supported the existence of both this broadly distributed genetic lineage within *A. carolinensis*, and the distinctiveness of *A. carolinensis* from southern Florida (Campbell-Staton et al. 2012, Tollis et al. 2012, Tollis & Boissinot 2014, Manthey et al. 2016).

The results reported here are in accord with these molecular genetic studies. Pacific *Anolis carolinensis* are essentially indistinguishable from *A. carolinensis* from South Carolina in head scale characteristics, a region that is within the range of the Gulf Coast/Atlantic lineage, while differing from those from South Florida. Thus, like Michaelides et al. (2018), we can conclude that Pacific *A. carolinensis* originate from this Gulf Coast/Atlantic region (although, unlike them, we cannot specify a specific origin site), and we can exclude southern Florida from the immediate ancestry of Pacific *A. carolinensis*.

Variation within Anolis carolinensis *and* A. porcatus.—While a number of studies have examined molecular genetic variation in *A. carolinensis* (see citations in previous section), there have been fewer morphological studies (e.g., Duellman & Schwartz 1958, Christman 1980, Camposano 2011), the most comprehensive being the work of Vance (1991). The latter author examined specimens from throughout its North American range and described *Anolis carolinensis seminolus* Vance, 1991 from the southwestern coast of Florida, with intergradation with the nominate form occurring throughout Florida and into Mississippi and South Carolina. Krysko et al. (2019) accept this subspecies as valid, while Powell et al. (2016) do not. Southern Florida genetic lineages identified by molecular genetic studies would all be either within the range of *A. c. seminolus* or the area of intergradation with *A. c. carolinensis*.

The situation of *A. carolinensis* in southern Florida is complicated by the presence of introduced *A. porcatus* (Powell et al. 2016, Krysko et al. 2019). Both of these sets of authors state that there are no morphological differences between the native and introduced form and that they interbreed (as confirmed by Wegener et al. 2019)

In stating that there are no morphological differences between *Anolis carolinensis* and *A. porcatus*, Krysko et al. (2019) explicitly relied upon the work of Camposano (2011). The latter author showed that *A. carolinensis*-group anoles in Miami-Dade County in southern Florida cannot be separated into two distinct moieties corresponding to *A. carolinensis* and *A. porcatus*. Rather, he found that there is a broad array of morphologies comprised of specimens typical of *A. carolinensis* from further north, specimens typical of *A. porcatus* from Cuba, and specimens of intermediate morphology. The situation he found with *A. carolinensis* from northern Florida (Leon, St. Johns, and Wakulla counties), however, was quite different. Although no single character was diagnostic, *A. carolinensis* from these counties could always be distinguished from Cuban *A. porcatus*.

These morphological results are in harmony with those reported here, and with the results of the molecular genetic studies cited above. Northern *Anolis carolinensis* (including those from northern Florida) are distinct from Cuban *A. porcatus*, both genetically and morphologically. Southern Florida *A. carolinensis* are distinct genetically from northern *A. carolinensis*, and in morphology approach the condition of Cuban *A. porcatus* (Fig. 2). The great morphological variation in Miami-Dade County doubtless results from the introduction of *A. porcatus* and subsequent

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interbreeding (Kolbe et al. 2007, Wegener et al. 2019) with *A. carolinensis*.

Within *Anolis porcatus* in Cuba, Ruibal & Williams (1961) identified three geographically-replacing forms, which they called western, central, and eastern, distinguishing them primarily on the basis of color pattern and shape of the canthal ridges. Rodríguez Schettino (1999) commented further on these forms and provided additional notes on the pattern of geographic variation. Glor et al. (2004, 2005) identified two genetic lineages within Cuban *A. porcatus*, a western one and an eastern one. The latter corresponds with Ruibal & Williams' (1961) eastern form of *A. porcatus*, whereas, based on its mapped occurrence, Glor et al.'s (2004: Fig. 1) western lineage includes both the western and central forms of Ruibal & Williams (1961). Glor et al. (2004, 2005) stated that the eastern lineage warranted status as a separate species but did not formally describe it.

The status of Anolis porcatus.—Although the situation of *Anolis porcatus* in Cuba needs further study, Glor et al. (2005) showed that *A. carolinensis* originated from within the western lineage of *A. porcatus*. Kolbe et al. (2007) and Wegener et al. (2019) have shown that the introduced *A. porcatus* in southeastern Florida have interbred to a considerable extent with the native *A. carolinensis*. The latter state that they are "not reproductively isolated and interbreed successfully after secondary contact, leading to a fusion of the previously distinct lineages"; Wegener et al. (2019:4144–4145) conclude that the western lineage of *A. porcatus* "should be subsumed into the earlier named A. *carolinensis*."

Under the biological species concept (Mayr 1942, 1963, Coyne & Orr 2004), species are recognized by their reproductive relations, conspecific populations interbreeding when they are in contact. The origin of *A. carolinensis* by colonization from Cuba (Glor et al. 2005, Campbell-Staton et al. 2012) created an extrinsic (sensu Mayr 1942, 1963) barrier that isolated the colonizing and source populations, allowing them to diverge. Secondary contact with interbreeding (Kolbe et al. 2007, Wegener et al. 2019) has shown that the two forms have not evolved reproductive isolating barriers and thus, are the same biological species. We thus concur with Wegener et al. (2019) that *A. carolinensis* and the western lineage of *A. porcatus* are conspecific.

Conclusions

The introduced green anole of the Pacific islands is *Anolis carolinensis* of the southeastern United States, originating from a source other than South Florida. This conclusion is in accord with the molecular genetic study of Michaelides et al. (2018), which identified a dual origin of Pacific green anoles, both from within their Gulf Coast/Atlantic lineage of *A. carolinensis*.

South Florida *A. carolinensis* are intermediate morphologically between *A. carolinensis* and the Cuban *A. porcatus*, and are genetically distinctive from other *carolinensis* lineages (Campbell-Staton et al. 2012, Tollis & Boissinot 2014, Manthey et al. 2016). Combined with the derivation of *A. carolinensis* from within the western genetic lineage of *A. porcatus* (Glor et al. 2004, 2005; Campbell-Staton et al. 2012) and the evidence for interbreeding between introduced *A. porcatus* and *A. carolinensis* in southern Florida (Kolbe et al. 2007, Powell et al. 2016, Wegener et al. 2019), these findings support the suggestion of Wegener et al. (2019) that the western lineage of *A. porcatus* and *A. carolinensis* are conspecific.

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of the American Museum of Natural History (AMNH), the California Academy of Sciences (CAS), the Museum of Comparative Zoology (MCZ), the San Diego Natural History Museum (SDNHM), and the United States National Museum of Natural History (USNM). We are especially grateful to Jose Rosado and George Zug. For assistance, discussion, and support of our studies, we are grateful to S. C. Adolph, R. I. Crombie, T. H. Fritts, W. R. Heyer, R. McDiarmid, G. Pregill, the late E. E. Williams, and G. R. Zug. JL's field work in Hawaii was supported by The Conservation Agency. B. D. Hollingsworth kindly provided the photos used in Fig. 1. In unpublished evaluations, E. E. Williams and the late B. Shreve independently came to the same conclusion regarding the specific identity of Pacific green anoles.

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Appendix

Specimens examined.—BONIN ISLANDS: Chichijima: MCZ 165214-17; MARIANAS: Guam: AMNH 74536, CAS 25632, MCZ 104504, 104506-

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08, 104510-11, 114646, USNM 192873-7, 192892-93, 216316-320, 301047-053; MARIANAS: Rota: USNM 284946-47; MARIANAS: Tinian: CAS 152033; MARIANAS: Saipan: USNM 212384-86, 257647-650, 257657; MARIANAS: Managaha: USNM 257646; YAP: MCZ 114642-45; HAWAII: Kauai: MCZ 172428-437; HAWAII: Oahu: MCZ 103854, 104503, 104512-13, 114646, 160013, 161238-242, Z-38001-06, USNM 279267-271, SDNHM 41049-051; SOUTH CAROLINA: USNM 80291-92, 218868, 218878-79, 246844, 267074, 286912-16; FLORIDA (all Monroe County): USNM 60583, 62079, 62086, 85200-01, 85203, 85205, 85207, 85222, 85225-28, 85230-31; CUBA: Pinar del Río: MCZ 55549, 93542-43; CUBA: Isla de la Juventud: MCZ 11127-130; CUBA: La Habana: USNM 194317, 194319, 194321-22, 194324, 194330-32, 194342, 194344, 194356, 194364, 194370; CUBA Camagüey: MCZ 60941, 68030-31; CUBA: Oriente: 60944, 60948, 61001-02, 61004-05, USNM 220716.

The listed specimen from Tinian, an adult male collected on 15 Mar 1978, is the basis for the occurrence of *Anolis carolinensis* on Tinian noted by Mayer & Lazell (1992). Based on a specimen collected in 1997, Vogt et al. (2001) discussed its occurrence on Tinian as a new record and noted failures to find it there during surveys in 1985 and 1989. The nearly 20-year gap between the first collected specimen and the one noted by Vogt et al. (2001) suggests that the introduction marked by the earlier specimen may have failed to result in an established population, or that it persisted at such low levels as to evade detection by searches during the 1980s.

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