

Evaluations of validity for some species of *Anolis*

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Background

Below I give justifications for the sample of *Anolis* species recognized in the key. I focus especially on cases where my list conflicts with the Reptile Database (Uetz et al. 2019), because this excellent resource has become the de facto authority for reptile species inferences. Some of these are cases where a published synonymy seems to have escaped public appreciation (e.g., *A. nigrolineatus*), but most are cases where, in my view, the publication review process should have headed off recognition of a species. These decisions are necessarily biased towards my own experience. Historically recognized forms like the green anoles of the *carolinensis* group (see Glor et al. 2005; Reynolds et al. 2018), *A. baleatus* and the giant anoles of Hispaniola and Cuba (e.g., see Mahler et al. 2016: ESM Figure 6), *bimaculatus*-group species/subspecies (see Stenson et al. 2004), eastern Andean Colombian "twig" anoles (*A. menta*, *A. ruizii*, *A. lamari*), *A. cryptolimifrons* and other *limifrons*-group anoles, the *frenatus/latifrons/princeps* triumvirate, and the *dunni-taylori* complex (see Kohler et al. 2014: Fig. 110) are examples of species and groups sorely in need of detailed analyses of species validity.

Species discussions are below. These treatments should not be construed as comments on the general quality of work from relevant authors. The workers involved generally made inferences based on their best interpretations of data in front of them, which is to say they acted according to appropriate scientific standards. In all cases discussed below, significant advances in understanding of anole intra- and interspecies variation were made in the cited publications. Here I dispute some of the resulting species inferences, in some cases based on new data but in most cases based on re-examination of presented data. These are practical decisions intended to help field workers attempting to identify species and comparative biologists seeking units for evolutionary analysis. Quite simply, it does not seem useful, or correct, to recognize parapatrically distributed "species" that cannot be distinguished based on morphology or DNA. I am interested to hear commentary on or correction to these verdicts from readers of these justifications and the pertinent descriptions.

Species Treatments

Anolis bocourtii*, *A. biscutiger

These species are recognized in the key but are considered synonyms in the Reptile Database. I tentatively recognize *A. biscutiger* because I have observed this form topotypically in life and find this species likely to be valid (see Taylor 1956). *Anolis biscutiger* is the version of *A. limifrons* in Southwestern Costa Rica. I tentatively associate the name *A. bocourtii* with the white-dewlapped version of *A. fuscoauratus* found near Nauta and Iquitos in Peru (Poe and Yanez-Miranda 2008).

Anolis anisolepis*, *A. bitectus*, *A. damulus*, *A. gibbiceps*, *A. impetigosus*, *A. lemniscatus*, *A. microlepis

These species are recognized in the Reptile Database but not in the key. I am preparing evidence that the names *Anolis anisolepis*, *A. bitectus*, *A. microlepis*, and *A. lemniscatus* are junior synonyms. I agree with previous authors that *A. damulus*, *A. impetigosus*, and *A. gibbiceps* are best considered nomina dubia (Nicholson et al. 2012; Rivas et al. 2012). Other species recognized in the Reptile Database but not in the key are discussed below.

Anolis osa

Anolis osa is still sometimes recognized as valid, even though this purported species is not monophyletic relative to *A. polylepis* according to mitochondrial DNA (Köhler et al. 2012: Fig. 2), interbreeds freely with *A. polylepis* (Köhler et al. 2012: 4), and differs from *A. polylepis* only in minor, continuously-varying details of hemipenial morphology (Köhler et al. 2012: Fig. 1; Köhler et al. 2010). For these reasons, I consider the name *A. osa* to be a junior synonym of *A. polylepis*.

Anolis Ibague

Anolis Ibague was described by Williams (1975) and diagnosed from the (at that time) poorly known species *A. sulcifrons* and similar (i.e., *pentaprion*-group) anole species based on its unusual headscales. In particular, Williams (1975: 5) stated that "The characters of *A. Ibague* that are extreme are the great size of the interparietal, of certain of the supraorbital scales, and of the sublabials." My group has visited the type locality of *A. Ibague* and collected individuals of *A. sulcifrons* there that display the listed diagnostic traits of *A. Ibague*. That is, we observed numerous individuals of *A. sulcifrons* at Ibagué with the interparietal in contact with the supraorbital semicircles, large supraorbital semicircles, and large sublabials. Williams' (1975) Table 1 suggests he was not aware of the considerable variation in traits that occurs within *A. sulcifrons*, as he listed point estimates for traits of *A. sulcifrons* (e.g., scales between interparietal and supraorbital semicircles) that are known to vary in all species of *Anolis* (Williams [1974] did not present a list of specimens examined). Thus, although I have not examined the type specimen of *A. Ibague*, I tentatively consider the name *A. Ibague* to be a junior synonym of *A. sulcifrons*.

Anolis nigrolineatus

Williams (1965) described *Anolis nigrolineatus* without reference to *A. festae*, but later (Williams 1982: 29) stated "*A. nigrolineatus* may be a strict synonym of *A. festae* Peracca (syntypes examined)." Future work may determine southern *A. festae* (i.e., *A. nigrolineatus*) to be distinct from *A. festae* proper, but my observations of northern and southern *A. festae* in life suggest to me that Williams' (1982) later view is correct and *A. nigrolineatus* should be treated as a synonym of *A. festae*.

Anolis delafuentei

Garrido (1982) described *Anolis delafuentei* based on a single male holotype from Sierra de Trinidad, central Cuba. Garrido (1982) noted extreme similarity between this form and its sympatric congener *A. ahli*. The traits listed to distinguish these two species are all conditions of trend or mode. For example, *A. delafuentei* is stated to differ from *A. ahli* in its smaller ventral scales, fewer scales between supraorbital semicircles, fewer postmental scales, and larger body size. However, the stated conditions for these traits for *A. delafuentei* are within the known ranges for *A. ahli* (personal observation). Male dewlap color of *A. delafuentei* was described as "rojizo o anarandado en vida" and "probablemente rojizo en vida," suggesting that the author did not see the dewlap of the holotype of *A. delafuentei* in life ("probablemente") and indicating that the hypothesized dewlap color of *A. delafuentei* is the same as the dewlap color of *A. ahli* (i.e., orangeish-red; Rodriguez-Schettino [1999]). Because no traits unambiguously diagnose *A. delafuentei* from *A. ahli*, I cautiously recommend that the name *A. delafuentei* be considered a junior synonym of *A. ahli*. This recommendation is influenced by the fact that Sierra de Trinidad is an easily accessible area that has been subject to numerous herpetological surveys with no new specimens of *A. delafuentei* produced.

Anolis deltae

Williams (1974) described *Anolis deltae* from a single specimen from the Orinoco delta of Venezuela. The characteristics of this specimen are distinct from all mainland South American *Anolis*, but accord well with Southern Lesser Antillean species of the *roquet* group of *Anolis*. In particular, the *deltae* holotype's combination of supraorbital semicircles in extensive contact with each other and with the interparietal scale, lack of postcloacal scales in males, and presence of tail crest is found only in *roquet* group *Anolis* from the Southern Lesser Antilles. Williams was unaware of the now well-documented invasion of Venezuela by *A. extremus* of the *roquet* group (Peters & Donoso-Barros 1970; Rivas et al. 2012). Although I have not examined the holotype of *A. extremus*, I tentatively recommend that the name *A. deltae* be treated as a junior synonym of *A. extremus* based on Williams' (1974) description. There are no data in that description that distinguish the *A. deltae* type specimen from *A. extremus*.

Anolis utilensis

Kohler (1996) described *Anolis utilensis* as a *pentaprion*-group anole endemic to Utila Island. My lab collected DNA sequence data from the cytochrome c oxidase subunit I gene for an individual of *A. utilensis* and multiple individuals of other *pentaprion*-group species, including *A. beckeri*. Degree of genetic divergence between *A. utilensis* and an individual of *A. beckeri* from a proximal mainland locality (Atlantida, Honduras) is low (p-distance of 2.7%). In particular, it is less than divergences between populations assigned to *A. beckeri* (up to at least 6.2%). Also, phylogenetic analysis estimates the Atlantida population of *A. beckeri* to be monophyletic with *A. utilensis* relative to slightly more geographically distant populations of *A. beckeri*. These results suggest ongoing gene flow between mainland and Utila populations of *pentaprion*-group *Anolis*. Additionally, I know of no morphological traits that consistently distinguish *A. beckeri* and *A. utilensis*, the male dewlaps of *A. utilensis* and *A. beckeri* appear identical, and the narrowness of the ecology of *A. utilensis* has been overstated (Poe 2016). For these reasons, *A. utilensis* seems best considered a junior synonym of *A. beckeri*.

Anolis quaggulus

Anolis quaggulus (Cope 1885) was diagnosed from *A. humilis* based on hemipenial structure and modal tendencies in some external traits (Kohler et al. 2006). Recent detailed molecular work has shown type-locality *A. quaggulus* to be phylogenetically nested within *A. humilis* (Phillips et al. 2015; i.e., *A. humilis* as currently recognized is paraphyletic), and that purported hemipenial differences between these species do not hold up to scrutiny. That is, for example, individuals with *quaggulus*-hemipenes were recorded from within the range of Phillips et al.'s (2015) "*N. humilis* 3"—a population of *A. humilis* that is phylogenetically separated from type-population *A. quaggulus* (compare range maps in Phillips et al. [2015], Kohler et al. [2006]). Phillips et al. (2015) found significant molecular structure within *A. humilis/quaggulus*, and I concur with those authors that the name *quaggulus* is likely to survive the completion of pertinent taxonomic work. For now, however, it seems practical to treat *A. quaggulus* as a junior synonym within *A. humilis*. There are no morphological traits with which to distinguish the type population of *A. quaggulus* from surrounding *A. humilis*, geographic species boundaries for a molecularly-diagnosed *A. quaggulus* are unclear (e.g., should Phillips et al.'s "*N. humilis* 5" be included in *A. quaggulus*?), and no suggested taxonomy exists for the other distinct lineages within currently-recognized *A. humilis* (see Phillips et al. [2015] for additional discussion).

Anolis lyra

Poe et al. (2009) recognized *Anolis lyra* as distinct from *A. vittigerus* based on analysis of external morphological traits. These purported species are identical in male dewlap color pattern (red with a dark central spot), and hypothesized external scale differences have not held up upon recent field work (pers. obs.). Recent molecular work has found a

reasonable species level divergence between type locality versions of these forms (9.8% p-distances for gene COI; data from Poe et al. 2017). But the continuous distribution of *A. vittigerus* and *A. lyra* from Panama to Ecuador suggests that such divergences may represent simple isolation by distance within a single species. Pending detailed multigene analysis with broad geographic sampling, it seems most prudent to recognize a single species, *A. vittigerus*, for the *lemurinus*-like anole distributed along the Pacific versant from central Panama to Ecuador. As with several species discussed here, it is likely that the newer name, *A. lyra*, will survive further molecular scrutiny, but likely in some altered geographic form. Until then, there seems little point in recognizing a species that is identifiable purely by geography.

Anolis leditzigorum*, *A. alocomyos

Anolis leditzigorum and *A. alocomyos* (Kohler, Vargas, & Lotzkat 2014) were described and compared to *A. tropidolepis*. These three Costa Rican species were diagnosed relative to each other based on 16S DNA, hemipenial structure, and dewlap coloration; according to the describing authors the forms are indistinguishable according to scalation and proportion (Kohler et al. 2014). Regarding the dewlap: "the dewlap of adult males of *N. leditzigorum* is purplish red, whereas that of *N. tropidolepis* is orange red." (Kohler et al. 2014: 271). But Figure 12c of Kohler et al. shows an individual assigned to *A. leditzigorum* with an orange-red dewlap. *Anolis alocomyos* is said to be "differentiated further from *N. benedikti*, *N. pachypus*, and *N. pseudopachypus* by the presence of a uniform purplish red male dewlap in life." However, figure 6B shows an individual assigned to *A. alocomyos* with an orange-red dewlap. The male dewlaps of figures 1B (*A. tropidolepis*), 6B (*A. leditzigorum*), and 12C (*A. alocomyos*) appear identical. Thus male dewlap coloration is not a diagnostic trait for any of these species relative to each other.

Regarding the hemipenes: The hemipenes of *Anolis tropidolepis* and *A. leditzigorum* appear indistinguishable in Kohler et al.'s (2014) Figure 3. The hemipenes of *A. alocomyos* (Fig. 3e, but see Fig. 8g also) appears to possess longer lobes than those of *A. tropidolepis/leditzigorum*. This trait was listed as the only diagnostic trait for *A. alocomyos* relative to *A. tropidolepis/leditzigorum*. However, one of the three listed male individuals of *A. alocomyos* was said to possess "the mitochondrial (i.e., maternal) genotype of *Norops [Anolis] alocomyos* while exhibiting hemipenial phenotype of the geographically neighboring *N. tropidolepis*." (Kohler et al. 2014: 276). That is, of the three individuals assigned to this species that by virtue of their maleness allows diagnosis of this species (assuming hemipenes were everted), one (1/3 of the sample) lacks the single diagnostic trait of this species relative to *A. tropidolepis*. The authors interpreted the combination of "*alocomyos* DNA" and "*tropidolepis/leditzigorum* hemipenes" to indicate hybridization between *A. alocomyos* and *A. tropidolepis*. Given the limited sampling of purported *A. alocomyos* and the known rapid evolution of hemipenes (Klaczko et al. 2015), a more parsimonious interpretation is simply that there

is some intraspecific variation in the degree of development of the hemipenial lobes. The number of specimens examined with everted hemipenes was not listed in Kohler et al. (2014).

Regarding the 16S results: There clearly is some mitochondrial structure within the species previously referred to as *Anolis tropidolepis* (Kohler et al. 2014: Fig. 2). Kohler et al. assigned names to some of these clades. The degrees of divergence (i.e., the p-distances) among these putative species are compatible with either conspecificity or separate species status for these forms (cited species with low divergences, such as *A. monteverde* and *A. altae*, may actually be conspecific). In such cases, one hopes for additional independent evidence--e.g., morphology, nuclear genes, chromosomes, allozymes--to corroborate these lineages (e.g., Jockusch et al 2012: *Batrachoseps*, Glor and Laport 2012: *Anolis distichus*; Nantararat et al. 2014: land snails). But as noted above, no additional traits have been found that unambiguously track the apparent mitochondrial lineages.

It is possible that the mitochondrial lineages recognized as species by Kohler et al. (2014) within *Anolis tropidolepis* are recently diverged species; this is the conclusion of these authors (Kohler et al. 2014: 260, 275). But there are numerous cases where mitochondrial results alone have been shown to be unreliable in species inferences (e.g., Ballard et al. 2004). The shallow mitochondrial splits, the geographical contiguity of the 'species' and, especially, the lack of diagnostic traits that corroborate the mitochondrial lineages suggest that the most realistic interpretation of these patterns is mitochondrial structure and normal intraspecific variation in hemipenes, male dewlap coloration, DNA, and external morphology in a single species *Anolis tropidolepis*. I adopt this interpretation of a single species cautiously and pragmatically: cautiously because the population structure in 16S is potentially suggestive of some evolutionary differentiation, and additional DNA work on this complex is warranted; pragmatically because there are no known diagnostic morphological or molecular traits with which workers in the field could distinguish these putative species. Alternatively to recognizing two species, *A. pachypus* and *A. tropidolepis*, it would be reasonable to recognize a "*tropidolepis species complex*" in recognition of the considerable variation discovered by Kohler et al. (2014).

Anolis carlliebi*, *A. sacamecatensis

Anolis carlliebi and *A. sacamecatensis* (Kohler, Trejo Perez, Petersen & Mendez de la Cruz 2014) were diagnosed relative to Mexican endemic *A. quercorum* according to genetic distance, hemipenial morphology, and "the ranges and average values of several morphometric and pholidotic characters." However, the reported genetic distances (4.8-7.1% for 16S) are compatible with either conspecific or separate species status for these species, and the hemipenes (reported as unilobed in *carlliebi*, "slightly to distinctly bilobed" in *A. quercorum* and *A. sacamecatensis*) appear very similar in the presented

photos (compare Kohler et al. 2014: Figs. 57, 64, 70). Hemipenes are known to evolve rapidly (Klaczko et al. 2015) and individuals from at least some populations recorded to display different hemipenes are able to interbreed (e.g., *A. polylepis* and *A. "osa"*; Kohler et al. 2012). Kohler et al. (2014) reported hemipenial morphology for only a single male of each of *A. carlliebi* and *A. sacamecatensis*.

Morphological differences of *Anolis carlliebi* and *A. sacamecatensis* relative to *A. quercorum* are stated to be "most obvious in (1) number of middorsal scales in one head length; (2) ratio shank length/HL; and (3) subdigital lamellae on Phalanges II–IV of Toe IV." However according to Table 9 of Kohler et al. (2014), the variation in these species in these traits is nearly completely enveloped by variation in *A. quercorum*: middorsals: *quercorum* (22-38), *carlliebi* (26-40), *sacamecatensis* (24-34); shank length: *quercorum* (0.82-0.96), *carlliebi* (0.92-1.03), *sacamecatensis* (0.81-0.93); lamellae: *quercorum* (19-26), *carlliebi* (20-24), *sacamecatensis* (19-22).

Anolis quercorum, *A. carlliebi*, and *A. sacamecatensis* display identical dewlaps (Kohler et al. 2014: Figs. 52a, 58a, 65a) and their hypothesized geographic ranges are not separated by geographic barriers. Although there may be some mitochondrial structure within what has been recognized as *A. quercorum* (Kohler et al. 2014: Fig. 51; but a test for isolation by distance is warranted), the lack of diagnostic traits correlated with recovered mitochondrial clades suggests caution in recognizing these clades as separate species. For now, the most prudent course seems to be to consider these three species as a single species, *A. quercorum*.

Anolis nietoi

Anolis nietoi (Kohler, Trejo Perez, Petersen & Mendez de la Cruz, 2014) was diagnosed from *A. nebuloides* and *A. megapholidotus* based on phylogenetic results and "the ranges and average values of several morphometric and pholidotic characters." However, the reported phylogenetic results are poorly supported (52% bootstrap value for the hypothesized *A. nietoi* clade in COI; see differing clade relationships between COI and 16S), and there are no traits listed that distinguish *A. nietoi* from *A. megapholidotus*. In particular, the species differences that are said to be "most obvious in (1) number of middorsal scales in one head length; and (2) number of subdigital lamellae on Phalanges II–IV of Toe IV" show near complete overlap in these traits in *A. nietoi* and *A. megapholidotus* (middorsals, *nietoi*: 16-24, *megapholidotus* 14-20; lamellae, *nietoi*: 20-24, *megapholidotus*: 17-23). Given the lack of diagnostic traits separating *A. nietoi* and *A. megapholidotus*, it seems most prudent not to recognize *A. nietoi* as a separate species from *A. megapholidotus* at this time.

Anolis stevepoei

Anolis stevepoei (Kohler, Trejo Perez, Petersen & Mendez de la Cruz, 2014) was diagnosed from *A. nebuloides* and *A. megapholidotus* by "(1) a rather gradual transition over 3 to 4 scales between the enlarged dorsal scales and the lateral body scales (vs. a more abrupt transition over only 1 or 2 scales); (2) the edges of the field of enlarged dorsal scale rows forming an undulating line due to single enlarged scales or groups thereof outside the main field (vs. the edges of this field well defined and in a more or less straight line) (3) and by having a pink to purple male dewlap (vs. more reddish)." Variation in middorsal scale rows in *nebuloides-megapholidotus Anolis* is evident but subtle, and continuously varying between populations (personal observation). For example, Kohler et al.'s (2014) Figure 49b (*A. nebuloides*) and Figure 31a (*A. stevepoei*) do not appear distinguishable based on the listed diagnostic middorsal traits. As for the purported dewlap difference, the range of variation depicted by Kohler et al. (2014) for *A. nebuloides* (Figures 45a-d) encompasses the dewlap variation shown for *A. megapholidotus* (Fig. 41a; which, incidentally, appears redder than my photo of an *A. megapholidotus* dewlap from its type locality) and *A. stevepoei*. Compare, for example, Kohler et al.'s (2014) Figure 45a (*A. nebuloides*) to their Figures 26a-b (*A. stevepoei*). As there appears to be no way to distinguish *A. stevepoei* and *A. nebuloides* in the field, and these species are similar according to mitochondrial DNA, it seems most prudent to consider *A. stevepoei* to be a junior synonym of *A. nebuloides*.

Anolis zapotecorum

Like *Anolis stevepoei*, *A. zapotecorum* (Kohler, Trejo Perez, Petersen & Mendez de la Cruz, 2014) was diagnosed from *A. nebuloides* and *A. megapholidotus* by "(1) a rather gradual transition over 3 to 4 scales between the enlarged dorsal scales and lateral body scales (vs. a more abrupt transition over only 1 or 2 scales); (2) the edges of the field of enlarged dorsal scale rows forming an undulating line due to single enlarged scales or groups thereof outside the main field (vs. the edges of this field forming well defined and in a more or less straight line) (3) and by having a pink male dewlap (vs. more reddish)." Also like *A. stevepoei*, these traits do not actually distinguish *A. zapotecorum* from *A. nebuloides* according to photos presented by Kohler et al. (2014; dewlap: compare Figure 33b, *A. zapotecorum* to Figure 45a, *A. nebuloides*; middorsals: compare Figure 38a, *A. zapotecorum*, to Figure 49b, *A. nebuloides*). As there is no consiliatory diagnostic support for the recovered mitochondrial clades in this group (Kohler et al., 2014: Fig. 19), it seems most realistic to recognize a pair of traditionally recognized and geographically coherent, but mitochondrially variable, species, *A. nebuloides* (including *A. zapotecorum*, *A. stevepoei*) and *A. megapholidotus* (including *A. nietoi*).

Anolis demissus

Anolis demissus was described as a subspecies of Hispaniolan *A. coelestinus* (Schwartz 1969) and diagnosed from the nominate form by Kohler and Hedges (2016) mainly using

traits of color pattern: "*Anolis demissus* differs from *A. coelestinus* by (1) usually not having a white subocular stripe and white streak above shoulder (vs. such a pattern usually present in *A. coelestinus*); (2) a dark gray to greenish gray male dewlap in life (vs. some shade of green in *A. coelestinus*); and (3) by lacking any pattern on flanks (vs. usually a pattern of pale green vertical bars or blotches present in *A. coelestinus*); (4) 5 supracaudals per caudal segment throughout all discernable segments (vs. 4 supracaudals per caudal segment, either throughout all discernable segments or having the reduction from 5 to 4 supracaudals per segment before the 5th segment); (3) usually smooth ventral scales (vs. usually weakly to distinctly keeled)." (In the Description section [p. 27], *A. demissus* is said to have ventral scales "usually faintly to distinctly keeled, occasionally smooth"). The use of the qualifier "usually" for the purportedly diagnostic traits indicates the overlap in these traits between *A. demissus* and *A. coelestinus*; unfortunately, Kohler and Hedges (2016) were unable to present photos of live examples of *A. demissus* for comparison of color pattern with *A. coelestinus*.

The overlap in trait values, the lack of molecular data for this form, and the proximity of localities for *Anolis demissus* and *A. coelestinus* (*A. demissus* is only known from Ile Grande Cayemite, a small island less than two kilometers from Haiti's Tiburon peninsula and localities for *A. coelestinus*) suggests caution in recognizing Schwartz's (1969) *A. coelestinus demissus* as an independently evolving lineage, i.e., a species. Pending additional study, it currently seems most prudent to consider the Grand Cayemite population of *A. coelestinus*, i.e. *A. demissus*, to be *A. coelestinus*.

Anolis pecuarius

Anolis pecuarius was described as a subspecies of *A. coelestinus* (Schwartz 1969) and diagnosed from the nominate form by Kohler and Hedges (2016; see also Schwartz 1969) using three traits of color pattern: "(1) usually not having a white subocular stripe and a white streak above shoulder (vs. such a pattern usually present in *A. coelestinus*); (2) a yellowish brown male dewlap in life (vs. some shade of green in *A. coelestinus*); and (3) by lacking any pattern on flanks (vs. usually a pattern of pale green vertical bars or blotches present in *A. coelestinus*." However, all of these traits are variable in *A. coelestinus* (see e.g., Kohler and Hedges, 2016: Figure 8) and the four specimens of *A. pecuarius* presented by Kohler and Hedges (2016: photographs in Figures 17a-d) each appear to possess the conditions that supposedly are characteristic of *A. coelestinus* rather than *A. pecuarius*: i.e., a subocular stripe, a streak above the shoulder, and (in the body shots, Figures 17c and d) pattern of vertical bars and blotches on the flanks. In particular, Figures 17c and 17d show individuals of *A. pecuarius* that appear more boldly patterned in subocular stripe, shoulder stripe, and flank pattern than the individual identified as *A. coelestinus* in Figure 7d. Perhaps most *A. pecuarius* lack the traits of *A. coelestinus*, but if so it is strange that the authors selected four examples for presentation that display the conditions characteristic of *A. coelestinus*. The dewlap of *A. coelestinus* is known to be variable (e.g., Kohler and Hedges 2016: Fig. 8), and Figure 8c of Kohler and Hedges (2016) appears more yellowish-brown than green.

Furthermore, Kohler and Hedges (2016:18) in their diagnosis of *A. coelestinus* describe its dewlap color as "yellowish green or brown (after metachrosis) in life"; i.e., displaying (at least sometimes) the dewlap color that supposedly is characteristic of *A. pecuarius*. Finally, genetic distances between *A. coelestinus* and *A. pecuarius* are low, and recognition of *A. pecuarius* renders *A. coelestinus* mitochondrially paraphyletic according to the tree presented by Kohler and Hedges (2016: Fig. 6).

Although none of these observations alone necessitates a conclusion of conspecific status between *Anolis coelestinus* and *A. pecuarius* (e.g., mitochondrially paraphyletic species might be valid given other evidence), taken together they call into question the initial decision to recognize *A. pecuarius* as a separate species. Pending additional study, it currently seems most prudent to consider the Ile-à-Vache population of *A. coelestinus*, i.e. *A. pecuarius*, to be *A. coelestinus*.

Anolis viridius

Anolis viridius is said to differ from *A. chlorodius* by having "an overall darker body coloration (Fig. 25), especially evident in the temporal region where the former species has blackish skin between the scales (vs. pale gray or dirty white skin in *A. chlorodius*). Also, the tail in *A. viridius* is dark and without distinctive pattern whereas that of *A. chlorodius* is pale with distinctive spots and bands (Fig. 26). Furthermore, *A. viridius* has lower supralabials and infralabials than *A. chlorodius* (ratio height of first supralabial / SVL >0.011 in *A. viridius* vs. <0.011 in *A. chlorodius*; Fig. 27), and the head bulges out less in *A. viridius* than in *A. chlorodius*." However, figure 25 in Kohler and Hedges (2016) show exceptions to these supposedly diagnostic color traits. For example, the leftmost specimen of *A. viridius* appears to have a lightly pigmented venter with a patterned tail, whereas the rightmost specimen of *A. viridius* appears relatively darkly pigmented with a patternless tail. The labial scale and "head bulges" traits are subtle at best, and not evident in presented figures. Given the meager mitochondrial distance between these purported species, their geographic contiguity, and the lack of diagnostic traits, it seems most prudent to recognize a single species, *A. chlorodius*.

Neither *Anolis chlorodius* nor *A. viridius* is distinguishable from *Anolis coelestinus* based on traits listed as diagnostic by Kohler and Hedges (2016; the ventral scales "usually" differ in degree of keeling). However, the deep mitochondrial split (Fig. 6) and geographic coherence of *chlorodius/viridius* versus *coelestinus* (Fig. 10) suggest continued recognition of the *chlorodius/viridius* complex as *A. chlorodius*.

Anolis peynadoi

Anolis peynadoi was diagnosed from *A. chlorocyanus* by Kohler and Hedges (2016) as "(1) having the the posterior portion of the dewlap skin in males solid black with widely spaced gorgetal scales (vs. only a weak suffusion of black pigment on the posterior

portion of the male dewlap with less widely spaced gorgetal scales in *A. chlorocyanus*); (2) a white streak on upper lip usually present, most obvious in life (vs. no white streak in *A. chlorocyanus*); (3) a more robust habitus (vs. a more slender habitus in *A. chlorocyanus*). *Anolis peynadoi* differs further from *A. chlorocyanus* by having moderately to greatly enlarged outer postmental scales, about three times the size of adjacent medial scales (vs. slightly to moderately enlarged outer postmental scales, less than three times the size of adjacent medial scales in *A. chlorocyanus*). However, none of these traits unambiguously separates these species. The depicted dewlaps of *A. chlorocyanus* and *A. peynadoi* appear to vary continuously (compare figures 39, 49), a white streak appears faint to absent in all figured *A. peynadoi* (Fig. 49) and present in at least some figured *A. chlorocyanus* (e.g., Figure 39b, d; i.e., the reverse of the stated diagnostic pattern), and a difference in outer postmental scales is not evident (compare the left postmental in Figure 36c [*chlorocyanus*] and Figure 48c [*peynadoi*]). An unquantified "robust" versus "slender" habitus is difficult to judge. Finally, *A. peynadoi* is mitochondrially paraphyletic relative to *A. chlorocyanus*, and genetic divergence between these species is shallow, according to the tree presented by Kohler and Hedges (2016: Fig. 6).

Although none of these observations alone necessitates a conclusion of conspecific status between *Anolis chlorocyanus* and *A. peynadoi*, taken together they call into question the initial decision to recognize *A. peynadoi* as a separate species. That is, there is no consistency of evidence suggesting separate species status for *A. peynadoi*. Pending additional study, it currently seems most prudent to consider *A. peynadoi* to be conspecific with *A. chlorocyanus*.

Anolis apletolepis

Anolis apletolepis was diagnosed by Kohler and Hedges (2016) from *A. aliniger* by "having the scales on anterior surface of thigh conspicuously enlarged, mostly higher than long (vs. these scales not or only slightly enlarged, not higher than long)." However, a difference in size and proportion of thigh scales is not apparent in the pertinent figures (Fig. 56g: *A. aliniger*; Fig. 80g: *A. apletolepis*; note differences in magnification in these figures). Considering also the mitochondrial similarity of these forms (Kohler and Hedges 2016: Fig. 6), it currently seems most prudent to consider *A. apletolepis* to be conspecific with *A. aliniger*.

Anolis leucodera

Anolis leucodera was diagnosed from *A. chlorocyanus* by Kohler and Hedges (2016) based on "the absence of suffusion of black pigment on the dewlap (vs. posterior portion of dewlap moderately to heavily suffused with black pigment in *A. cyanostictus*, *A. chlorocyanus*, and *A. peynadoi*) and "having faintly to weakly keeled ventrals (vs. smooth in *A. chlorocyanus* and *A. peynadoi*)." However, the only color information

provided for *A. leucodera* was from specimens that had been preserved for 16 years. Dark markings may fade in preservative over time, and some specimens of *A. chlorocyanus* display only weak suffusion of black on the dewlap even in life (e.g., Kohler and Hedges 2016: Fig. 39c). Regarding the trait of ventral keeling, Kohler and Hedges (2016) variously described the condition in *A. chlorocyanus* as "usually smooth" (e.g., p. 51; diagnosis of *A. chlorocyanus*) or "smooth" (e.g., p. 73; the diagnosis of *A. leucodera*). The condition "usually smooth" in *A. chlorocyanus* overlaps with the condition "faintly keeled" in *A. leucodera*. Given the mitochondrial similarity of *A. leucodera* and *A. chlorocyanus* (Kohler and Hedges 2016: Fig. 6; note also that inclusion of *A. peynadoi* as *A. chlorocyanus* [see above] renders *A. chlorocyanus* paraphyletic relative to *A. leucodera*) and the questionability of the diagnostic morphological traits, it seems most prudent at this time to consider *A. leucodera* to be a junior synonym of *A. chlorocyanus*. Color notes of live specimens and/or dewlap photos of *A. chlorocyanus* from Northwestern Haiti, as well as additional molecular data, may overturn this verdict in the future.

Anolis wampuensis*, *A. spilorhipis*, *A. macraniei*, *A. wilsoni

Kohler et al. (2016) divided *Anolis tropidonotus* into four species including *A. spilorhipis* (previously described as a subspecies of *A. tropidonotus*), *A. mccraniei*, and *A. wilsoni*. *Anolis wampuensis* (McCranie and Kohler 2001) was described previously as indistinguishable from *A. tropidonotus* but for its smaller body size and lack of a dark streak on the dewlap.

Anolis wampuensis was not included in Kohler et al.'s (2016) review of *A. tropidonotus*, even though one of their new *tropidonotus*-like species (*A. mccraniei*) is found within 20 km of localities for *A. wampuensis* and *A. wampuensis* is acknowledged to be a vicariant form of *A. tropidonotus* (McCranie and Kohler 2001). McCranie and Kohler (2016: p. 203) stated with reference to *A. tropidonotus* that "Were it not for the extreme differences in habitat between the two nominal forms (see below), we would consider them [i.e., *A. wampuensis* and *A. tropidonotus*] conspecific." I concur that the stated morphological differences between *A. tropidonotus* and *A. wampuensis* are not compelling evidence of separate species status (the body size difference is based on seven male specimens of *A. wampuensis*, and *A. tropidonotus* [sensu lato] is variable in the presence of a dark blotch or streak on the dewlap according to Alvarez del Toro and Smith [1956]; see also McCranie and Kohler [2016]: Fig. 72B). The diagnostic habitat difference was described by McCranie and Kohler (2016: p. 203) as *A. wampuensis* occurring in "undisturbed broadleaf rainforest," a habitat in which "*Norops tropidonotus* has also never been found." However, those authors noted finding *A. wampuensis* in a disturbed area ("the edge of a cornfield"), and clearly *A. tropidonotus* occurred in "undisturbed" areas before humans arrived. I have found *A. tropidonotus* in deep forest, but I have not visited the Wampu river area and so I cannot assess whether that forest is substantially different from forested areas where I have found *A. tropidonotus*. But even

granting the habitat difference, it seems unlikely that a small radius of eastern localities harbors a distinct species that is identical to a surrounding species but for its existence in remnant habitat. *Anolis wampuensis* may eventually be the valid name for some eastern populations of *A. tropidonotus/mccraniei*. For now, however, it seems most prudent to consider *A. wampuensis* to be a junior synonym of *A. tropidonotus*.

The remaining *tropidonotus*-complex species also are in need of scrutiny. These species were identified based on phylogenetic analysis of 16S DNA data, with corroboration attempted using morphological traits. In particular, the species were said to differ in hemipenes, dewlap color pattern, and some scale counts.

The genetic distances between purported species (minimum of 2.9-3.2%) would be among the lowest in *Anolis*; they are compatible with either conspecific or separate species status. The presented phylogenetic tree (Kohler et al. 2016: Fig. 1) depicts an explosive speciation event whereby four species result—there are zero-length branches for a polytomy of three species and an unsupported branch showing *A. wilsoni* as sister to these three. The simultaneous radiation of four species would be interesting and remarkable if true. However, a more parsimonious interpretation is that the four clades simply show normal intraspecific variation in a mitochondrial gene within a single species. The use of single mitochondrial genes in species diagnoses has been criticized (e.g., Ballard and Whitlock 2004), but certainly such evidence is telling if it can be corroborated with independent evidence such as that from morphology or additional genes. Unfortunately, the additional evidence in Kohler et al. (2016) is equivocal at best.

The hemipenes represent a strong possibility of corroborating evidence, as the unilobed organ of *Anolis tropidonotus* (Kohler et al. 2016: Fig. 2B) appears distinctly different from the bilobed anatomies of the other three species. However, Kohler et al. (2016) do not present a list of localities from which hemipenes were examined, so it is impossible to know the geographic distribution of this trait, its consistency within populations or hypothesized species, or its condition at apparent areas of parapatry for these species (*A. mccraniei* and *A. wilsoni* appear nearly sympatric in the presented range map [Kohler et al. 2016: Fig. 9], and *A. tropidonotus* is presented as geographically bracketing *A. spilorhipis*). Neighboring *Anolis* populations with very different hemipenes may interbreed freely (e.g., *Anolis polylepis* and the Osa peninsula population of *A. polylepis* that was recognized as *A. osa*; Kohler et al. 2012). The dewlap variation is similarly unhelpful, as there is no mention in Kohler et al. (2016) of the observed geographic distribution of purported differences, and intraspecific variation in the supposedly diagnostic dewlap trait (the presence and structure of a dark blotch/streak) is known to be common in *A. tropidonotus* (e.g., Alvarez del Toro and Smith 1956; pers. obs.). Other mentioned diagnostic traits are acknowledged to overlap in these species (see Kohler et al. 2016: Table 2).

Kohler et al. (2016) and others (e.g., Alvarez del Toro and Smith 1956; Phillips et al. 2015) have documented interesting molecular and morphological variation within *Anolis tropidonotus sensu lato*, and it would be surprising if such a widespread form did

not harbor multiple species. However, based on the above arguments, I currently recognize all of these forms as a composite *A. tropidonotus* complex. I do not doubt that some or all of the names *A. spilorhipis*, *A. wilsoni*, *A. mccraniei*, and *A. wampuensis* may survive upon more geographically detailed analyses. However, I do not see value in recognizing the current taxonomy and distribution. The molecular and hemipenes sampling is too thin, the species boundaries are too fuzzy, the mitochondrial divergences too shallow, and the external diagnoses (which workers must use to identify which form they have in hand) are unhelpful.

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