A REVISION OF THE GENUS *AUDANTIA* OF HISPANIOLA WITH DESCRIPTION OF FOUR NEW SPECIES (REPTILIA: SQUAMATA: DACTYLOIDAE)

Una revisión del género *Audantia* de la Hispaniola con descripción de cuatro especies nuevas (Reptilia: Squamata: Dactyloidae)

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ABSTRACT

We revise the species of *Audantia*, a genus of dactyloid lizards endemic to Hispaniola. Based on our analyses of morphological and genetic data we recognize 14 species in this genus, four of which we describe as new species (*A. aridius* sp. nov., *A. australis* sp. nov., *A. higuey* sp. nov., and *A. hispaniolae* sp. nov.), and two are resurrected from the synonymy of *A. cybotes* (*A. doris* comb. nov., *A. ravifaux* comb. nov.). Also, we place *Anolis citrinellus* Cope, 1864 in the synonymy of *Ctenonotus distichus* (Cope, 1861); *Anolis haetianus* Garman, 1887 in the synonymy of *Audantia cybotes* (Cope, 1863); and *Anolis whitemani* Williams, 1963 in the synonymy of *Audantia saxatilis* (Mertens, 1938). Finally, we designate a lectotype for *Anolis cybotes* Cope, 1863, and for *Anolis riisei* Reinhardt & Lütken, 1863. Our main focus is on the populations of anoles formerly referred to as *Audantia cybotes* which we demonstrate to be a complex of seven distinct species. For these seven species we provide a standardized description of external morphology, color descriptions in life, color photographs in life, description and illustration of hemipenis morphology (if available), distribution maps based on the specimens examined, comments on the conservation status, and natural history notes. Finally, we provide a dichotomous key for the identification of the 14 species of the genus *Audantia* occuring on Hispaniola.

Keywords: *Anolis, Audantia*, Dominican Republic, Haiti, lectotype designation, new species, phylogeny, taxonomy.

RESUMEN

Nosotros revisamos las especies del género *Audantia* que ocurren en la Hispaniola. Basados en nuestros análisis de datos morfológicos y moleculares, reconocemos 14 especies del género *Audantia*, cuatro de las cuales describimos como nuevas especies (*A. aridius* sp. nov., *A. australis* sp. nov., *A. higuey* sp. nov. y *A. hispaniolae* sp. nov.), y dos son recuperadas de sinonimias de *A. cybotes* (*A. doris* comb. nov., *A. ravifaux* comb. nov.). Además, situamos a *Anolis citrinellus* Cope, 1864 en la sinonimia de *Ctenonotus distichus* (Cope, 1861); *Anolis haetianus* Garman, 1887 en la sinonimia de *Audantia cybotes* (Cope, 1862); y *Anolis whitemani* Williams, 1963 en la sinonimia de *Audantia saxatilis* (Mertens, 1938). Finalmente, designamos un lectotipo para *Anolis cybotes* Cope, 1863, y otro para *Anolis riisei* Reinhardt & Lütken, 1863. Nuestro enfoque principal es sobre las poblaciones de las especies previamente referidas como *Audantia cybotes*, para lo cual demostramos que en realidad es un complejo de siete especies diferentes. Para estas siete especies nosotros proveemos una

descripción estandarizada de morfología externa, descripciones de color en vida, fotografías a color en vida, descripción e ilustración de la morfología de los hemipenes (cuando estuvieron disponibles), mapa de distribución basados en los especímenes examinados, comentarios sobre el estado de conservación, y notas de historia natural. Finalmente, nosotros proveemos una clave dicotómica para la identificación de las 14 especies del género *Audantia* que ocurren en la Hispaniola.

Palabras clave: *Anolis*, *Audantia*, República Dominicana, Haití, designación de lectotipo, especies nuevas, filogenia, taxonomía.

INTRODUCTION

Anoles of the family Dactyloidae are a prominent faunal component on the major Antillean island of Hispaniola. Indeed, with 54 species, anoles form one of the most species-rich groups of amphibians and reptiles (total 261 species) on this island (Hedges, 2018). One group of anoles endemic to Hispaniola is the genus *Audantia* Cochran, 1934, formerly the *Anolis cybotes* series or subseries (Williams, 1976; Burnell & Hedges, 1990) and often informally referred to as the 'cybotoids' (Schwartz, 1979). The genus includes species that characteristically perch low to the ground (trunk/ground ecomorph) on bushes and trees and are among the most abundant anoles on the island, often occurring in degraded habitats (Henderson & Powell, 2009). The nine currently recognized species of *Audantia* (Schwartz, 1980; Schwartz & Henderson, 1982, 1991; Henderson & Powell, 2009; Nicholson *et al*., 2012, 2018) are *A. armouri* Cochran, 1934, *A. breslini* (Schwartz, 1980), *A. cybotes* (Cope, 1863), *A. haetianus* (Garman, 1887), *A. longitibialis* (Noble, 1923), *A. marcanoi* (Williams, 1975), *A. shrevei* Cochran, 1939, *A. strahmi* (Schwartz, 1979), and *A. whitemani* (Williams, 1963).

We are aware of the contentious debate between recognizing *Anolis* as a single genus and recognizing multiple genera (Nicholson *et al.,* 2012; Nicholson *et al.,* 2014; Poe, 2013; Poe *et al.,* 2017; Nicholson *et al.,* 2018). Here we follow Nicholson *et al.* (2018) and therefore recognize the genus *Audantia* Cochran, 1934 (sensu Nicholson *et al.*, 2018) for the anole species in the *cybotes* series, while recognizing the criticisms of the multiple-genera taxonomy. The genus *Audantia* sensu Nicholson *et al.* (2018) corresponds to clade *Audantia* of Poe *et al.* (2017).

Cope (1863) introduced the new species *Anolis cybotes* based on five syntypes, ANSP 7604–05, MCZ 3619 (destroyed in 1939 according to Rosado, personal communication to Gunther Köhler, 25 April 2018) and MCZ 14346–47, that were collected in "Western Hayti; from near Jeremie". Reinhardt & Lütken (1863) described *Anolis riisei* based on two syntypes (now NHMD R3796 and R3793) from "Haiti". The new species *Anolis citrinellus* from "Hayti" was introduced by Cope (1864). Garman (1887) described *Anolis haetianus* based on three syntypes (MCZ 6191) from "Tiburon, Hayti". According to Rosado, MCZ (personal communication to G. Köhler, 25 April, 2018), the three syntypes of *A. haetianus* are "a jumble of parts mixed together in pieces in a bottle". In 1923, Noble "spent four days on Beata Island off the southwestern coast of the Dominican Republic" where he "made an effort to secure a representative collection". Amongst the material collected was an adult male that became the holotype of his new species, *Anolis longitibialis* (now AMNH 24329), from "Beata Island, Dominican Republic" (Noble, 1923a). Cochran (1934; 1941) regarded this nominal taxon as a subspecies of *A. cybotes*. Other authors (e.g., Schwartz & Henderson, 1991; Nicholson *et al.,* 2005) didn't share this view and treated *A. longitibialis* as a distinct species. Barbour (1925) described the new species *Anolis doris* based on an adult male (now MCZ 13739) from "Gonave or Gonaive Island, off the west coast of Haiti" (= Île de la Gonâve, Haiti). Most authors have regarded this nominal taxon as a subspecies of *A. cybotes* (Cochran, 1941; Schwartz & Henderson, 1988).

Cochran (1934) described the new species *Audantia armouri* based on an adult male (now MCZ 37523) "from Peak La Selle, Haiti". This taxon was assigned to the genus *Anolis* by Etheridge (1960). In 1963, Williams recognized it as a subspecies of *A. cybotes*, but later treated it as a full species (Williams, 1976). This opinion was followed by Schwartz & Henderson (1991) and Nicholson *et al.* (2005). *Anolis cybotes saxatilis* was described by Mertens (1938) based on an adult male (now SMF 25032) from "Südlich von Fondo Negro, Gebiet des unteren Rio Yaque, Südwest-Santo Domingo" (= south of Fondo Negro, region of lower Rio Yaque, southwestern Dominican Republic).

Cochran (1941) placed the three nominal taxa *A. riisei, A. citrinellus,* and *A. cybotes saxatilis* in the synonymy of *Anolis cybotes cybotes* where they remained ever since (Uetz *et al*., 2019). Cochran (1939) introduced the new species *Audantia shrevei* based on an adult male (MCZ 44365) from "Valle Nuevo, in the Cordillera Central, southeast of Constanza, Dominican Republic, at 6000 to 8000 feet elevation," which "resembles *Audantia armouri* Cochran, but has a large nuchal patch of enlarged keeled scales, has a darker and more uniform coloration, and attains a lager adult size". This nominal taxon was listed as a synonym of *A. armouri* by most authors until now (Etheridge, 1960; Schwartz & Henderson, 1991). In 1963, Williams described *Anolis whitemani* based on an adult male (MCZ 60055) that was collected on a "road to Eaux Gaillees, Haiti". He stated that it was similar to *A. cybotes* "but differing in squamation (…), and in color". Williams (1975) introduced his new species *Anolis marcanoi*, which was named in honor of Professor Eugenio de Jesús Marcano, based on an adult male (holotype MCZ 131837) from "ca 5 km N La Horma, Peravia Province, Dominican Republic". He stated that *A. marcanoi* is "quite distinct from *A. cybotes* in electrophoretic characters but nearly indistinguishable in squamation".

Schwartz (1979) described the new taxon *A. longitibialis specuum* based on an adult male (now MCZ 132370) from "17 km NW of Oviedo Nuevo, Pedernales Province, República, 183 m". Schwartz (1979) also described the new species *Anolis strahmi* with two subspecies: *Anolis strahmi strahmi* based on an adult male (holotype MCZ 132371) from "3 km NE of El Aguacate, Independencia Province, 854 m, República Dominicana" and *Anolis strahmi abditus* based on an adult male (MCZ 146827) that was collected from a "dirt road to Las Mercedes, 2.9 km from intersection (= 5 km SE, 2.9 km N of Pedernales), Pedernales Province, República Dominicana". Schwartz (1980) described two new taxa of anoles from Haiti, both as subspecies of *A. whitemani*: *Anolis whitemani lapidosus* (holotype MCZ 156206) from "Terre Sonnain, 1.6 km N Les Poteaux, 122 m, Département de l'Artibonite, Haiti" and *Anolis whitemani breslini* (holotype MCZ 156204) from "Môle St. Nicholas, Département du Nord-Ouest, Haiti". The latter was elevated to full species status by Glor *et al.* (2003) who concluded that its "morphological distinctness, monophyly of sampled mtDNA haplotypes, deep divergence from all other sampled haplotypes (~10 % or more), and geographical isolation collectively support separate species status for *A. breslini*". Schwartz & Henderson (1982) introduced the new subspecies *Anolis cybotes ravifaux* based on an adult male (holotype MCZ 156221) from "environs of Mano Juan, Isla Saona, República Dominicana".

Despite an enormous activity in herpetological research in the Caribbean in general (see compilations e.g., in Schwartz & Henderson, 1991; Henderson & Powell, 2009) and with Caribbean anoles specifically (e.g., Losos, 2009 and references therein), the taxonomy of the cybotoid anoles of Hispaniola has not been addressed since the early 1980s. Our study of variation in genetic and morphological characters generated evidence for much more diversity than is reflected by the current taxonomy of this group of anoles, leading to this revision.

OBJECTIVES

- The objective of the present study is to revise the genus *Audantia*, using morphological and molecular data as lines of evidence, in order to define the morphological and geographical species boundaries in this group of lizards.

MATERIALS AND METHODS

For this study, we examined a total of 674 specimens of the genus *Audantia* (see Appendix 1). Abbreviations for museum collections follow Sabaj (2016) except for MNHNSD (Museo Nacional de Historia Natural "Prof. Eugenio de Jesús Marcano", Santo Domingo, Dominican Republic). Coordinates and elevation were recorded using Garmin GPS receivers with built-in altimeters. All coordinates are in decimal degrees, WGS 1984 datum, and rounded to the appropriate decimal place given precision of the measurement. Prior to preservation of collected specimens in the field, we took color photographs of each individual's extended dewlap. For this purpose, Gunther Köhler (GK) preferably utilized the standard forceps of genuine Swiss Army knives since their broad, flat apex prevents even thin-skinned dewlaps from damage and functions as an approximate scale (width = 3 mm in the models of both suppliers). Immediately after euthanasia via a pericardian injection of T61 (Intervet International, Unterschleißheim, Germany), relative hind limb length was determined by recording the point reached by the tip of the fourth toe when the extended hind limb was adpressed along the straightened specimen. Tissue samples were cut from the tip of the tail of selected individuals before they came in contact with formalin, stored in 98 % non-denatured ethanol.

Whenever possible, we everted the hemipenes of male specimens by injecting 70 % ethanol into the hemipenial pockets after manually pre-everting the hemipenes. Specimens were then preserved by injecting a solution of 5–10 mL absolute (i.e., 36 %) formalin in 1 L of 96 % ethanol into the body cavity and thighs, preferably also sprinkling everted hemipenes and extended dewlaps with this solution, and stored in 70 % ethanol. The collected specimens have been deposited in the collection of the Senckenberg Forschungsinstitut Frankfurt (SMF), Museo Nacional de Historia Natural "Prof. Eugenio de Jesús Marcano", Santo Domingo, Dominican Republic (MNHNSD), and the Smithsonian Institution (USNM).

The capitalized colors and color codes (the latter in parentheses) are those of Köhler (2012). Terminology of markings used in color descriptions follow Köhler (2012). Nomenclature of scale characters follows that of Köhler (2014). Head length was measured from the tip of the snout to the anterior margin of the ear opening. Snout length was measured from the tip of the snout to the anterior border of the orbit. Head width was determined with the broad tips of the calipers aligned with the levels of posterior margin of eye and supralabial scales, respectively, with the calipers held in a vertical position relative to the head. Dorsal and ventral scales were counted at midbody along the midline. Tail height and width were measured at the point reached by the heel of the extended hind leg. Subdigital lamellae were counted on Phalanges II to IV of Toe IV of the hind limbs, and separately on distal phalanx. We considered the scale directly anterior to the circumnasal to be a prenasal.

Abbreviations used are AGD (axilla-groin distance), dorsAG (number of medial dorsal scales between levels of axilla and groin), dorsHL (number of medial dorsal scales in one head length), HDT (horizontal diameter of tail), HL (head length), HW (head width), IFL (infralabials), IP (interparietal plate), SAM (scales around midbody), ShL (shank length), SL (snout length), SO (subocular scales), SPL (supralabial scales), SS (supraorbital semicircles), SVL (snout-vent length), TL (tail length), VDT (vertical diameter of tail),

ventrAG (number of medial ventral scales between levels of axilla and groin), and ventrHL (number of medial ventral scales in one head length). Synonymies in the species accounts are restricted to the major checklists of the Caribbean herpetofauna, regional treatments, and relevant taxonomic works.

Discriminant function analysis (DFA) was used to evaluate the phenetic distinctness of *a priori* groups (i.e., genetic clusters). The DFAs were created with the aid of the computer programm STATISTICA 6 (StatSoft, Inc. 2003). Discriminant scores (DS) were calculated by multiplying selected standardized variables (raw variables minus their associated mean value and divided by their associated standard deviation) by their associated unstandardized canonical coefficients. Each specimen was then plotted along the axes providing maximal separation of the a priori groups.

It is known that Hispaniola is a composite of two separate paleo-islands that collided about 10 million years ago (Hedges, 1996). Herein we refer to the southern and northern regions as the South Island and North Island, respectively, following Mertens (1939) and Schwartz (1978). Today they are connected by dry land that is below sea level, the Valle de Neiba (Dominican Republic) and Cul de Sac (Haiti).

As lines of evidence for species delimitation, we apply a phenotypic criterion (external morphology: coloration, morphometrics, and pholidosis, all structures coded by nuclear genes) and a criterion for reproductive isolation (genetic distinctness of the mitochondrial cytochrome B and ND2 genes). Genomic DNA was extracted from tissue using the DNeasy Blood and Tissue kit (Qiagen, Massachusetts, USA). For degraded samples and those for which sufficient yield was not obtained with the Qiagen kit, phenol chloroform extractions were completed. PCR amplification was performed under standard reaction conditions as outlined elsewhere (Hedges *et al*., 2008).

For this study, we have added a total of 267 new cytB sequences and 280 ND2 sequences (Appendix 2), with 142 ND2 sequences obtained from Glor *et al.* (2003). It should be noted that S.Blair Hedges (SBH) provided tissues for use in Glor *et al*. (2003) but they were reported incorrectly in that study as "USNM" catalog numbers when instead they were field and laboratory numbers used by SBH. They are represented in this tree with their correct "SBH" field numbers (see Appendix 2). The primers used to obtain these sequences were as follows: cytB – cytBL3 5' ATACAYTACACAGCRGAYAT 3' and cytBH3 5'TGGGTGTTCKACTGGTTGTCC3'; ND2 (from Macey *et al* 1997) – L4437 5'AAGCTTTCGGGCCCATACC3' and H4980 5'ATTTTTCGTAGTTGGGTTTGRTT3'. Sequences from 426 ingroup and three outgroup taxa were analyzed resulting in a total of 1691 aligned sites. Gene alignments were performed independently in Geneious 11.0.4 (https://www.geneious.com) using MAFFT 7.388 with default parameters (Katoh & Standley, 2013). Protein translations were reviewed to ensure correct alignment with respect to reading frames and individual gene trees were constructed as an additional check on data quality. Best-fit model selection for each gene was performed in MEGA X (Kumar *et al.*, 2018) and a maximum likelihood (ML) analysis was completed using RAxML 8.2.11 (Stamatakis, 2014), in Geneious 11.0.4. Evolutionary rates and base frequencies were estimated independently per gene, using the evolutionary model GTR + I + Γ. Gaps were treated as missing data. All parameters for the ML analyses were estimated by the program during the run. Branch support in the trees was provided by standard bootstrap analysis (2,000 replicates).

RESULTS

Taxonomy of anoles of the genus *Audantia*

The species of the genus *Audantia* are readily differentiated from all other Hispaniolan anoles (family Dactyloidae) by the combination of having (1) a very large head in adult males (ratio head length/SVL >0.3); (2) predominantly grayish-brown overall coloration in life; (3) usually a double row of slightly to greatly enlarged vetrebral scales, not forming a serrated crest (4) moderately long hind legs (fourth toe of adpressed hind leg reaching to a point between of posterior margin of eye and tip of snout); (5) the ventral scales at midbody smooth or keeled; (6) 24–35 subdigital lamellae on Phalanges II–IV of Toe IV of hind limbs; (7) male dewlap dirty white, greenish, yellowish, or orange; (8) males with a pair of distinctly enlarged postcloacal scales.

The analysis of our molecular data revealed 14 distinct genetic clusters among the specimens of the genus *Audantia* we studied (Fig. 1). We take this high level of genetic differentiation among these clusters (Table I) as evidence for lack of gene flow. Also, we documented morphological differences among these 14 genetic clusters, both in single characters of external morphology (Table II) as well as in multivariate statistical analyses.

Table I. Percent pairwise genetic distances (*p*-distances) separating each of the 14 species of *Audantia*

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. *A. hispaniolae*													
2. *A. armouri*	11.6												
3. *A. doris*	9.5	10.3											
4. *A. shrevei*	12.6	10.7	13.1										
5. *A. higuey*	13.3	11.4	12.9	11.9									
6. *A. ravifaux*	13.4	13.0	13.8	13.0	13.1								
7. *A. aridius*	14.0	13.5	13.7	12.8	13.6	13.9							
8. *A. cybotes*	14.5	13.4	14.1	13.3	13.3	13.2	12.8						
9. *A. australis*	14.0	12.8	13.6	12.0	13.0	12.4	13.8	10.5					
10. *A. breslini*	15.1	15.2	15.8	15.1	14.2	15.2	13.9	14.6	14.3				
11. *A. saxatilis*	18.2	17.7	17.7	17.5	16.5	17.5	16.9	18.4	17.6	16.7			
12. *A. longitibialis*	18.5	18.3	19.4	18.8	17.8	19.6	17.5	17.8	18.1	18.1	19.0		
13. *A. marcanoi*	21.2	21.0	22.0	21.3	20.0	21.1	20.2	19.4	19.9	19.1	22.2	21.7	
14. *A. strahmi*	17.7	16.9	17.2	18.2	16.5	18.5	17.0	15.9	17.6	18.0	18.0	13.6	20.5

Table II. Selected measurements, proportions and scale characters of the *cybotes* series species studied in detail here. Range is followed by mean value and standard deviation in parentheses. For abbreviations see text.

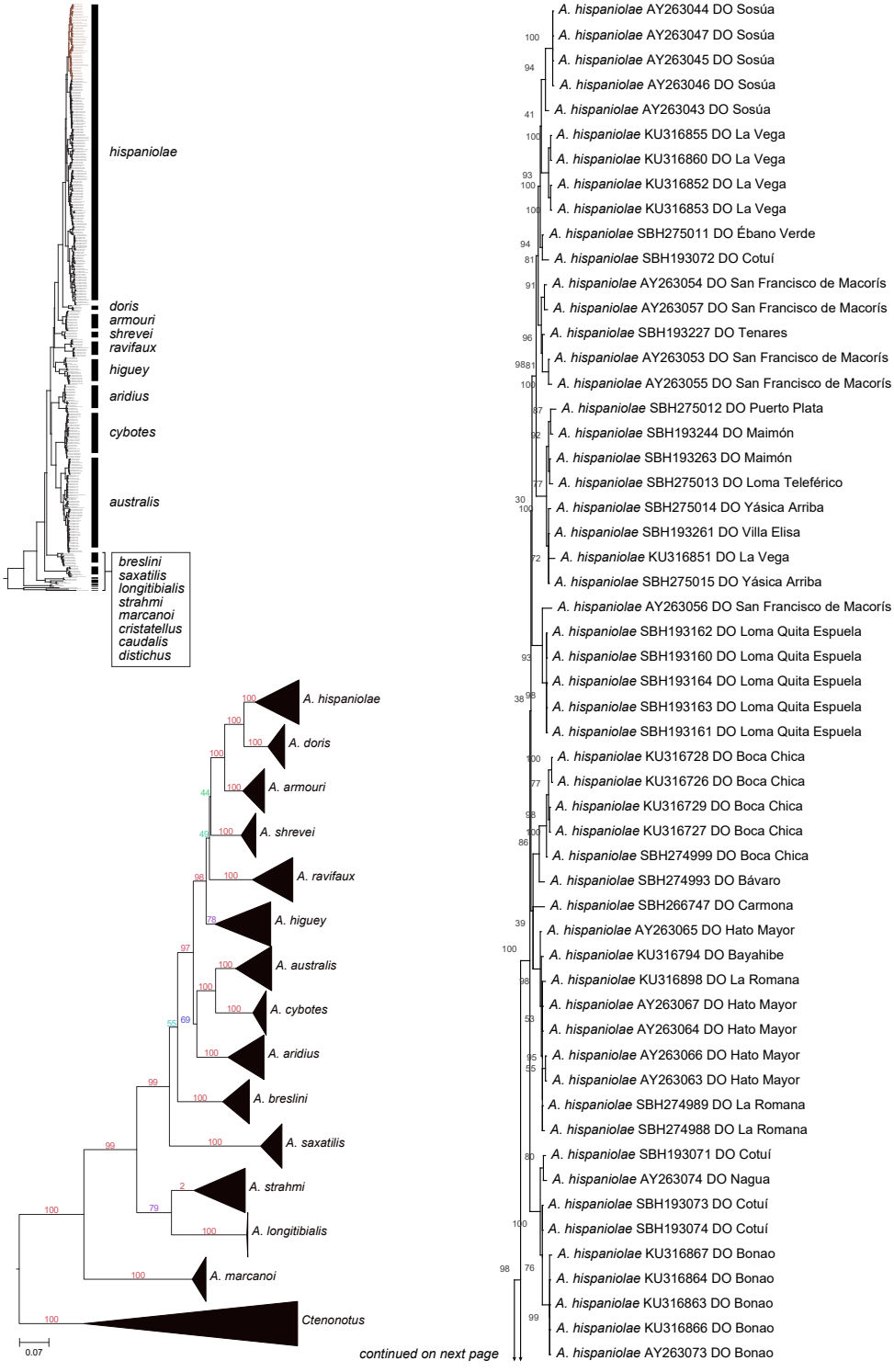
		Audantia aridius ♂ 9 ♀ 3	***Audantia australis*** ♂ 14 ♀ 26	***Audantia cybotes*** ♂ 14 ♀ 10	***Audantia doris*** ♂ 4 ♀ 3	***Audantia higuey*** ♂ 9 ♀ 3	***Audantia hispaniolae*** ♂ 20 ♀ 10	***Audantia ravifaux*** N = 24
maximum SVL	males	70.0	69.0	79.0	63.0	69.0	67.0	59
	females	52.5	64.0	57.0	47.0	51.0	56.0	44
TL/SVL	males	1.82–1.96 (1.89±0.06)	1.69–1.94 (1.81±0.09)	1.66–1.98 (1.80±0.13)	–	1.86–2.00 (1.95±0.08)	1.98–2.10 (2.03±0.06)	–
	females	–	1.68–1.94 (1.77±0.10)	1.47–2.11 (1.70±0.24)	–	1.88–1.97 (1.94±0.05)	1.76–1.85 (1.81±0.07)	–
VDT/HDT	males	1.32–1.95 (1.52±0.20)	1.35–1.82 (1.60±0.13)	1.38–2.00 (1.56±0.19)	2.26–2.50 (2.38±0.17)	1.42–2.40 (1.71±0.35)	1.31–1.67 (1.48±0.11)	–
	females	1.28–1.53 (1.40±0.18)	1.16–1.73 (1.34±0.16)	1.33–1.69 (1.45±0.11)	–	1.28–2.30 (1.82±0.51)	1.14–1.42 (1.31±0.11)	–
AGD/SVL	males	0.33–0.37 (0.35±0.01)	0.38–0.55 (0.41±0.04)	0.20–0.42 (0.36±0.05)	0.35–0.38 (0.37±0.01)	0.33–0.40 (0.35±0.02)	0.33–0.39 (0.36±0.02)	–
	females	0.35–0.39 (0.38±0.02)	0.34–0.43 (0.39±0.02)	0.38–0.42 (0.40±0.01)	0.39–0.45 (0.42±0.03)	0.36–0.39 (0.37±0.01)	0.37–0.41 (0.40±0.02)	–
HL/SVL	males	0.29–0.32 (0.31±0.01)	0.29–0.33 (0.30±0.01)	0.30–0.32 (0.31±0.01)	0.32–0.34 (0.33±0.01)	0.30–0.32 (0.31±0.01)	0.29–0.32 (0.31±0.01)	–
	females	0.29–0.30 (0.30±0.00)	0.26–0.32 (0.30±0.01)	0.28–0.31 (0.29±0.01)	0.29 (0.29±0.00)	0.28–0.32 (0.31±0.02)	0.27–0.30 (0.29±0.01)	–
HL/HW	males	1.67–1.82 (1.73±0.05)	1.65–1.79 (1.73±0.05)	1.64–1.87 (1.75±0.06)	1.77–1.85 (1.82±0.04)	1.71–1.96 (1.82±0.06)	1.66–2.03 (1.78±0.11)	–
	females	1.64–1.74 (1.68±0.05)	1.58–1.80 (1.68±0.05)	1.68–1.81 (1.72±0.04)	1.67–1.78 (1.72±0.05)	1.76–2.07 (1.82±0.13)	1.63–1.78 (1.69±0.04)	–
SL/SVL	males	0.13–0.14 (0.14±0.00)	0.12–0.13 (0.13±0.00)	0.12–0.14 (0.13±0.01)	0.14–0.15 (0.14±0.00)	0.13–0.14 (0.14±0.00)	0.12–0.14 (0.13±0.01)	–
	females	0.12–0.13 (0.13±0.01)	0.12–0.13 (0.13±0.00)	0.11–0.13 (0.12±0.01)	0.12–0.13 (0.13±0.00)	0.13–0.15 (0.14±0.01)	0.12–0.14 (0.13±0.01)	–

Table II. Continuation

		Audantia aridius ♂ 9 ♀ 3	***Audantia australis*** ♂ 14 ♀ 26	***Audantia cybotes*** ♂ 14 ♀ 10	***Audantia doris*** ♂ 4 ♀ 3	***Audantia higuey*** ♂ 9 ♀ 3	***Audantia hispaniolae*** ♂ 20 ♀ 10	***Audantia ravifaux*** N = 24
SL/HL	males	0.42–0.45 (0.43±0.01)	0.41–0.43 (0.42±0.01)	0.40–0.44 (0.43±0.01)	0.43–0.45 (0.44±0.01)	0.43–0.46 (0.44±0.01)	0.40–0.46 (0.43±0.02)	–
	females	0.40–0.45 (0.43±0.03)	0.41–0.44 (0.42±0.01)	0.40–0.44 (0.42±0.01)	0.43–0.45 (0.44±0.02)	0.44–0.47 (0.45±0.01)	0.42–0.49 (0.44±0.02)	–
ShL/SVL	males	0.28–0.32 (0.31±0.01)	0.28–0.32 (0.30±0.01)	0.16–0.32 (0.29±0.04)	0.30–0.33 (0.32±0.01)	0.30–0.33 (0.32±0.01)	0.28–0.33 (0.30±0.01)	–
	females	0.29–0.30(0.29±0.01)	0.27–0.31 (0.30±0.01)	0.29–0.32 (0.30±0.01)	0.29–0.31 (0.30±0.01)	0.27–0.31 (0.29±0.02)	0.27–0.31 (0.29±0.01)	–
ShL/HL	males	0.94–1.05 (0.99±0.04)	0.95–1.08 (1.00±0.04)	0.49–1.05 (0.92±0.14)	1.92–1.02 (0.96±0.04)	1.01–1.03 (1.02±0.01)	0.89–1.05 (0.99±0.05)	–
	females	0.98–1.05 (1.00±0.03)	0.94–1.06 (1.01±0.03)	0.97–1.11 (1.01±0.04)	1.00–1.07 (1.04±0.03)	0.85–1.02 (0.94±0.06)	0.93–1.07 (1.01±0.05)	–
ToeLam p		26–33 (29.8±2.1)	27–34 (29.8±2.1)	28–35 (30.8±2.1)	24–32 (28.7±2.6)	27–31 (28.6±1.2)	27–32 (29.6±1.6)	–
ToeLam d / IO		7–11 (9.4±1.1) 0–1 (0.4±0.5)	8–11 (9.1±0.9) 0–1 (0.3±0.5)	8–12 (9.3±0.9) 0–1 (0.2±0.4)	9–10 (9.4±0.5) 0–1 (0.1±0.4)	8–11 (9.8±0.8) 0–1 (0.2±0.4)	8–11 (9.5±0.9) 0–1 (0.4±0.5)	– 0–1 (0.0±0.2)
IP/IO		1–3 (2.2±0.5)	2.0–3.5 (2.3±0.4)	1–3 (2.1±0.6)	2–3 (2.6±0.5)	1.0–2.5 (2.0±0.4)	1–3 (2.2±0.5)	1–3 (1.7±0.5)
SO/SPL		0–1 (0.9±0.3)	0–1 (0.9±0.3)	0–1 (0.8±0.4)	0–1 (0.9±0.2)	0–1 (0.7±0.5)	0–1 (0.9±0.3)	0.0–1.5 (0.4±0.5)
SPL		6–7 (6.2±0.4)	5–7 (6.2±0.5)	5–8 (6.2±0.7)	6–7 (6.4±0.5)	6–7 (6.3±0.5)	6–7 (6.4±0.5)	–
IFL		6–7 (6.2±0.4)	5–7 (5.9±0.5)	5–7 (5.9±0.7)	6–7 (6.3±0.5)	5–8 (6.3±0.8)	5–7 (6.2±0.6)	–
LST		24–49 (36.3±8.1)	28–72 (40.3.5±8.7)	32–66 (45.8±9.6)	26–41 (35.0±4.9)	35–59 (46.5±6.6)	20–72 (41.7±12.3)	–

	Audantia aridius ♂ 9 ♀ 3	***Audantia australis*** ♂ 14 ♀ 26	***Audantia cybotes*** ♂ 14 ♀ 10	***Audantia doris*** ♂ 4 ♀ 3	***Audantia higuey*** ♂ 9 ♀ 3	***Audantia hispaniolae*** ♂ 20 ♀ 10	***Audantia ravifaux*** N = 24
LSR	4–7 (6.2±0.9)	5–8 (6.6±0.8)	5–9 (6.8±0.8)	5–7 (6.1±0.7)	6–7 (6.6±0.5)	5–9 (6.9±1.1)	5–7 (5.8)
PR	6–7 (6.3±0.5)	4–7 (6.4±0.8)	5–7 (6.5±0.6)	6–7 (6.4±0.5)	6–7 (6.8±0.4)	5–7 (6.4±0.6)	3–5 (3.7)
PM	4–9 (6.0±1.1)	4–9 (6.1±0.9)	4–8 (6.3±0.9)	6–7 (6.1±0.4)	6–9 (7.2±0.8)	4–8 (6.1±0.9)	4–8 (4.8)
SubL / IN	1–2 (1,9±0.3) 5–8 (6.3±0.8)	1.0–2.5 (1.6±0.5) 4–8 (6.0±0.6)	1–2 (1.7±0.4) 5–7 (6.1±0.5)	2.0–2.5 (2.1±0.2) 5–6 (5.9±0.4)	2–3 (2.2±0.4) 6–7 (6.1±0.3)	0.5–2.5 (1.9±0.5) 4–7 (5.9±0.7)	– –
ESO (greatly) / ESO (moderately) / 2Canths	0 3–7 (4.8±1.3) 6–8 (7.3±0.8)	0.5–1.0 (0.7±0.3) 2–7 (4.7±1.1) 5–8 (6.6±1.0)	0.5 (0.5±0.0) 1.5–6.5 (5.5±1.4) 5–10 (7.0±1.3)	0 2.5–5.0 (3.8±0.9) 6–7 (6.3±0.5)	0 2.5–7.0 (4.3±1.2) 5–8 (6.0±1.1)	0.5 2.0–6.5 (4.5±1.0) 5–9 (6.6±1.4)	– – 4–7 (5.5)
1Canths	6–9 (8.0±1.0)	6–12 (9.0±1.2)	7–12 (8.6±1.2)	8–9 (8.4±0.5)	8–9 (8.1±0.3)	6–12 (8.7±1.6)	–
dorsHL	42–58 (39.3±4.4)	36–52 (44.4±3.9)	30–56 (42.0±5.0)	32–48 (38.3±5.1)	38–50 (45.3±3.7)	38–66 (47.0±7.4)	35–54 (44.9)
ventrHL	28–44 (36.5±4.9)	24–42 (31.2±4.6)	22–42 (31.7±5.1)	22–40 (30.0±7.0)	26–40 (35.3±4.4)	22–50 (31.5±6.7)	27–51 (36.5)
dorsAG	62–80 (68.2±6.2)	52–87 (72.0±7.8)	55–86 (69.4±9.3)	45–75 (55.7±10.4)	53–70 (63.1±5.2)	56–99 (75.6±10.2)	–
ventrAG / SAM / RED	43–50 (45.9±2.7) 186–234 (216.8±14.0) 2 (2±0)	35–57 (45.3±5.7) 178–242 (216.3±14.8) 2 (2±0)	35–53 (44.6±5.1) 160–232 (203.6±17.3) 2 (2±0)	38–51 (42.4±4.5) 164–184 (173.1±7.6) 2 (2±0)	38–49 (43.3±2.9) 166–212 (184.5±13.8) 2 (2±0)	37–55 (42.0±4.2) 166–240 (204.8±20.3) 2 (2±0)	– – –

FIGURE 1



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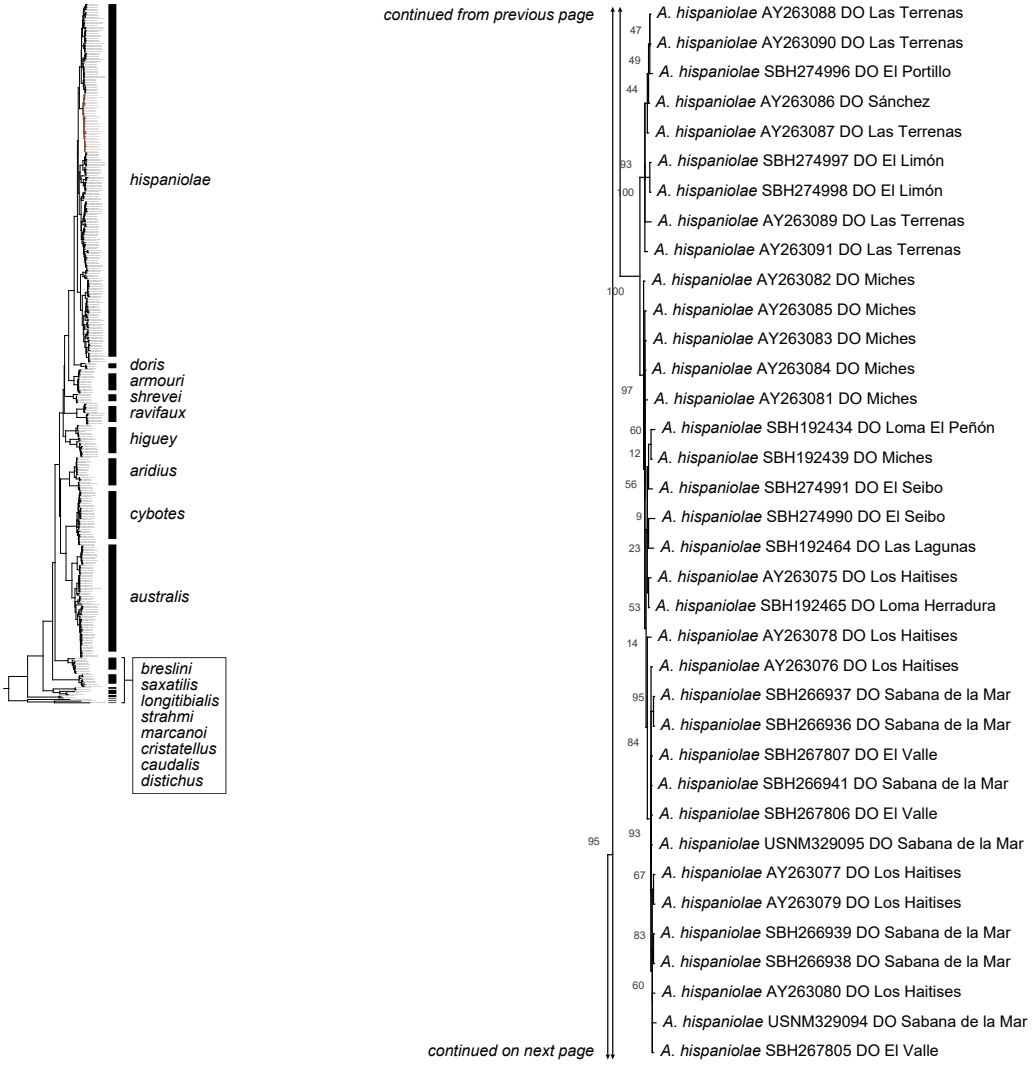
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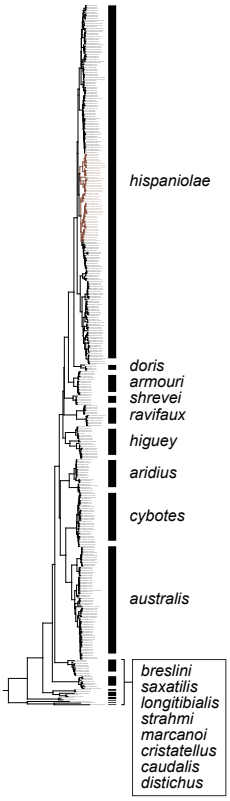

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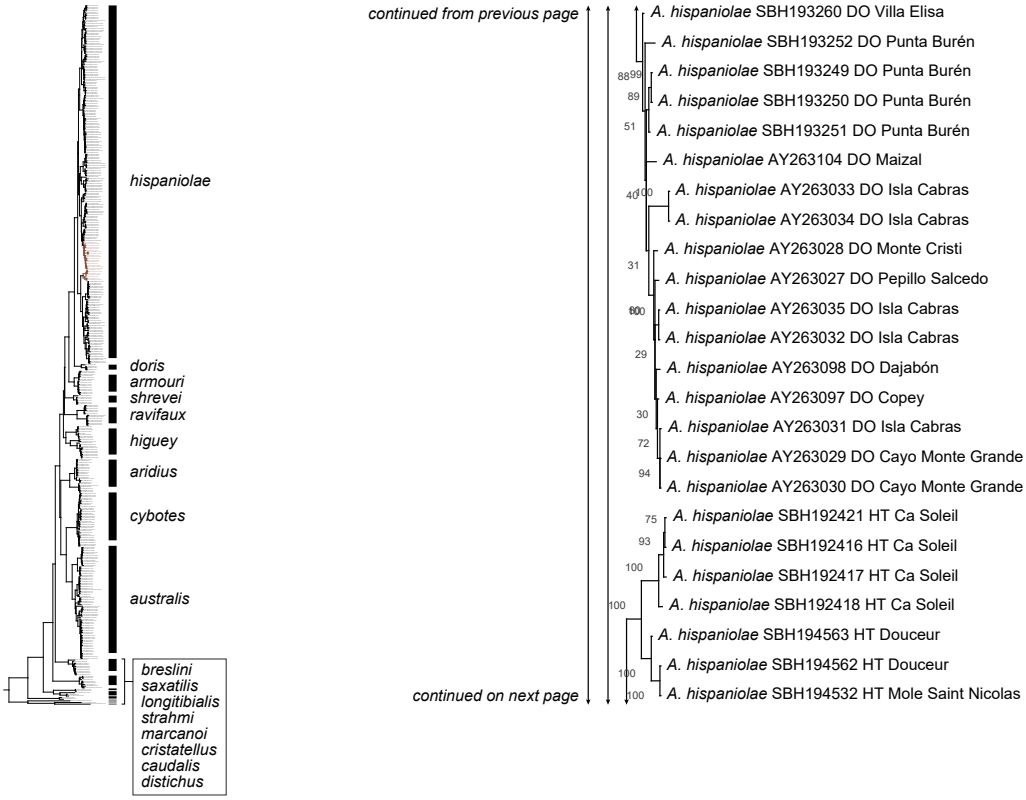
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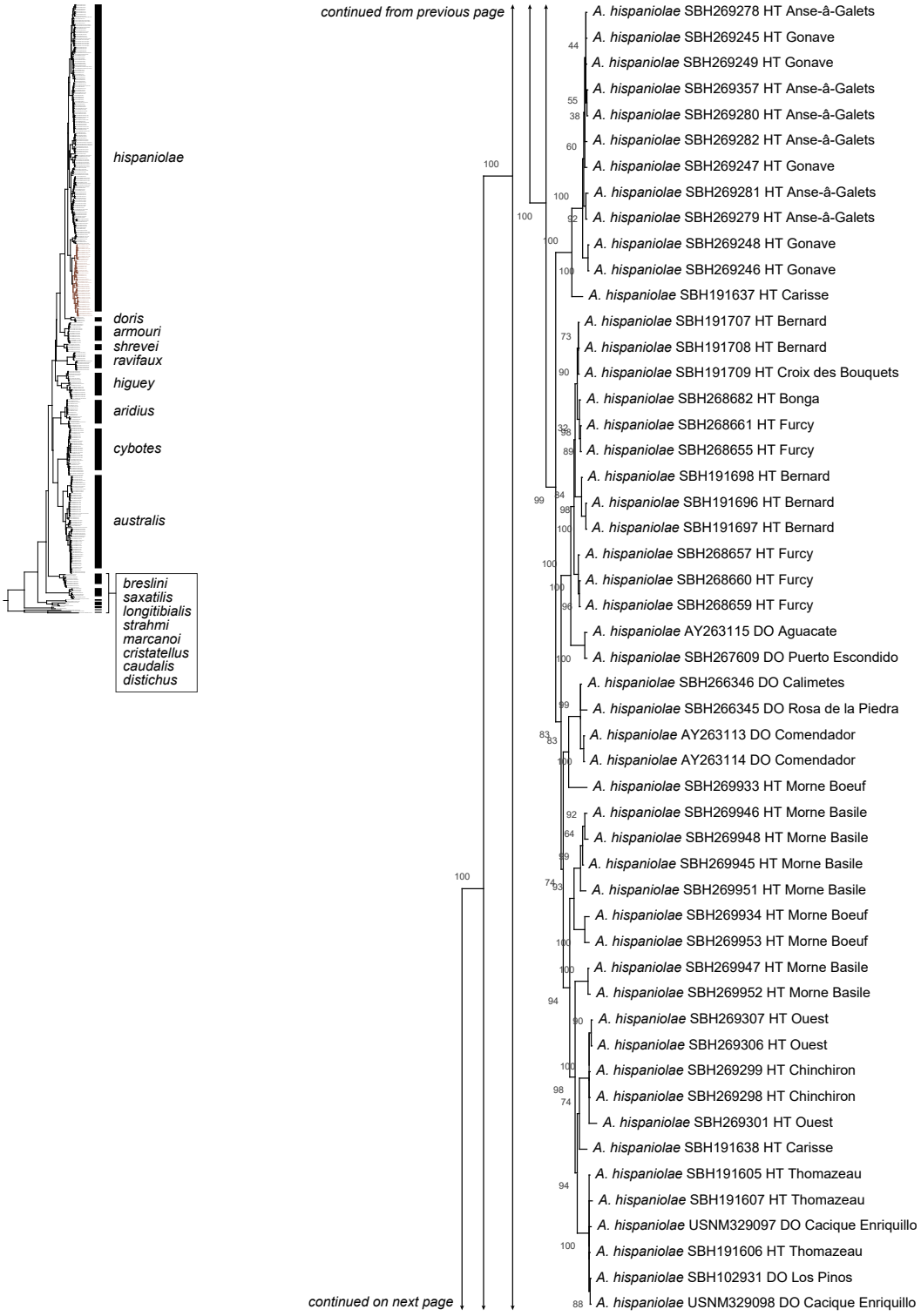
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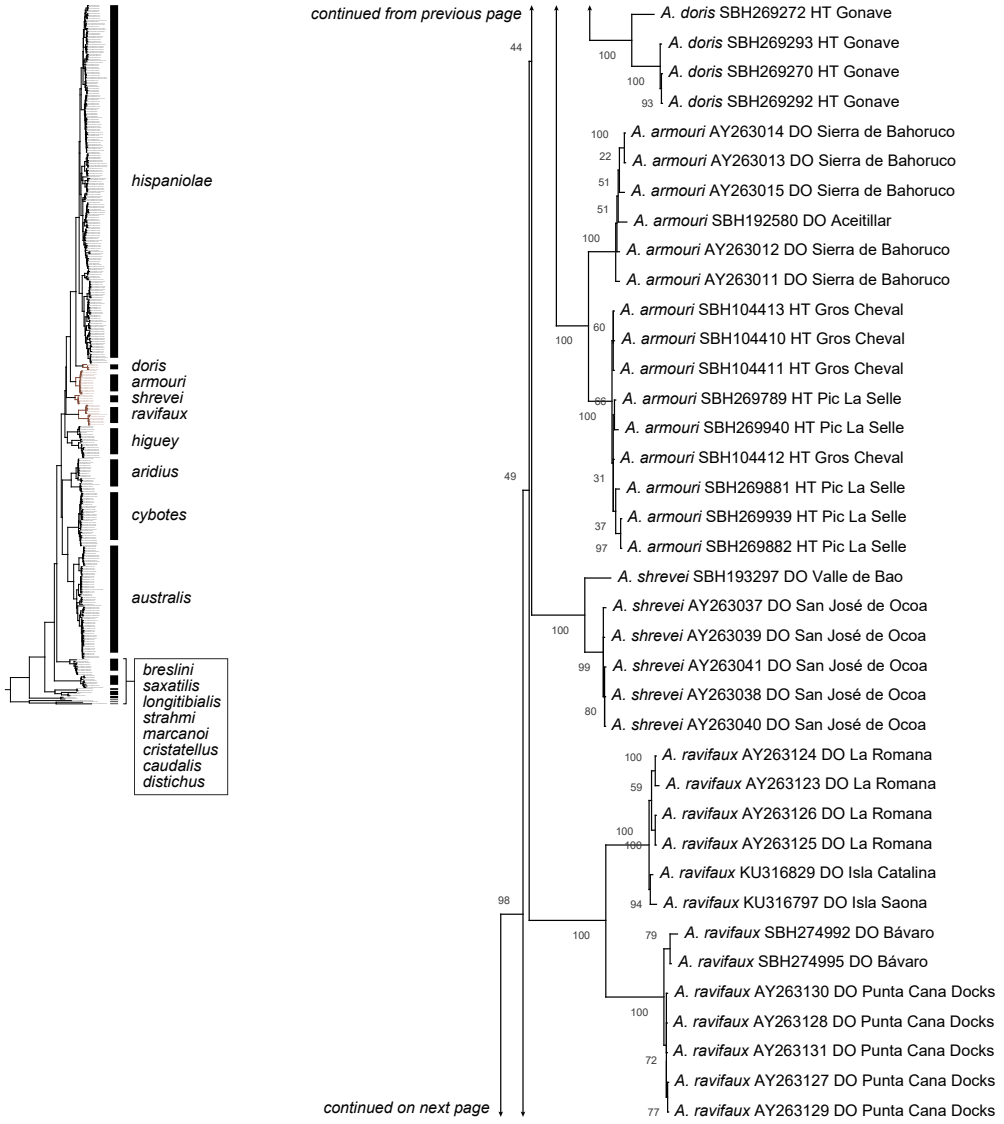
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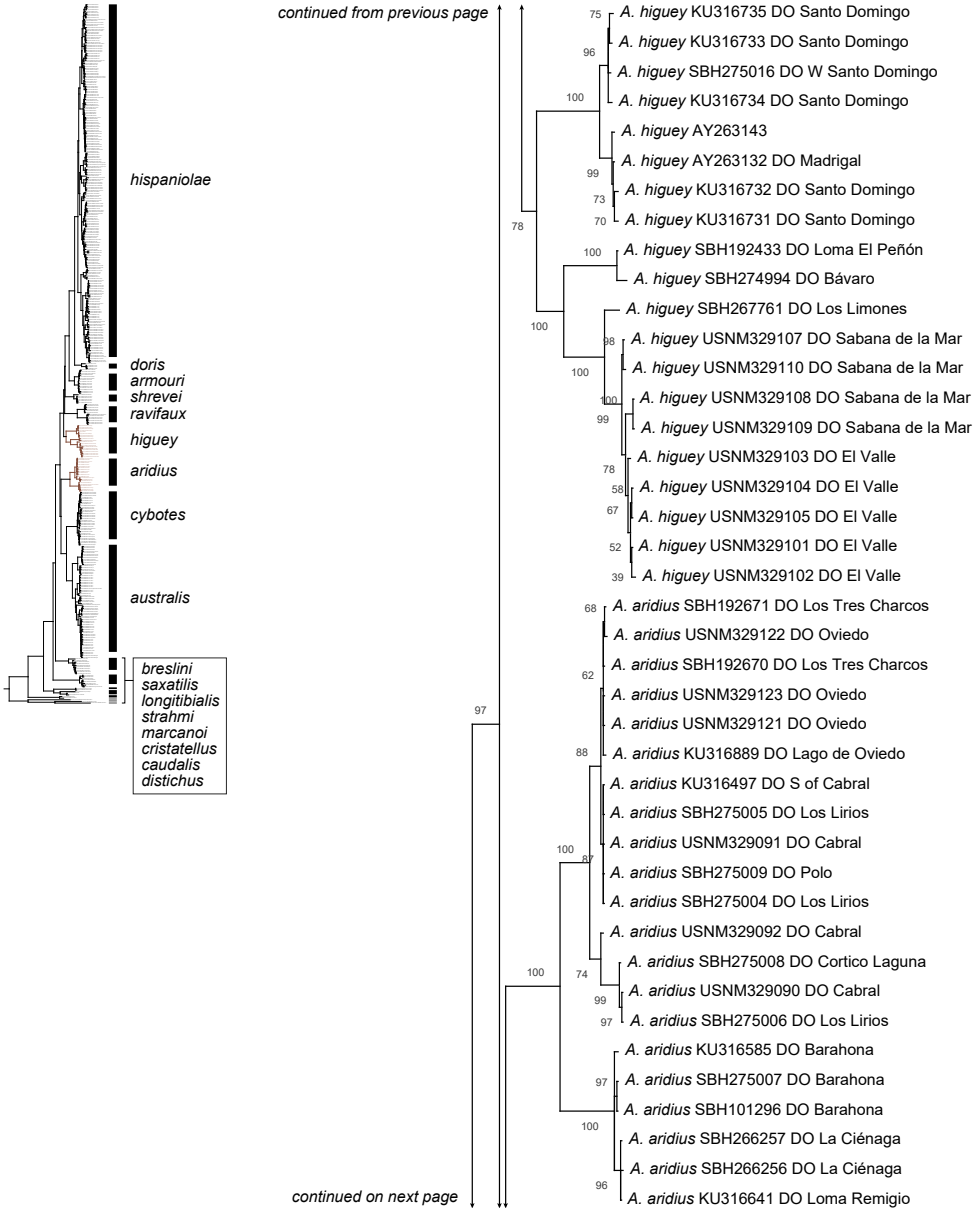
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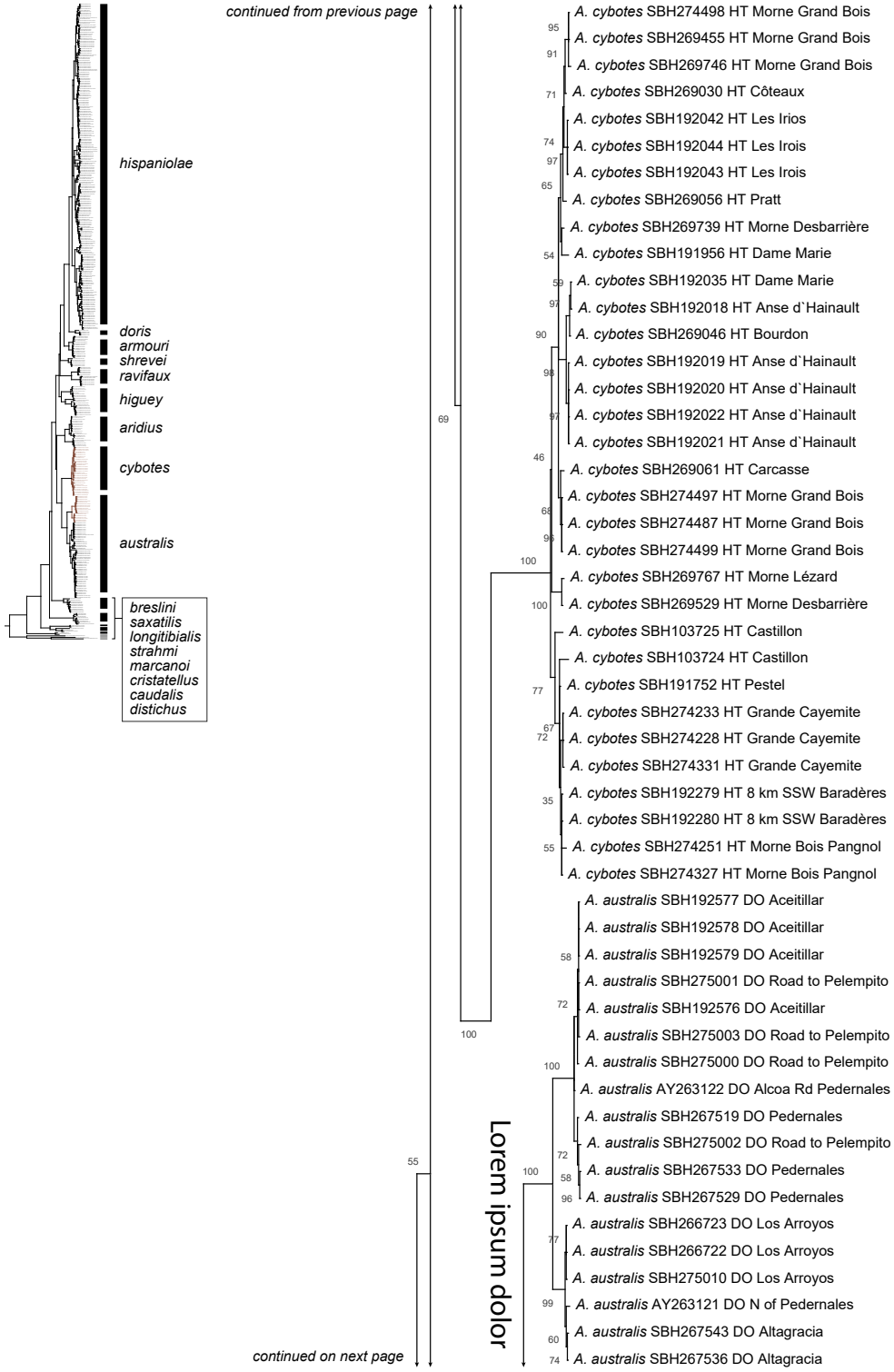
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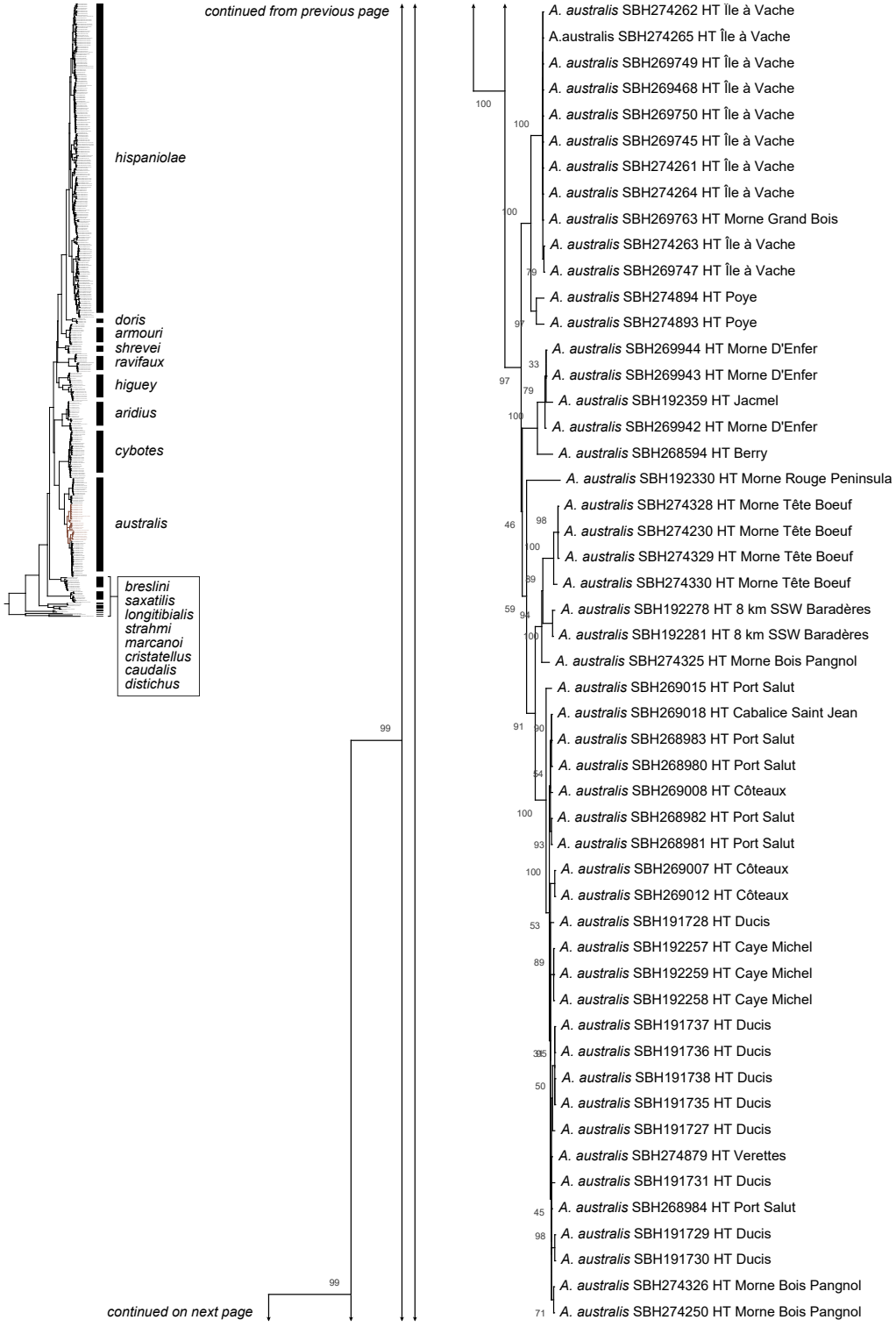
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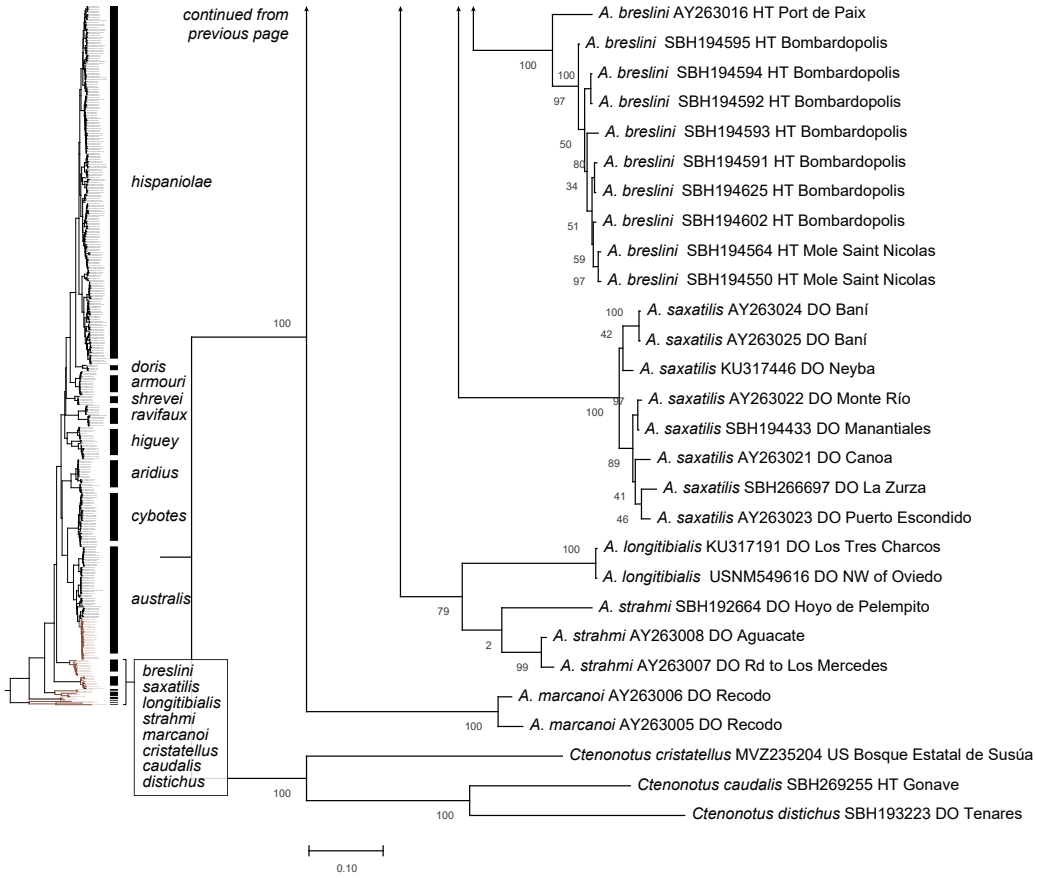

Figure 1. Phylogenetic tree of specimens of the genus *Audantia* from a maximum-likelihood analysis of DNA sequences of two mitochondrial genes: cytochrome b and ND2. A scale bar is indicated. The numbers at nodes are bootstrap values. The tree is rooted with the species *Ctenonotus caudalis*, *C. cristatellus*, and *C. distichus*. A locator tree is shown on each page identifying the clade or clades (red) that are displayed on the same page. For ease of viewing, a species-level tree is shown as an inset in the lower left corner of the first page, with same topology, branch lengths, and support values as in the full tree. Black triangles are proportional to the number of individuals within each species in the full tree.

Figures 2–7 show the results of discriminant function analyses (DFA). The best discriminating characters were relative size of body scales, number of loreal scales, as well as the ratios shank/SVL and AGD/SVL.

Figure 2 shows the results of an analysis based on six morphological characters (ventrHL, dorsHL, LST, SAM, shank/SVL, and AGD/SVL) of males of the species *Audantia cybotes*, Species 3 "*australis*", and Species 4 "*aridius*". The first and second discriminant functions correctly classified 80.0 % of the specimens of *A. cybotes*, 84.6 % of Species 3 "*australis*", and 80.0 % of Species 4 "*aridius*". The first discriminant function is DS = 0.048747 [ventrHL] -0.901191 [dorsHL] + 0.754006 [LST] -0.436889 [SAM] -0.381972 [shank/SVL] + 0.052856 [AGD/SVL]. The second discriminant function is DS = -0.138031 [ventrHL] + 0.183618 [dorsHL] + 0.064224 [LST] -0.168316 [SAM] -0.317627 [shank/SVL] -0.948841 [AGD/SVL]. The polygons of all three species hardly overlap.

Figure 3 shows the results of an analysis based on six morphological characters (ventrHL, dorsHL, LSR, LST, SAM, and ToeLam prox) of females of the species *A. cybotes*, Species 3 "*australis*", and Species 4 "*aridius*". The first and second discriminant functions correctly classified 41.7% of the specimens of *A. cybotes*, 90.5 % of Species 3 "*australis*", and 33.3 % of Species 4 "*aridius*". The first discriminant function is DS = 0.222672 [ventrHL] + 0.723711 [dorsHL] -0.552333 [LST] -0.175056 [SAM] + 0.300687 [shank/SVL] -0.406005 [A-GD/SVL]. The second discriminant function is DS = -0.265324 [ventrHL] + 0.275709 [dorsHL] -0.540854 [LST] + 0.565826 [SAM] + 0.425727 [shank/SVL] -0.168236 [A-GD/SVL]. The polygone of Species 4 "*aridius*" does slightly overlap with the polygone of *A. cybotes*, whereas *A. cybotes'* and Species 3 "*australis*"*'* polygons have a high degree of overlap.

The results of an analysis based on six morphological characters (ventrHL, dorsHL, ToeLam prox, LST, SAM, and AGD/SVL) of males of the species Species 2 "*higuey*", Species 1 "*hispaniolae*", *A. doris,* and *A. ravifaux* are shown in Figure 4. The first and second discriminant functions correctly classified 77.8 % of the specimens of Species 2 "*higuey*" and 81.8 % of Species 1 "*hispaniolae*", 71.4 % of *A. doris*, and 91.7 % of *A. ravifaux*. The first discriminant function is DS = -0.390318 [ventrHL] -0.054148 [dorsHL] + 0.837806 [SAM] + 0.448478 [LST] + 0.183539 [AGD/SVL]. The second discriminant function is DS = 0.731362 [ventrHL] + 0.296961 [dorsHL] + 0.523924 [SAM] -0.946471 [LST] + 0.140161 [AGD/SVL]. The polygone of *A. ravifaux* does not overlap with any of the other polygons, whereas whereas the polygons of the remaining three species slightly overlap with each other.

Figure 5 shows the results of an analysis based on five morphological characters (ventrHL, dorsHL, ToeLam prox, SAM, and AGD/SVL) of females of the Species 2 "*higuey*", Species 1 "*hispaniolae*", and *A. doris*. The first and second discriminant functions correctly classified 100.0 % of all three specimens. The first discriminant function is DS = -0.618265 [ventrHL] -0.331903 [dorsHL] -0.952501 [LST] + 1.533832 [SAM] + 0.966015 [AGD/SVL]. The second discriminant function is DS = -0.17553 [ventrHL] -1.15786 [dorsHL] -1.32790 [LST] -0.61151 [SAM] + 0.00630 [AGD/SVL]. All three polygons do not overlap.

To further evaluate the patterns of morphological variation in the genetic clusters that occur sympatrically at several localities, we placed the genetically defined specimens in the area of sympatry in OTUs separate from those outside of this area. In the case of *A. cybotes* and Species 3 "*australis*", this resulted in completely separated polygons for the allopatric OTUs of these taxa, whereas the polygons of the OTUs in the area of sympatry strongly overlap, with only 33.3–66.6 % of the OTUs in the area of sympatry being classified correctly (Figs. 6 and 7). For the males, the first discriminant function is DS = -0.16628 [ToeLam prox] + 0.80227 [LST] -0.73931 [SAM] -0.56962 [dorsAG]. The second discriminant function is DS = 0.34617 [ToeLam prox] + 0.13400 [LST] -0.62410 [SAM] + 1.00712 [dorsAG]. For the females, the first discriminant function is DS = 0.06983 [ToeLam prox] -0.88473 [ToeLam dist] + 0.07918 [LST] + 0.42101 [IO] -0.41888 [SAM] + 0.09967 [dorsAG]. The second discriminant function is DS = -0.37742 [ToeLam prox] + 0.42339 [ToeLam dist] -0.59342 [LST] + 0.66923 [IO] + 0.22095 [SAM] + 0.13491 [dorsAG].

In conclusion, we recognize these 14 clusters as species level units. The majority of the species level units we recognize can be readily assigned to a nominal taxon based on the geographic provenance of the respective type material (i.e., *Audantia armouri, A. breslini, A. doris, A. longitibialis, A. marcanoi, A. ravifaux, A. shrevei, A. strahmi, A. whitemani*). The type locality of *Anolis cybotes* Cope, 1863 is "Western Hayti; from near Jeremie".

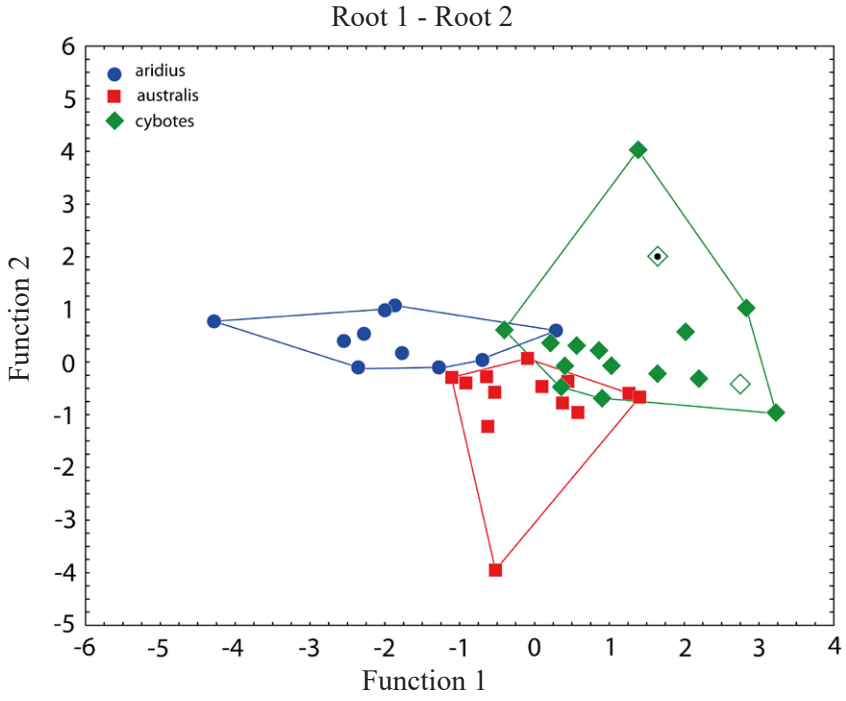

Figure 2. Discriminant function analysis of species of the genus *Audantia* based on six morphological characters (ventrHL, dorsHL, LST, SAM, shank/SVL, and AGD/SVL) of males of the species *A. cybotes*, Species 3 "*australis*", and Species 4 "*aridius*". Open square = lectotype of *Anolis riisei* Reinhardt & Lütken, 1863 (NHMD R3796); open square with black dot = lectotype of *Anolis cybotes* Cope, 1863 (MCZ 14346). See text for details.

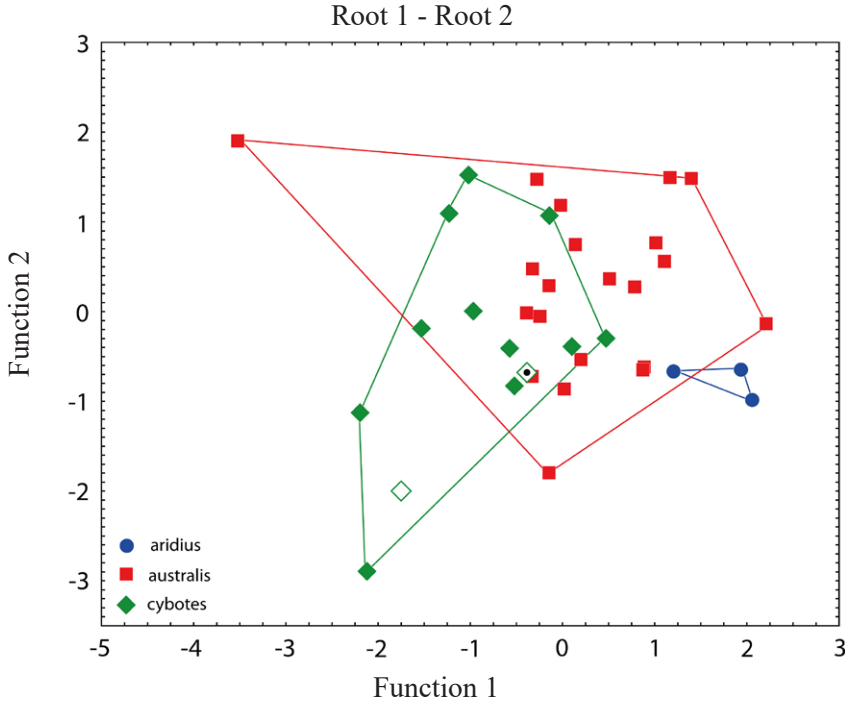

Figure 3. Discriminant function analysis of species of the genus *Audantia* based on six morphological characters (ventrHL, dorsHL, LSR, LST, SAM, and ToeLam prox) of females of the species *A. cybotes*, Species 3 "*australis*", and Species 4 "*aridius*". Open square = paralectotype of *Anolis riisei* Reinhardt & Lütken, 1863 (NHMD R3797); open square with black dot = paralectotype of *Anolis cybotes* Cope, 1863 (MCZ 14347). See text for details.

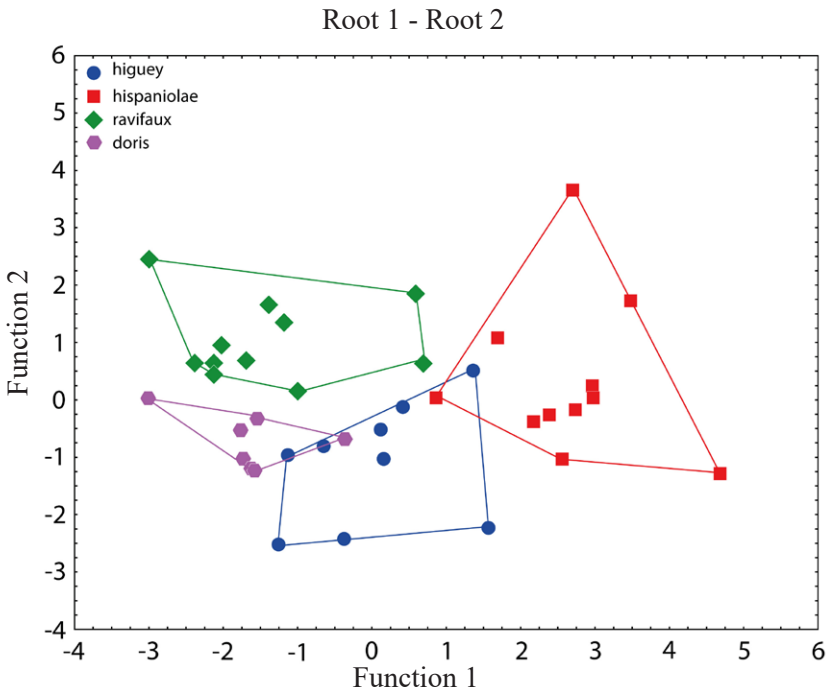

Figure 4. Discriminant function analysis of species of the genus *Audantia* based on six morphological characters (ventrHL, dorsHL, ToeLam prox, LST, SAM, and AGD/SVL) of males of the species Species 2 "*higuey*", Species 1 "*hispaniolae*", *A. doris*, and *A. ravifaux*. See text for details.

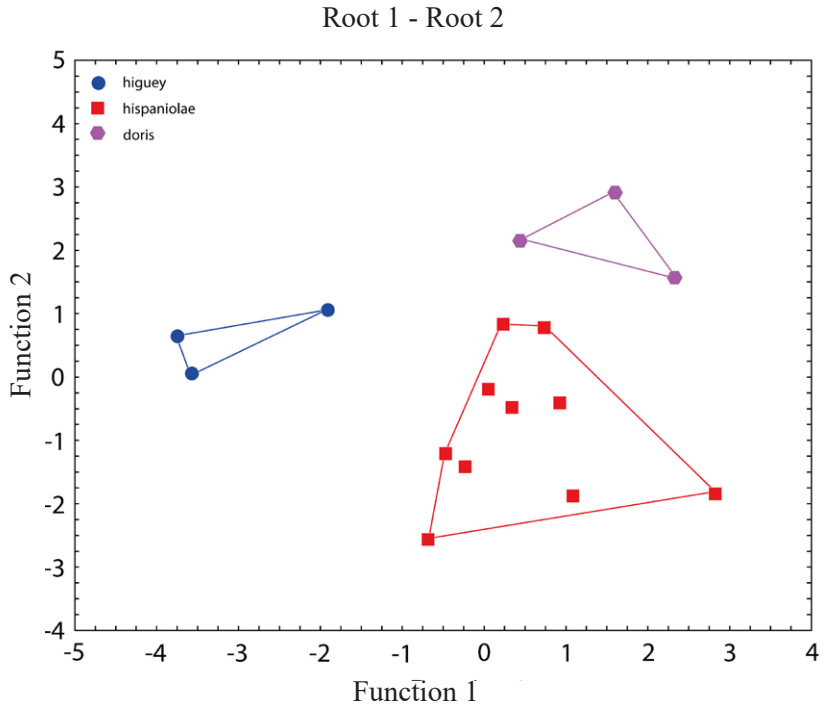

Figure 5. Discriminant function analysis of species of the genus *Audantia* based on five morphological characters (ventrHL, dorsHL, ToeLam prox, SAM, and AGD/SVL) of females of the Species 2 "*higuey*", Species 1 "*hispaniolae*", and *A. doris*. See text for details.

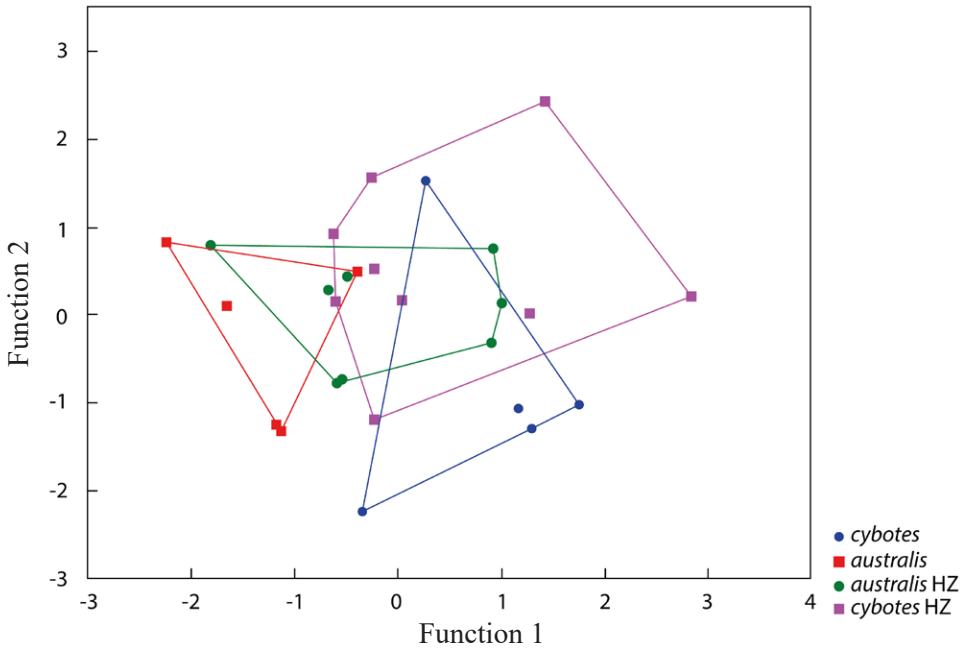

Figure 6. Discriminant function analysis of males of species of the species *A. cybotes* and Species 3 "*australis*" with the populations in the area of sympatry (called "*cybotes* HZ" and "*australis* HZ" here) grouped as OTUs separate from those outside of this area (those are called "*cybotes*" and "*australis*" here). This analysis is based on four morphological characters (dorsAG, LST, SAM, and ToeLam prox). See text for details.

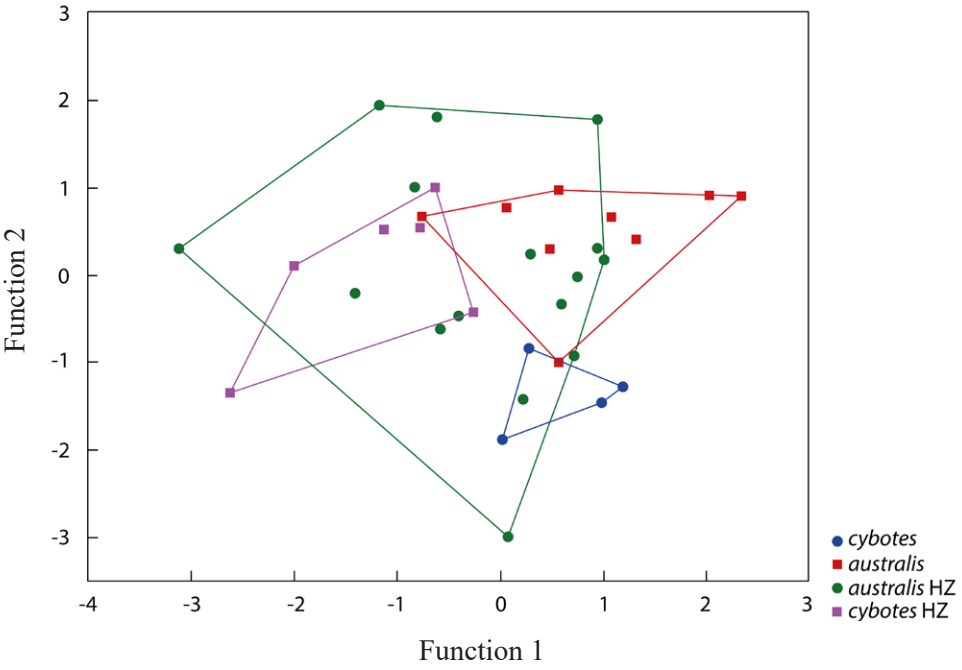

Figure 7. Discriminant function analysis of males of species of the species *A. cybotes* and Species 3 "*australis*" with the populations in the area of sympatry (called "*cybotes* HZ" and "*australis* HZ" here) grouped as OTUs separate from those outside of this area (those are called "*cybotes*" and "*australis*" here). This analysis is based on six morphological characters (dorsAG, LST, SAM, IO, ToeLam dist, and ToeLam prox). See text for details.

Therefore, we assign the genetic clade that contains specimens from the extreme western portion of the Tiburón Peninsula, Haiti, to *A. cybotes* sensu stricto. Also, we here designate as the lectotype of *Anolis cybotes* Cope, 1863 MCZ 14346, an adult male. Given its type locality and the poor state of conservation of its type material (see introduction and Fig. 8), and the genetic evidence, we assign the nominal taxon *Anolis haetianus* Garman, 1887 to the synonymy of *A. cybotes* Cope, 1863. Our data support the recognition of the nominal taxa *Anolis cybotes ravifaux* Schwartz & Henderson, 1982 and *Anolis doris* Barbour, 1925, respectively, as distinct species. Finally, we examined the holotype of *Anolis citrinellus* Cope, 1864 (BMNH 1946.8.5./1) and were surprised to learn that this specimen is not a species of the genus *Audantia* but rather represents an adult female of *Ctenonotus distichus* (**new synonymy**; Figs. 9–10; Table III). Furthermore, the holotype of *Anolis cybotes saxatilis* Mertens, 1938 (Figs. 11–12; Table III) is actually a specimen of the biological species currently referred to as *A. whitemani*, not of *A. cybotes*, as characterized by having dark brown crossbands on neck and anterior dorsum, keeled ventral scales; homogeneously distributed, widely spaced small gorgetals with more skin covered than uncovered by scales; no dark gular streaks; and a double row of weakly enlarged, but distinct vertebral scales. Therefore, we consider *Anolis cybotes saxatilis* Mertens, 1938 and *Anolis whitemani* Williams, 1963 to be conspecific and place the latter name into the synonymy of the former. Thus, in this work we use the name *A. saxatilis* for the species formerly referred to as *A. whitemani*.

A somewhat complicated issue is the taxonomic identity of *Anolis riisei* Reinhardt & Lütken, 1863. This taxon was descibed based on two syntypes, NHMD R3796 (adult male) and R3793 (adult female) from "Haiti," a term that was used for the whole island of Hispaniola at that time. Herewith we designate the male syntype, NHMD R3796 (Fig. 13), as the lectotype of *Anolis riisei* Reinhardt & Lütken, 1863 and in the following provide a redescription of this specimen.

NHMD R3796, adult male, as indicated by well-developed dewlap, and presence of a pair of greatly enlarged postcloacal scales; SVL 65.0 mm; tail length 113.0 mm (complete); tail distinctly compressed in cross section, tail height 4.0 mm and width 1.9 mm; axilla to groin distance 25.3 mm; head length 19.0 mm, head length/SVL ratio 0.29; snout length 8.3 mm; head width 10.6 mm; longest toe of adpressed hind limb reaching to level of anterior margin of eye; shank length 18.0 mm, shank length/head length ratio 0.95; longest finger of extended forelimb reaching to 5 mm past snout; longest finger of adpressed forelimb reaching to 2 mm past anterior insertion of hind limbs. Dorsal head scales mostly keeled, some rugose or smooth, especially in frontal and parietal regions; 7 postrostrals; 7 scales between nasals; 1 elongate prenasal scale on each side, distinct from circumnasal and in contact with both rostral and first supralabial; circumnasal separated from first supralabial by two scales; scales in deep prefrontal depression mostly slightly keeled; supraorbital semicircles well-developed, broadly in contact medially; supraorbital disc composed of 4 to 5 moderately enlarged, keeled scales arranged in three to four rows; circumorbital row complete, therefore, enlarged supraorbital scales separated from supraorbital semicircles; a very large elongated superciliary, followed posteriorly by a much smaller, overlapping one and by several small, keeled scales; about five rows of small keeled scales extending between enlarged supraorbitals and large superciliary; a parietal depression present; interparietal scale well-developed, 2.3 x 1.5 mm (length x width), surrounded by scales of moderate size; 2 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 3 large and 2 small anterior canthal scales; 8 scales present between second canthals; 9 scales present between posterior canthals; 46 (right) – 49 (left) mostly keeled loreal scales in a maximum of 9 horizontal rows; 7 keeled subocular scales arranged in a single row; 6 supralabials to level below center of eye; suboculars separated from supralabials by a complete scale row; ear opening 1.3 x 1.9 mm (length x height); mental distinctly wider

than long, almost completely divided medially, bordered posteriorly by 6 postmentals, outer ones much larger than median ones; 6 infralabials to level below center of eye; sublabials greatly enlarged (< four times the size of medial postmental scales), one in contact with infralabials; scales in sublabial row much larger than scales medially adjacent to this row; granular scales present on chin and throat; dewlap large, extending from level below anterior margin of eye onto chest; a nuchal crest and a dorsal ridge present; dorsum of body with keeled, granular scales; 2 medial rows distinctly enlarged, mostly usually less than twice the size of adjacent scales; largest dorsal scales about 0.40 x 0.30 mm (length x width); about 46 medial dorsal scales in one head length; about 70 medial dorsal scales between levels of axilla and groin; lateral scales keeled, granular and more or less homogeneous in size, average size 0.10 mm in diameter; ventrals at midbody smooth, flat, almost cycloid, imbricate, about 0.45 x 0.75 mm (length x width); about 32 medial ventral scales in one head length; about 46 medial ventral scales between levels of axilla and groin; 190 scales around midbody; all caudal scales keeled; middorsal caudal scales distinctly enlarged, forming a low crest; lateral caudal scales without whorls of enlarged scales, although an indistinct division in segments is discernible; a pair of greatly enlarged postcloacal scales present, about 1.1 mm wide; no tube-like axillary pocket present; scales on dorsal surface of upper forelimb strongly keeled, mucronate, imbricate; scales on anterior surface of thigh keeled, mucronate, imbricate; digital pads dilated, dilated pad three times the width of non-dilated distal phalanx; distal phalanx narrower than and raised from dilated pad; 32 lamellae under Phalanges II–IV of Toe IV of hind limbs; 10 scales under distal phalanx of Toe IV of hind limbs.

In external morphology, the *A. riisei* lectotype NHMD R3796 agrees well with the specimens from the western portion of the Tiburón Peninsula, Haiti, that we have assigned to *A. cybotes*. This observation is supported in a multivariate analysis, where the lectotype of *A. riisei* is placed in the center of the *A. cybotes* morphospace. Thus, we consider the primary type specimens of *Anolis cybotes* Cope, 1863 and *Anolis riisei* Reinhardt & Lütken, 1863 to belong to the same biological species.

The publication "Bidrag til det vestindiske Øriges og navnligen de dansk-vestindiske Øers Herpetologie" has often been cited as "Reinhard & Lütken, 1863". However, the publication from 1863, printed in Copenhagen by "Bianco Lunos Bogtrykkeri ved F.S. Muhle," appears to be a reproduction of a work that was originally communicated on 14 February 1862 in the journal "Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjöbenhavn". In the former publication the original date of publication (14 February 1862) is in fact mentioned on page 1, which corresponds to page 153 in the latter paper. Hence, the content of both publications is identical (with the exception of the first page, which includes additional information on journal number etc. in the original paper) but the page numbering differs.

Interestingly, something similar appears to be the case with the journal containing the Cope paper describing *Anolis cybotes*. That journal was also printed in 1863. At the bottom of the cover page of the journal it says "Philadelphia: Printed for the Academy. 1863". The journal contains papers that were "presented for publication" (i.e., not published) between January and December 1862. The Cope paper is first mentioned on page 160, where it says "April 22d, 1862. Forty members present. The following papers were presented for publication: Contributions to Neotropical Saurology, by E. D. Cope" The Cope paper begins on page 176 and on the bottom of that page is printed "[April," and on page 177 "1862.]". Thus, although both works (i.e., that of Cope and that of Reinhard & Lütken) have been presented in some way in 1862, both seem to have been printed in 1863. There is no indication that either article was released as a single individual paper prior to the publication of the entire volume in 1863. We have no information as to the exact date when these two articles were actually published in 1863,

and therefore are unable to determine which one has been published first. Given the long usage of the name *Anolis cybotes* Cope, 1863 for a well-known biological species, we continue to use this name and maintain *Anolis riisei* Reinhardt & Lütken, 1863 in the synonymy of *Anolis cybotes* Cope, 1863, a species name we restrict to the populations inhabiting the western portion of the Tiburón Peninsula, Haiti.

In conclusion, we recognize 14 species of anoles in the genus *Audantia* (i.e., *A. armouri, A. breslini, A. cybotes, A. doris, A. longitibialis, A. marcanoi, A. ravifaux, A. saxatilis, A. shrevei, A. strahmi*, as well as four undescribed species). In the standard characters of external morphology, these 14 species are not easily differentiated (Table II). However, subtle differences in body and dewlap scalation, morphometrics, and dewlap coloration among these species are useful to differentiate them. No names are available for four of our species level units, and therefore we describe each of them as a new species below.

In the following, we provide species accounts for *Audantia cybotes, A. doris,* and *A. ravifaux,* as well as the four new species. The two species that are restricted to the highlands of Hispaniola (i.e., *A. armouri* and *A. shrevei*), are only considered in the respective diagnosis sections of the seven species treated here in detail. The same applies to those species that are only distantly related to those five species as evidenced by our genetic analyses (*A. breslini, A. longitibialis, A. marcanoi, A. strahmi,* and *A. saxatilis*).

Table III. Selected measurements, proportions and scale characters of the holotypes of *A. citrinellus* and *A. cybotes saxatilis*. For abbreviations see text.

	Anolis citrinellus **BMNH 1946.8.5./1** ♀ **1**	***Anolis cybotes saxatilis*** **SMF 25032** ♂ **1**
maximum SVL	40	63
TL/SVL	1.86	—
VDT/HDT	1.54	1.60
AGD/SVL	0.38	0.36
HL/SVL	0.27	0.32
HL/HW	1.33	1.86
SL/SVL	0.12	0.13
SL/HL	0.45	0.42
ShL/SVL	0.24	0.30
ShL/HL	0.90	0.94
ToeLam p	31	30

	Anolis citrinellus **BMNH 1946.8.5./1** ♀ **1**	***Anolis cybotes saxatilis*** **SMF 25032** ♂ **1**
ToeLam d	9	8
IO	0	0
IP/IO	2	2
SO/SPL	5/5	2/2
SPL	6	7
IFL	6	7
LST	28	34
LSR	5	6
PR	8	6
PM	9	6
SubL	1	2
IN	6	6
ESO (greatly)	1	0
ESO (moderately)	2/3	6/7
2Canths	5	7
1Canths	9	9
dorsHL	42	46
ventrHL	38	38
dorsAG	54	59
ventr AG	53	52
SAM	112	158
RED	2	2

Figure 8. Syntypes of *Anolis haetianus* (MCZ 6191). Photo by Museum of Comparative Zoology, Harvard University.

Figure 9. Holotype of *Anolis citrinellus* Cope, 1864 (BMNH 1946.8.5./1): (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; (f) ventral view of head. Scale bars equal 5.0 mm in (a–c) and 1.0 mm in (d–f), respectively. Photos by Gunther Köhler.

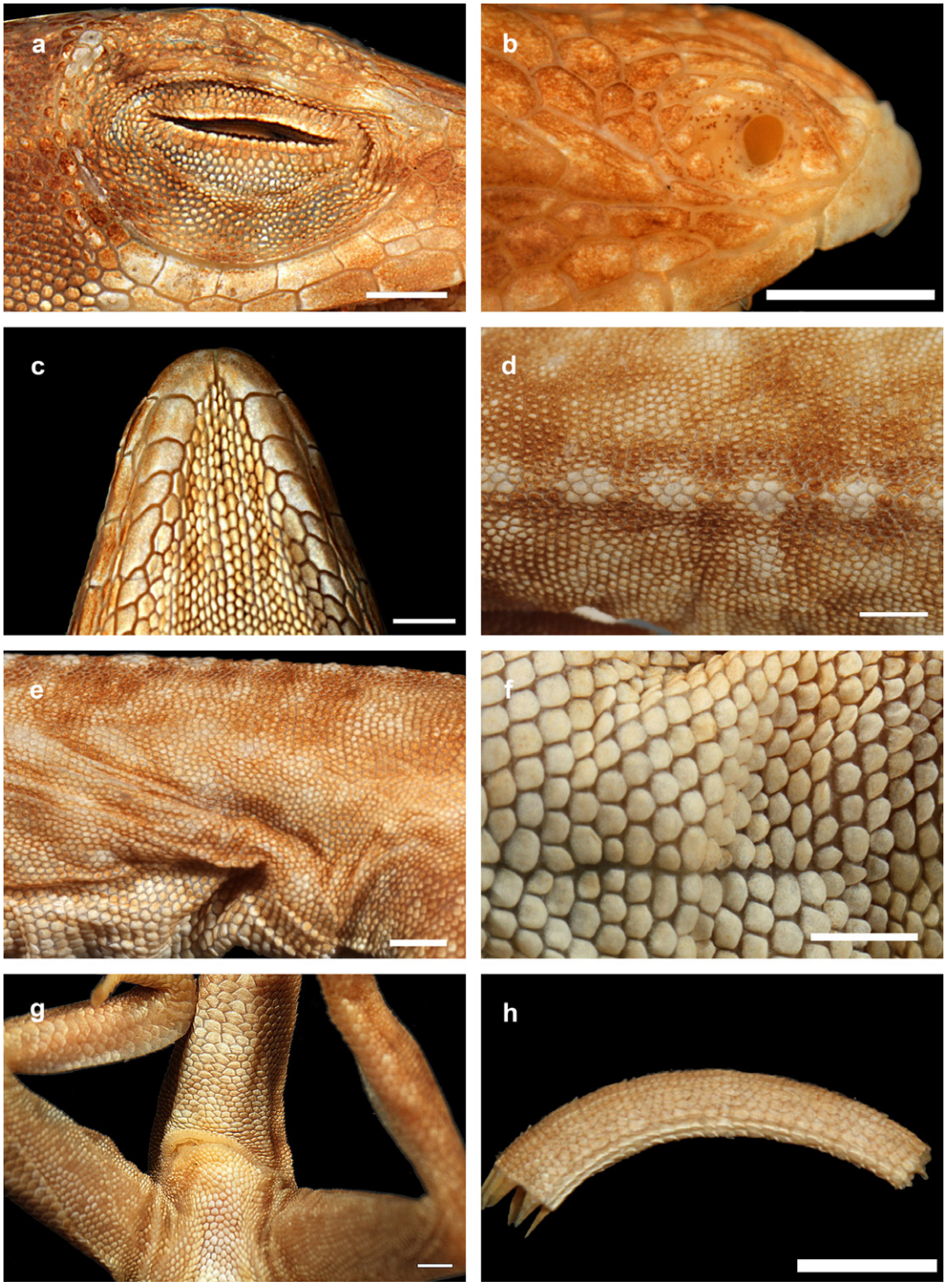

Figure 10. Holotype of *Anolis citrinellus* Cope, 1864 (BMNH 1946.8.5./1): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region (e) flank region; (f) midventer; (g) cloacal region; (h) lateral view of tail. Scale bars equal 1.0 mm. Photos by Gunther Köhler.

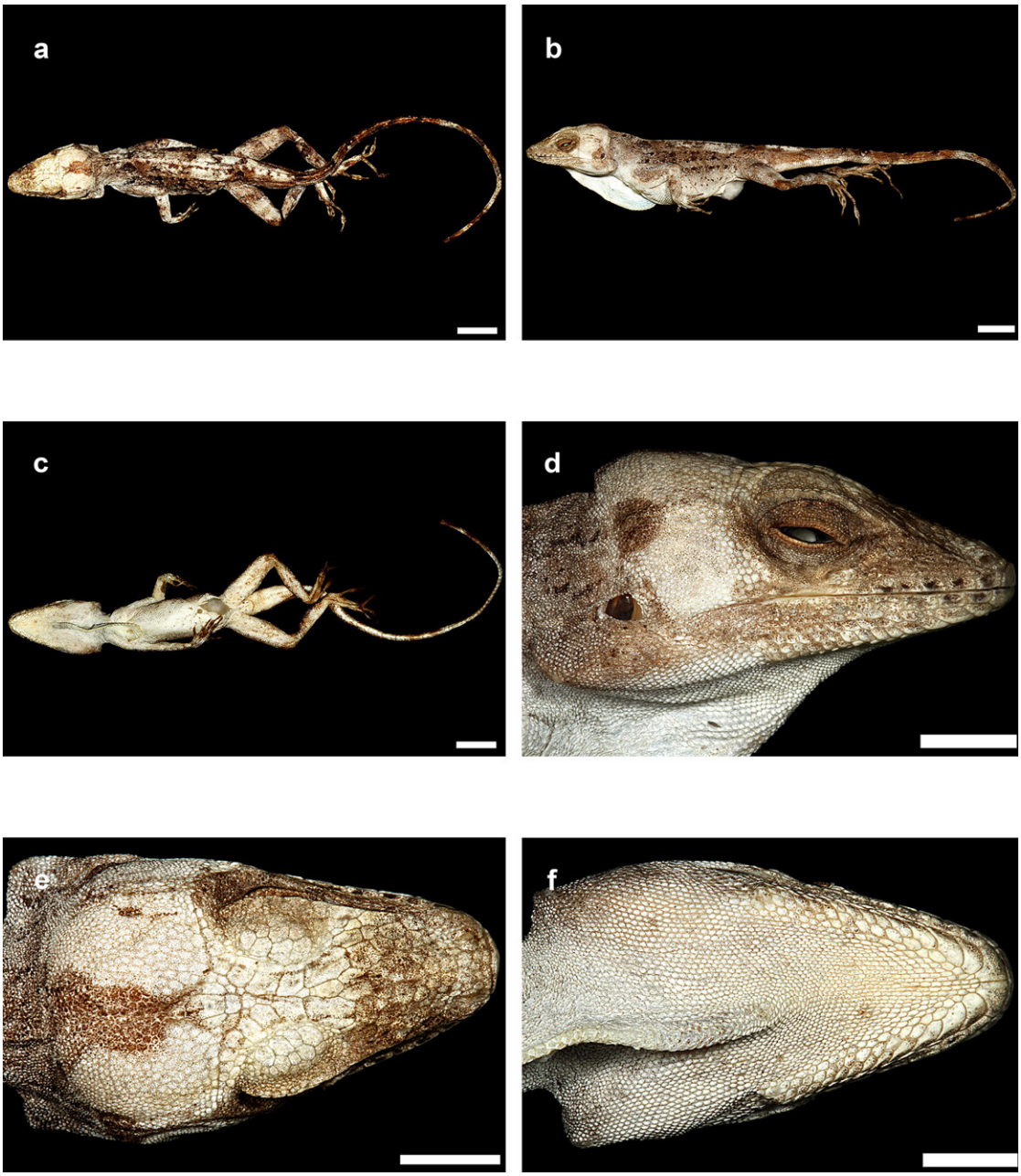

Figure 11. Holotype of *Anolis cybotes saxatilis* Mertens, 1938 (SMF 25032): (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; (f) ventral view of head. Scale bars equal 10.0 mm in (a–c) and 5.0 mm in (d–f), respectively. Photos by Gunther Köhler.

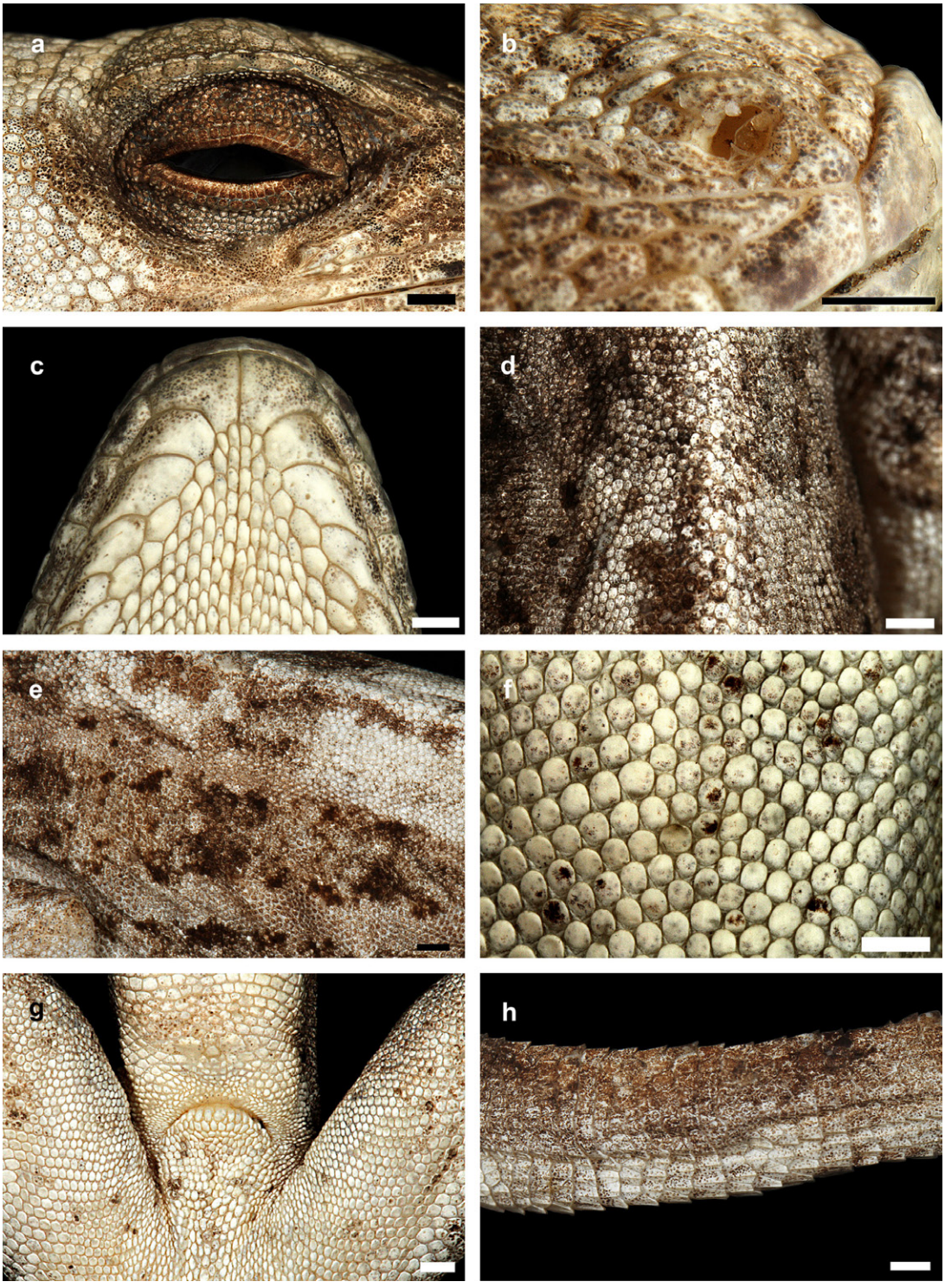

Figure 12. Holotype of *Anolis cybotes saxatilis* Mertens, 1938 (SMF 25032): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region (e) flank region; (f) midventer; (g) cloacal region; (h) base of tail. Scale bars equal 1.0 mm. Photos by Gunther Köhler.

Figure 13. Lectotype of *Anolis riisei* Reinhardt & Lütken, 1863 (NHMD R3796): (a) dorsal view; (b) lateral view; (c) ventral view; (d) dorsal view of head; (e) lateral view of head; (f) ventral view of head. Scale bars equal 5.0 mm in (a–c) and 1.0 mm in (d–f), respectively. Photos by Daniel Klingberg Johansson.

***Audantia cybotes* (Cope, 1863)**

Tiburon Stout Anole

Figs. 14–16

Anolis (*Anolis*) *cybotes* Cope, 1863: 177; type locality: Haiti, near Jeremie. Lectotype: MCZ 14346. Boulenger, 1885 (in part.); Schmidt, 1921 (in part.); Barbour & Loveridge, 1929 (in part.); Barbour, 1930a (in part.); Barbour, 1930b (in part.); Schwartz & Thomas, 1975 (in part.); Schwartz, 1979 (in part.); Wyles & Gorman, 1980 (in part.); Schwartz, 1980 (in part.); Henderson *et al*., 1984 (in part.); Henderson & Schwartz, 1984 (in part.); Burnell & Hedges, 1990 (in part.); Olson, 1990; Powell *et al.,* 1996 (in part.); Queiroz *et al.*, 1998 (in part.); Powell *et al.*, 1999 (in part.); Poe, 2004 (in part.); Nicholson *et al.*, 2005 (in part.); Henderson & Powell, 2009 (in part.); Boistel *et al.*, 2011 (in part.); Kolbe *et al.,* 2011 (in part.); Poe, 2013 (in part.); Köhler, 2014 (in part.); Muñoz *et al*., 2014a (in part.);

Klaczko *et al.*, 2015 (in part.); Giovannotti *et al*., 2017 (in part.); Poe *et al.*, 2017 (in part.); Barbour, 1914 (in part.); Schwartz, 1989 (in part.).

Anolis cybotes cybotes: Cochran, 1934 (in part.); Barbour, 1935 (in part.); Barbour, 1937 (in part.); Mertens, 1938 (in part.); Mertens, 1939 (in part.); Cochran, 1941 (in part.); Schwartz & Thomas, 1975 (in part.); MacLean *et al.,* 1977 (in part.); Henderson & Schwartz, 1984 (in part.); Henderson *et al*., 1984 (in part.); Schwartz & Henderson, 1991 (in part.); Fobes *et al*., 1993 (in part.); Powell *et al.*, 1999 (in part.); Powell & Henderson, 2012 (in part.).

Anolis cybotes haetianus: Schwartz & Thomas, 1975; MacLean *et al.,* 1977; Henderson & Schwartz, 1984, Henderson *et al.,* 1984.

Anolis haetianus: Garman, 1887; Schwartz & Henderson, 1982; Barbour, 1914; Schwartz, 1989; Powell *et al*., 1996; Powell *et al.*, 1999.

Anolis riisei Reinhardt & Lütken 1863: 264; type locality: "Haiti". Lectotype: NHMD R3796.
Audantia cybotes cybotes: Nicholson *et al.*, 2012 (in part.); Nicholson *et al.*, 2018 (in part.).

Audantia cybotes: Nicholson *et al.*, 2014 (in part.).

Audantia haetiana: Nicholson *et al.*, 2012; Nicholson *et al.*, 2018. An incorrect spelling, because the original species name is a noun that does not change gender.

Ctenonotus cybotes: Savage & Guyer, 1989 (in part.).

Ctenonotus haetianus: Savage & Guyer, 1989.

Diagnosis. A species of the genus *Audantia* that differs from all congeners by the combination of having (1) usually keeled ventral scales; (2) male dewlap dirty white without yellowish or orange suffusions, and with homogeneously distributed, narrowly spaced gorgetal scales, all large on posterior half of dewlap; (3) dark gular streaks in males present (Fig. 16e, f); (4) no patch of enlarged scales in nuchal region; (5) a double row of greatly enlarged (at least three times the size of adjacent scales), keeled and mucronate vertebral scales; (6) usually two sublabial scales in contact with infralabials; (7) 180–222 scales around midbody in males; and (8) keeled scales on dorsal surfaces of upper forelimb and anterior surface of thigh.

Audantia cybotes differs from *A. armouri, A. breslini, A. shrevei,* and *A. saxatilis* by having dark gular streaks (vs. usually absent); by having a double row of greatly enlarged, at least three times the size of adjacent scales, keeled and mucronate vertebral scales (vs. those scales only weakly enlarged, usually less than twice the size of adjacent scales, non-mucronate); and by having one or two well-defined pale longitudinal lateral stripes, usually edged with orange or olive-green (vs. such stripes absent). *Audantia cybotes* differs further from *A. armouri* by having 180–222 scales around midbody in males (vs. 118–172). *Audantia cybotes* differs further from *A. shrevei* by lacking a patch of greatly enlarged scales in nuchal region (vs. such a patch present). *Audantia cybotes* differs from *A. doris* by having dark gular streaks (vs. usually absent); by having a male dewlap with homogeneously distributed, narrowly spaced gorgetal scales, all large on posterior half of dewlap (vs. heterogeneously distributed with groups of cluttered scales, scales reduced in size in central portion of dewlap); and by having 180–222 scales around midbody in males (vs. 166–184). *Audantia cybotes* differs from *A. marcanoi* and *A. strahmi* by having a dirty white male dewlap (vs. rose-red at the edge, more orangish anteriorly and posteriorly, but purplish or even bluish toward the center in *A. marcanoi*, and orange with paler center in *A. strahmi*). *Audantia cybotes* differs further from *A. marcanoi* by having

a double row of abruptly and greatly enlarged, at least three times the size of adjacent scales, keeled vertebral scales (vs. vertebral scales gradually and weakly enlarged, not forming a regular double row). *Audantia cybotes* differs from *A. longitibialis* by having usually keeled ventral scales (vs. smooth); and a male dewlap dirty white without yellowish or orange suffusions, and with homogeneously distributed, narrowly spaced gorgetal scales, all large on posterior half of dewlap (vs. heterogeneously distributed, somewhat spaced, and with groups of cluttered scales, scales smaller in central region of dewlap or all gorgetals small). *Audantia cybotes* differs from *A. ravifaux* by having keeled ventrals (vs. smooth); by having keeled scales on dorsal surface of upper forelimb and anterior surface of thigh (vs. smooth); by having a double row of greatly enlarged, at least three times the size of adjacent scales, keeled and mucronate vertebral scales (vs. those scales only weakly enlarged, usually less than twice the size of adjacent scales, smooth and non-mucronate); and by having homogeneously distributed, narrowly spaced gorgetal scales, all large on posterior half of dewlap (vs. heterogeneously distributed, somewhat spaced, and with groups of cluttered scales, scales smaller in central region of dewlap). For differences between *A. cybotes* and the species described below, see the respective accounts of the new species.

Description of lectotype. Adult male, as indicated by well-developed dewlap, and presence of a pair of greatly enlarged postcloacal scales (Figs. 14–15); SVL 64.0 mm; tail incomplete; axilla to groin distance 20.4 mm; head length 20.0 mm, head length/SVL ratio 0.31; snout length 8.6 mm; head width 10.8 mm; shank length 18.3 mm, shank length/head length ratio 0.92. Dorsal head scales smooth or rugose, except weakly keeled scales on snout and supraoculars; 7 postrostrals; 6 scales between nasals; 1 elongate prenasal scale on each side, distinct from circumnasal and in contact with both rostral and first supralabial; circumnasal separated from first supralabial by one scale; scales in deep prefrontal depression smooth or rugose; supraorbital semicircles well-developed, broadly in contact medially; supraorbital disc composed of 3 moderately enlarged, keeled scales arranged in two rows; circumorbital row incomplete, therefore, some enlarged supraorbital scales contacting supraorbital semicircles; a very large elongated superciliary, followed posteriorly by a much smaller, overlapping one and by several small, keeled scales; 2–3 rows of small keeled scales extending between enlarged supraorbitals and large superciliary; a deep parietal depression present; interparietal scale well-developed, 2.5 x 1.5 mm (length x width), surrounded by scales of moderate size; 2 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 3 large and 2 small anterior canthal scales; 7 scales present between second canthals; 9 scales present between posterior canthals; 74 (right) mostly keeled loreal scales in a maximum of 9 (right) horizontal rows; 8 keeled subocular scales arranged in a single row; 6 supralabials to level below center of eye; suboculars separated from supralabials by one scale row; ear opening 1.4 x 1.9 mm (length x height); mental distinctly wider than long, almost completely divided medially, bordered posteriorly by 7 postmentals, outer ones much larger than median ones; 6 infralabials to level below center of eye; sublabials greatly enlarged (< four times the size of medial postmental scales), 2 in contact with infralabials; scales in sublabial row much larger than scales medially adjacent to this row; pointed granular scales present on chin and throat; dewlap large, extending from level below anterior margin of eye onto chest; a nuchal crest and a dorsal ridge present; dorsum of body with mostly smooth, some weakly keeled, granular scales; 2 medial rows slightly enlarged, usually at least twice the size of adjacent scales; about 54 medial dorsal scales in one head length; about 62 medial dorsal scales between levels of axilla and groin; lateral scales mostly smooth, granular and more or less homogeneous in size; ventrals at midbody smooth, flat, almost cycloid, subimbricate; about 36 medial ventral scales in one head length; about 40 medial ventral scales between levels of axilla and groin; 186 scales around midbody; ventral basal caudal scales smooth; a pair of greatly enlarged postcloacal scales present, about 1.5 mm wide; no tube-like axillary pocket present; scales on dorsal surface of upper forelimb keeled, imbricate; scales on anterior surface of thigh enlarged, keeled, imbricate; digital pads dilated, dilated pad three times the width of

non-dilated distal phalanx; distal phalanx narrower than and raised from dilated pad; 34 lamellae under Phalanges II–IV of Toe IV of hind limbs; 9 scales under distal phalanx of Toe IV of hind limbs.

Geographic distribution. As currently known, *Audantia cybotes* is restricted to the western portion of the Tiburón Peninsula, Haiti, from near sea level to 1–780 m a. s. l. (Fig. 18).

Natural history notes. Audantia cybotes seems to be quite adaptable in regard of the tolerated habitats and even seems to prefer disturbed habitat, forest edges, and villages as long as trees and bushes provide shade and humidity (Fig. 17). At night these lizards sleep on leafs and twigs 1 to 2 m above the ground but have also been found under rocks and logs. Henderson & Powell (2009) provided a summary of the natural history of "*Anolis cybotes*" which under our concept is represented by several species.

Conservation. Given its usual abundance wherever this species occurs, we consider the conservation status of *Audantia cybotes* as Least Concern based on the IUCN Red List Categories and Criteria (IUCN, 2012).

Figure 14. Lectotype of *Anolis cybotes* Cope, 1863 (MCZ 14346): (a) dorsal view; (b) lateral view; (c) ventral view; (d) dorsal view of head; (e) lateral view of head; (f) ventral view of head. Scale bars equal 5.0 mm. Photos by Gunther Köhler.

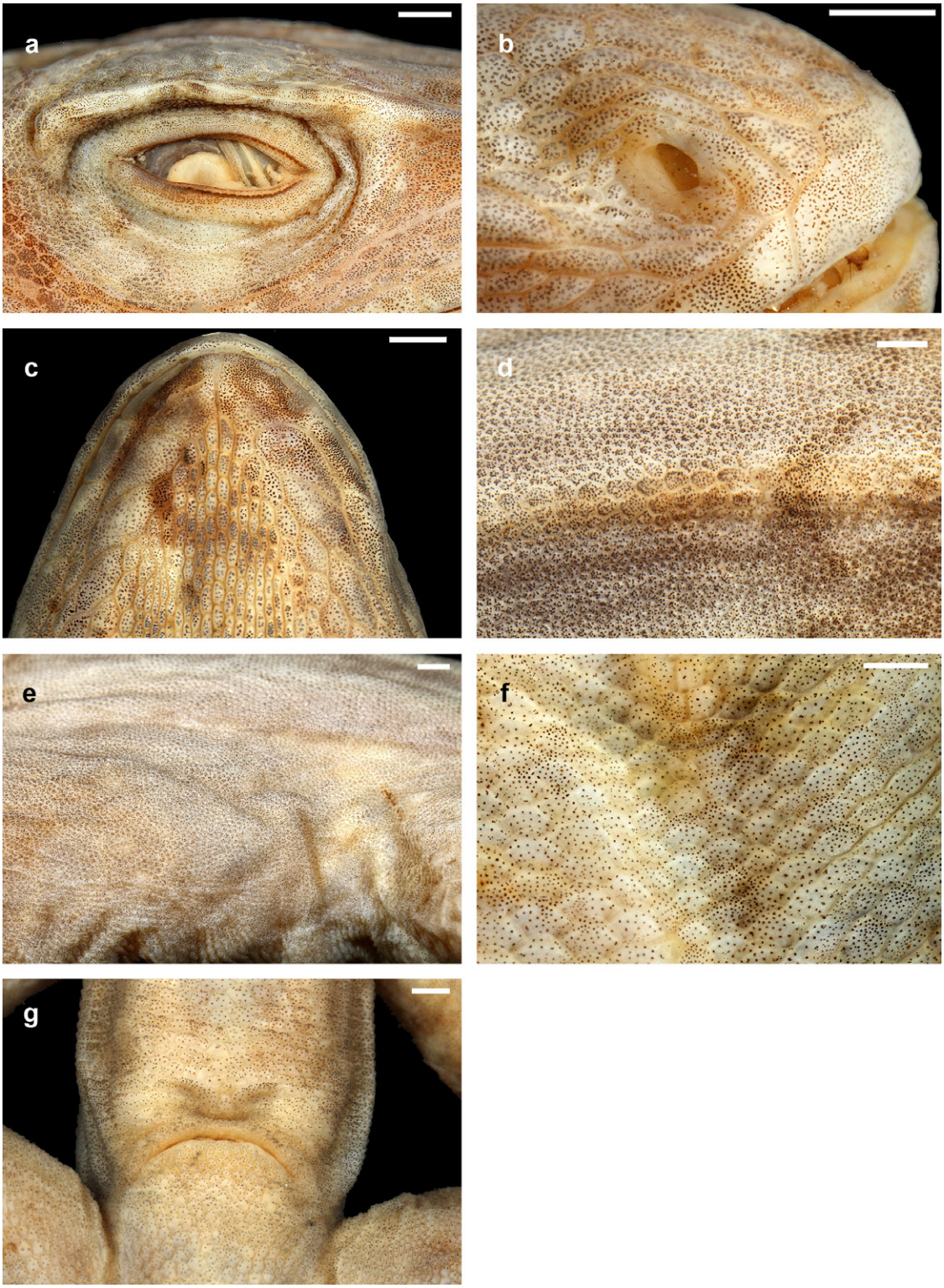

Figure 15. Lectotype of *Anolis cybotes* Cope, 1863 (MCZ 14346): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region (e) flank region; (f) midventer; (g) cloacal region. Scale bars equal 1.0 mm. Photos by Gunther Köhler.

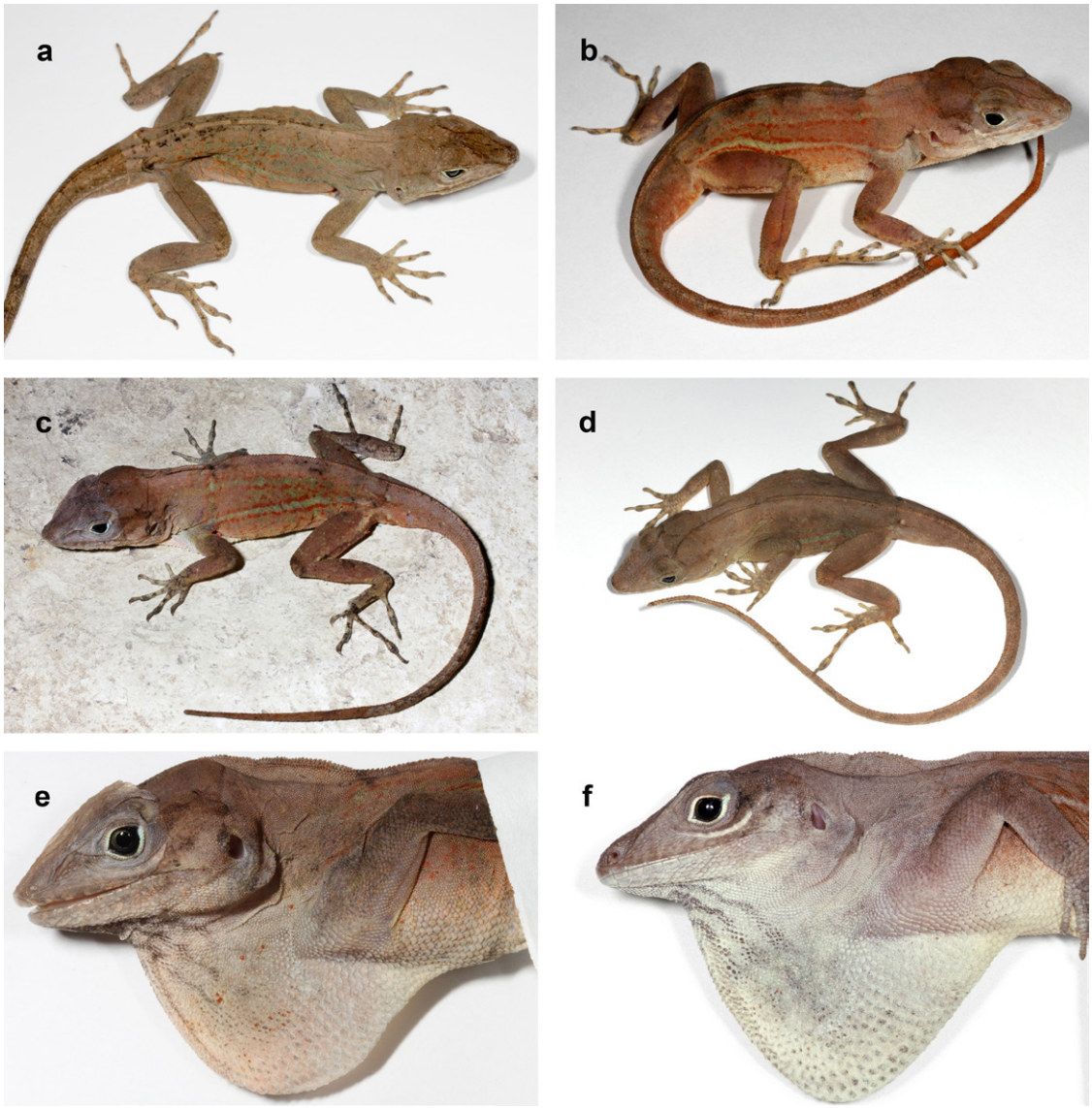

Figure 16. *Audantia cybotes* in life (all males). (a) SMF 104199; (b) SMF 104196; (c) SMF 104197; (d) SMF 104201; (e) SMF 104197; (f) uncatalogued specimen from 1.8 km E of Anse D'Hainault, Grand'Anse, Haiti. Photos by S. Blair Hedges.

Figure 17. Habitat of *Audantia cybotes* (a) Morne Bois Pangnol, Nippes, Haiti, 1170 m a.s.l. (20 June 2012); (b) 5 km NW Duplantin, on Morne Lezard, Grande Colline, Sud, Haiti, 1 177 m a.s.l. (25 July 2011). Photos by S. Blair Hedges.

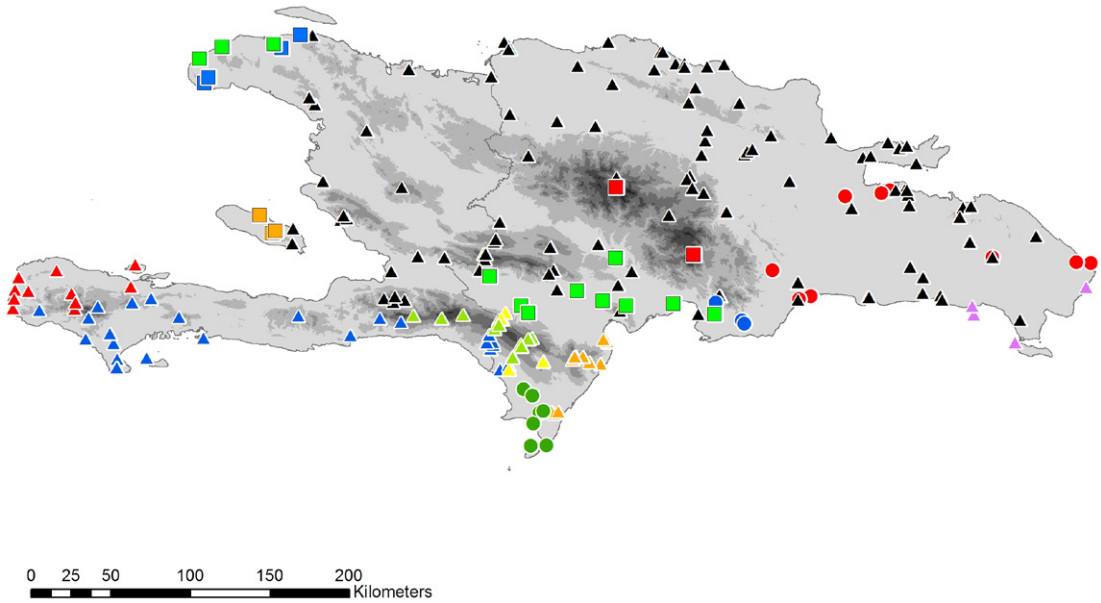

Figure 18. Map indicating collecting localities of the species of the genus *Audantia*. Each symbol can represent one or more adjacent localities. Areas above 500 and 1 000 m are shaded medium dark and dark gray, respectively. Red triangles: *Audantia cybotes*; blue triangles: *A. australis*; green triangles: *A. armouri*; yellow triangles: *A. strahmi*; blue squares: *A. breslini*; green squares: *A. saxatilis*; green circles: *A. longitibialis*; orange triangles: *A. aridius*; red squares: *A. shrevei*; blue circles: *A. marcanoi*; black triangles: *A. hispaniolae*; red circles: *A. higuey*; orange squares: *A. doris*; pink triangles: *A. ravifaux*.

***Audantia doris* (Barbour, 1925)**
Gonave Stout Anole
Figs. 19–21

Anolis cybotes: Boulenger, 1885 (in part.); Schmidt, 1921 (in part.); Schwartz, 1979 (in part.); Wyles & Gorman, 1980 (in part.); Schwartz, 1980 (in part.); Henderson *et al*., 1984 (in part.); Schwartz, 1989 (in part.); Burnell & Hedges, 1990 (in part.); Powell *et al*., 1996 (in part.); Queiroz *et al.*, 1998 (in part.); Poe, 2004 (in part.); Nicholson *et al.*, 2005 (in part.); Henderson & Powell, 2009 (in part.); Boistel *et al.*, 2011 (in part.); Kolbe *et al.,* 2011 (in part.); Poe, 2013 (in part.); Köhler, 2014 (in part.); Muñoz *et al*., 2014 a (in part.); Klaczko *et al.*, 2015 (in part.); Giovannotti *et al.*, 2017 (in part.); Poe *et al.*, 2017 (in part.).

Anolis doris Barbour, 1925: 101; type locality: Île de la Gonâve. Holotype: MCZ 13739. Cochran, 1928, Barbour & Loveridge, 1929; Barbour, 1930a; Barbour, 1930b.

Anolis cybotes doris: Cochran, 1934; Barbour, 1935; Barbour, 1937; Cochran, 1941; Schwartz & Thomas, 1975 (in part.); MacLean *et al*., 1977; Schwartz *et al.*, 1982; Henderson & Schwartz, 1984; Henderson *et al*., 1984 (in part.); Schwartz & Henderson, 1991; Fobes *et al.*, 1993; Powell *et al.*, 1999; Powell & Henderson, 2012.

Audantia cybotes: Nicholson *et al.*, 2014 (in part.).

Audantia cybotes doris: Nicholson *et al.*, 2012; Nicholson *et al.*, 2018.

Ctenonotus cybotes: Savage & Guyer, 1989 (in part.).

Diagnosis. A species of the genus *Audantia* that differs from all congeners by the combination of having (1) smooth ventral scales; (2) male dewlap creme white with central orange blotch (Fig. 21b)**,** and with heterogeneously distributed, intermediate spaced gorgetal scales, that are cluttered in groups, and reduced in size in central portion; (3) no dark gular streaks in males; (4) no patch of enlarged scales in nuchal region; (5) a double row of greatly enlarged (at least three times the size of adjacent scales), keeled and mucronate vertebral scales; (6) usually two sublabial scales in contact with infralabials; (7) 166–184 scales around midbody in males; and (8) keeled scales on dorsal surfaces of upper forelimb and anterior surface of thigh.

Audantia doris differs from A. breslini, A. cybotes, A. shrevei, and *A. saxatilis* by having smooth ventrals (vs. keeled, some individuals of *A. breslini* and *A. cybotes* with smooth ventrals); by having an orange blotch in the center on the male dewlap (vs. absent); and by having heterogeneously distributed gorgetals with groups of cluttered scales (vs. homogeneously distributed gorgetals). *Audantia doris* differs further from *A. shrevei* by lacking a patch of greatly enlarged scales in nuchal region (vs. such a patch present). *Audantia doris* differs from *A. armouri* by having a double row of greatly enlarged, at least three times the size of adjacent scales, keeled and mucronate vertebral scales (vs. those scales only weakly enlarged, usually less than twice the size of adjacent scales, non-mucronate); by having 166–184 scales around midbody in males (vs. 118–172); by having an orange blotch arranged in the center on the male dewlap (vs. absent); and by having heterogeneously distributed gorgetals with groups of cluttered scales (vs. homogeneously distributed gorgetals). *Audantia doris* differs from *A. cybotes* by having no dark gular streaks (present); by having the gorgetal scales reduced in size in central portion of posterior half of male dewlap (vs. all gorgetals large on posterior half of dewlap); and by having heterogeneously distributed gorgetals with groups of cluttered scales (vs. homogeneously distributed gorgetals). *Audantia doris* differs from *A. marcanoi* and *A. strahmi* by having a creme white male dewlap with an orange blotch arranged

in the center (vs. rose-red at the edge, more orangish anteriorly and posteriorly, but purplish or even bluish toward the center in *A. marcanoi*, and orange with paler center in *A. strahmi*). *Audantia doris* differs from *A. longitibialis* by having a creme white dewlap with a central orange blotch (vs. yellow without central orange blotch); and by having mucronate middorsals (vs. non-mucronate middorsals). *Audantia doris* differs from *A. ravifaux* by having keeled scales on dorsal surface of upper forelimb and anterior surface of thigh (vs. smooth); by having a double row of greatly enlarged, at least three times the size of adjacent scales, keeled and mucronate vertebral scales (vs. those scales only weakly enlarged, usually less than twice the size of adjacent scales, smooth and non-mucronate); and by having a male dewlap with an orange blotch arranged in the center (vs. absent). For differences between *A. doris* and the species described below, see the respective accounts of the new species.

Description of lectotype. Adult male, as indicated by well-developed dewlap, and presence of a pair of greatly enlarged postcloacal scales (Figs. 19–20); SVL 59.0 mm; tail length 105 mm (complete); axilla to groin distance 18.1 mm; head length 18.9 mm, head length/SVL ratio 0.32; snout length 8.3 mm; head width 10.3 mm; shank length 18.7 mm, shank length/head length ratio 0.99. Dorsal head scales smooth or rugose, except weakly keeled scales on snout and supraoculars; 5 postrostrals; 6 scales between nasals; 1 elongate prenasal scale on each side, distinct from circumnasal and in contact with both rostral and first supralabial; circumnasal in contact with first supralabial; scales in moderate prefrontal depression smooth or rugose; supraorbital semicircles well-developed, broadly in contact medially; supraorbital disc composed of 3 moderately enlarged, keeled scales arranged in two rows; circumorbital row complete, therefore, enlarged supraorbital scales separated from supraorbital semicircles; a very large elongated superciliary, followed posteriorly by a much smaller, overlapping one and by several small, keeled scales; 2–3 rows of small keeled scales extending between enlarged supraorbitals and large superciliary; a shallow parietal depression present; interparietal scale well-developed, 2.4 x 0.7 mm (length x width), surrounded by scales of moderate size; 2 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 3 large and 2 small anterior canthal scales; 6 scales present between second canthals; 9 scales present between posterior canthals; 38 (both sides) mostly keeled loreal scales in a maximum of 7 (both sides) horizontal rows; 7 keeled subocular scales arranged in a single row; 7 supralabials to level below center of eye; suboculars separated from supralabials by one scale row; ear opening 1.5 x 1.9 mm (length x height); mental distinctly wider than long, almost completely divided medially, bordered posteriorly by 6 postmentals, outer ones much larger than median ones; 6 infralabials to level below center of eye; sublabials greatly enlarged (< four times the size of medial postmental scales), 2 in contact with infralabials; scales in sublabial row much larger than scales medially adjacent to this row; pointed granular scales present on chin and throat; dewlap large, extending from level below anterior margin of eye onto chest; a nuchal crest and a dorsal ridge present; dorsum of body with mostly smooth, some weakly keeled, granular scales; 2 medial rows slightly enlarged, usually at least twice the size of adjacent scales; about 34 medial dorsal scales in one head length; about 46 medial dorsal scales between levels of axilla and groin; lateral scales mostly smooth, granular and more or less homogeneous in size; ventrals at midbody smooth, flat, almost cycloid, subimbricate; about 40 medial ventral scales in one head length; about 41 medial ventral scales between levels of axilla and groin; 180 scales around midbody; ventral basal caudal scales smooth, all other caudal scales keeled; middorsal caudal scales distinctly enlarged, forming a low crest; lateral caudal scales with whorls of enlarged scales; a pair of greatly enlarged postcloacal scales present, about 1.7 mm wide; no tube-like axillary pocket present; scales on dorsal surface of upper forelimb keeled, imbricate; scales on anterior surface of thigh enlarged, keeled, imbricate; digital pads dilated, dilated pad three times the width of non-dilated distal phalanx; distal phalanx narrower than and raised from dilated pad; 26 lamellae under Phalanges II–IV of Toe IV of hind limbs; 8 scales under distal phalanx of Toe IV of hind limbs.

Geographic distribution. As currently known, *Audantia doris* is restricted to Île de la Gonâve, Haiti, from near sea level to 445 m a. s. l. (Fig. 18).

Natural history notes. Henderson & Powell (2009) provided a summary of the natural history of "*Anolis cybotes*" which under our concept is represented by several species. SBH collected this species in various habitats on Île de la Gonâve, Haiti, including open coastal vegetation with coconut palm trees (Fig. 22).

Conservation. Given that two closely related species of the genus *Audantia* occur on Île de la Gonâve (i.e., *A. doris* and a species described below) it is possible that gene introgression between these two species occurs as indicated by the intermediate morphology of the Gonave specimens of the species described below compared to their mainland conspecifics.

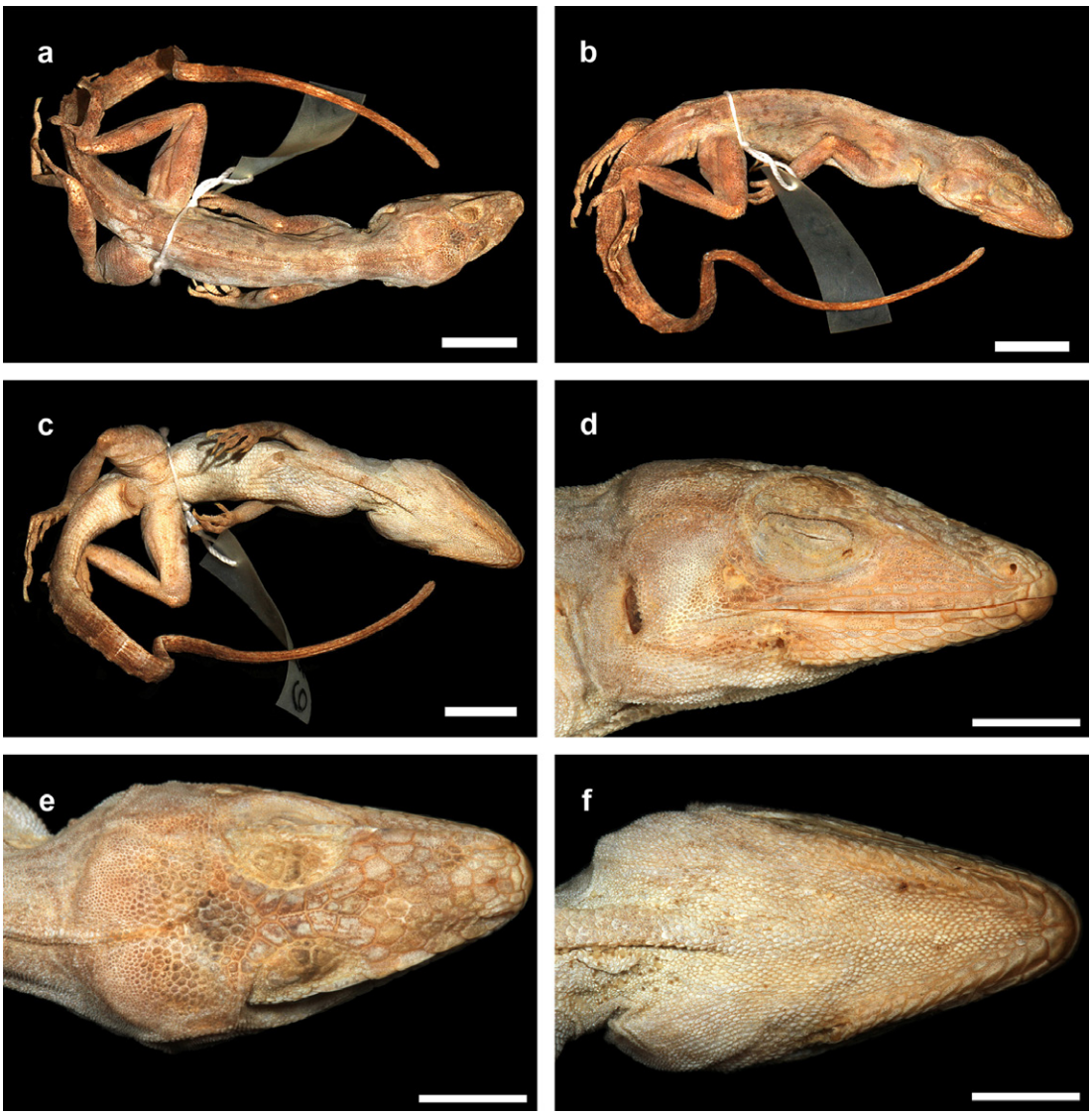

Figure 19. Holotype of *Anolis cybotes doris* Barbour, 1925 (MCZ 13739): (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; (f) ventral view of head. Scale bars equal 10.0 mm in (a–c) and 5.0 mm in (d–f), respectively. Photos by Gunther Köhler.

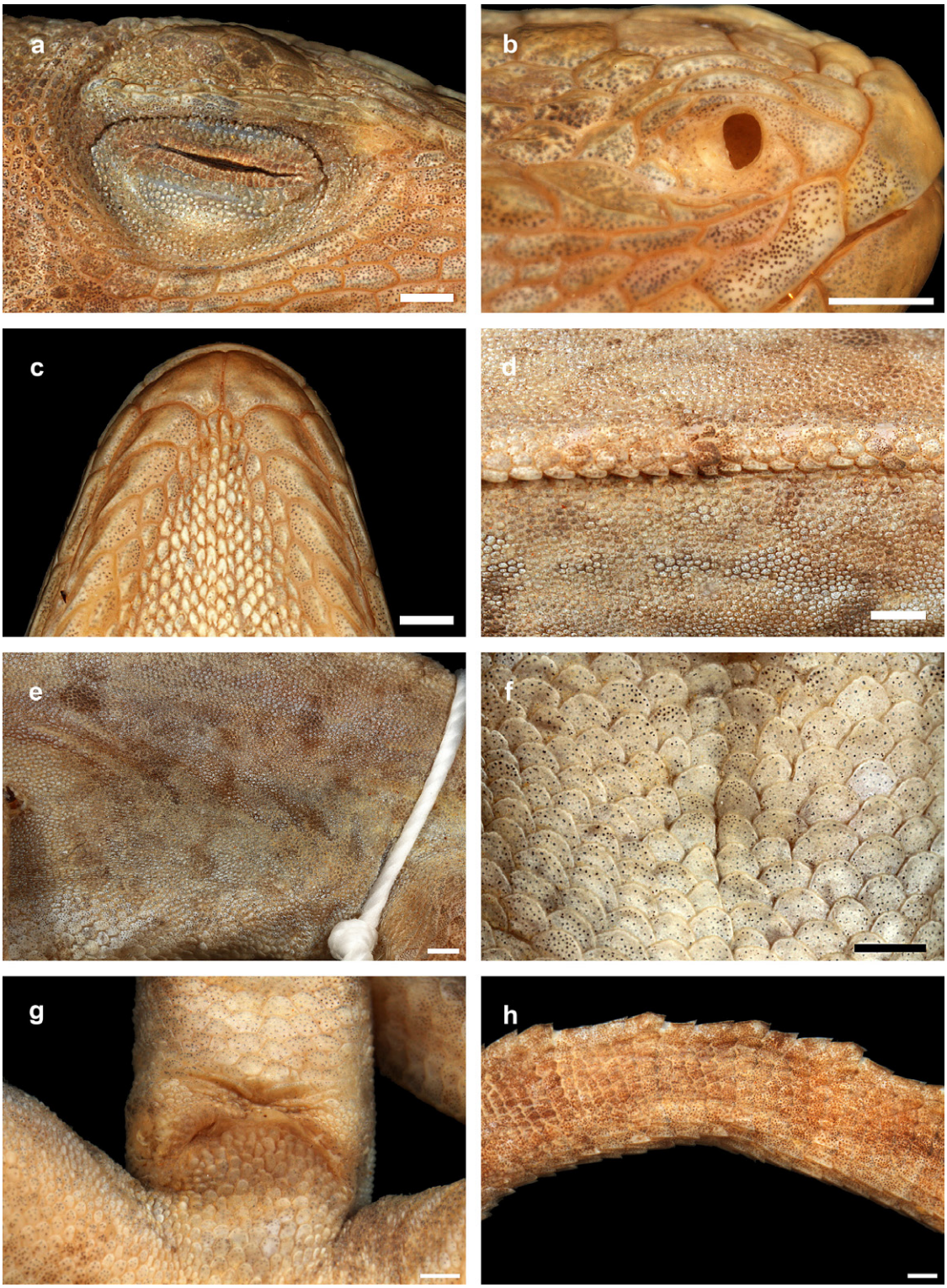

Figure 20. Holotype of *Anolis cybotes doris* Barbour, 1925 (MCZ 13739): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region (e) flank region; (f) midventer; (g) cloacal region; (h) base of tail. Scale bars equal 1.0 mm. Photos by Gunther Köhler.

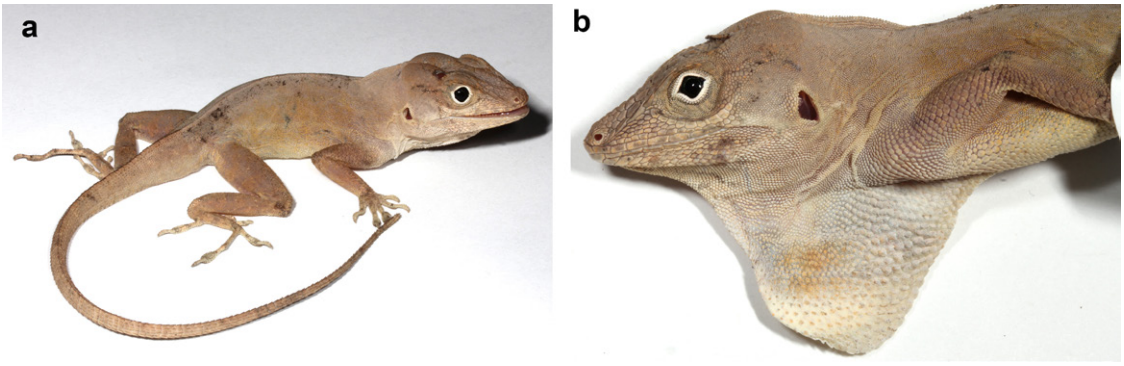

Figure 21. Adult male of *Audantia doris* in life (SBH 269292 to be catalogued at USNM) from Île de la Gonâve, Gran Source, Artibonite, Haiti (3 April 2011). Photos by S. Blair Hedges.

Figure 22. Habitat of *Audantia doris* near Richard on coast road, Île de la Gonâve, Artibonite, Haiti (2 April 2011). Photo by S. Blair Hedges.

***Audantia ravifaux* (Schwartz & Henderson, 1982)**
Saona Stout Anole
Figs. 23–26

Anolis cybotes: Boulenger, 1885 (in part.); Schmidt, 1921 (in part.); Barbour & Loveridge, 1929 (in part.); Barbour, 1930a (in part.); Barbour, 1930b (in part.); Schwartz, 1979 (in part.); Wyles & Gorman, 1980 (in part.); Schwartz, 1980 (in part.); Henderson *et al*., 1984 (in part.); Schwartz, 1989 (in part.); Burnell & Hedges, 1990 (in part.); Powell *et al*., 1996 (in part.); Queiroz *et al.*, 1998 (in part.); Poe, 2004 (in part.); Nicholson *et al.*, 2005 (in part.); Henderson & Powell, 2009 (in part.); Boistel *et al.*, 2011 (in part.); Kolbe *et al*., 2011 (in part.); Poe, 2013 (in part.); Köhler, 2014 (in part.); Muñoz *et al*., 2014a (in part.); Klaczko *et al.*, 2015 (in part.); Giovannotti *et al*., 2017 (in part.); Poe *et al.*, 2017 (in part.).

Anolis cybotes ravifaux Schwartz & Henderson, 1982: 3; type locality: environs of Mano Juan, Isla Saona, República Dominicana. Holotype: MCZ 156221. Schwartz *et al*., 1982; Henderson & Schwartz, 1984; Henderson *et al*., 1984 (in part.); Schwartz & Henderson, 1991; Powell *et al.*, 1999; Powell & Henderson, 2012.

Anolis cybotes cybotes: Cochran, 1934 (in part.); Barbour, 1935 (in part.); Barbour, 1937 (in part.); Fobes *et al*., 1993 (in part.); Cochran, 1941 (in part.); MacLean *et al*., 1977 (in part.).

Audantia cybotes ravifaux: Nicholson *et al.*, 2012; Nicholson *et al.*, 2018.

Audantia cybotes: Nicholson *et al.*, 2014 (in part.).

Ctenonotus cybotes: Savage & Guyer, 1989 (in part.).

Diagnosis. A species of the genus *Audantia* that differs from all congeners by the combination of having (1) smooth ventral scales; (2) male dewlap dirty white with or without yellow suffusions; (3) no dark gular streaks in males; (4) no patch of enlarged scales in nuchal region; (5) a double row of weakly enlarged (usually less than twice the size of adjacent scales), smooth and non-mucronate vertebral scales; (6) two or three sublabial scales in contact with infralabials; (7) 170–204 scales around midbody in males; and (8) enlarged scales on anterior surface of thigh smooth (Fig. 23).

Audantia ravifaux differs from *A. breslini*, *A. cybotes*, *A. saxatilis*, and *A. shrevei* by having smooth enlarged scales on anterior surface of thigh (vs. keeled); and by having smooth ventrals (vs. keeled, some individuals of *A. breslini* and *A. cybotes* with smooth ventrals). *Audantia ravifaux* differs further from *A. shrevei* by lacking a patch of greatly enlarged scales in nuchal region (vs. such a patch present). *Audantia ravifaux* differs from *A. marcanoi* and *A. strahmi* by having smooth enlarged scales on anterior surface of thigh (vs. keeled); and by having a dirty white male dewlap (vs. rose-red at the edge, more orangish anteriorly and posteriorly, but purplish or even bluish toward the center in *A. marcanoi*, and orange with paler center in *A. strahmi*). *Audantia ravifaux* differs from *A. armouri*, *A. doris*, and *A. longitibialis* by having smooth enlarged scales on anterior surface of thigh (vs. keeled). *Audantia ravifaux* differs further from *A. doris* by having a double row of weakly enlarged, usually less than twice the size of adjacent scales, smooth and non-mucronate vertebral scales (vs. greatly enlarged, at least three times the size of adjacent scales, keeled and mucronate vertebral scales). For differences between *A. ravifaux* and the species described below, see the respective accounts of the new species.

Description of holotype. Adult male, as indicated by well-developed dewlap, and presence of a pair of greatly enlarged postcloacal scales (Figs. 24 and 25); SVL 58.0 mm; tail length 83.0 mm (incomplete); tail distinctly compressed in cross section, tail height 3.2 mm and width 1.8 mm; axilla to groin distance 21.7 mm; head length 18.9 mm, head length/SVL ratio 0.33; snout length 8.4 mm; head width 10.5 mm; longest toe of adpressed hind limb reaching to point between eye and nostril; shank length 18.2 mm, shank length/head length ratio 0.96; longest finger of extended forelimb reaching to 3 mm beyond tip of snout; longest finger of adpressed forelimb reaching to 4 mm past anterior insertion of hind limbs. Dorsal head scales smooth or rugose, except weakly keeled scales on snout and supraoculars; 5 postrostrals; 6 scales between nasals; 1 elongate prenasal scale on each side, distinct from circumnasal and in contact with both rostral and first supralabial; circumnasal in contact with first supralabial; scales in deep prefrontal depression smooth or rugose; supraorbital semicircles well-developed, broadly in contact medially; supraorbital disc composed of 5 moderately enlarged, keeled scales arranged in two rows; circumorbital row complete, therefore, enlarged supraorbital scales separated from supraorbital semicircles; a very large elongated superciliary, followed posteriorly by a much smaller, overlapping one, and by three small, keeled scales; 2-3 rows of small keeled scales extending between enlarged supraorbitals and large superciliary; a deep parietal depression present; interparietal scale well-developed, 2.3 x 1.3 mm (length x width), surrounded by scales of moderate size; 2 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 3 large and 2 small anterior canthal scales; 5 scales present between second canthals; 8 scales present between posterior canthals; 35 (right) mostly keeled loreal scales in a maximum of 7 (right) horizontal rows; 8 keeled subocular scales arranged in a single row; 7 supralabials to level below center of eye; suboculars narrowly in contact with supralabials; ear opening 1.5 x 2.2 mm (length x height); mental distinctly wider than long, almost completely divided medially, bordered posteriorly by 8 postmentals, outer ones much larger than median ones; 6 infralabials to level below center of eye; sublabials greatly enlarged (< four times the size of medial postmental scales), 3 (right)–4 (left) in contact with infralabials; scales in sublabial row much larger than scales medially adjacent to this row; pointed granular scales present on chin and throat; dewlap large, extending from level below anterior margin of eye onto chest; a nuchal crest and a dorsal ridge present; dorsum of body with mostly smooth, some weakly keeled, granular scales; 2 medial rows slightly enlarged, usually less than twice the size of adjacent scales; largest dorsal scales about 0.50 x 0.30 mm (length x width); about 45 medial dorsal scales in one head length; about 61 medial dorsal scales between levels of axilla and groin; lateral scales keeled, granular and more or less homogeneous in size, average size 0.15 mm in diameter; ventrals at midbody smooth, flat, almost cycloid, subimbricate, about 0.40 x 0.60 mm (length x width); about 42 medial ventral scales in one head length; about 49 medial ventral scales between levels of axilla and groin; 170 scales around midbody; ventral basal caudal scales smooth, all other caudal scales keeled; middorsal caudal scales distinctly enlarged, forming a low crest; lateral caudal scales with whorls of enlarged scales; a pair of greatly enlarged postcloacal scales present, about 1.1 mm wide; no tube-like axillary pocket present; scales on dorsal surface of upper forelimb smooth, imbricate; scales on anterior surface of thigh enlarged, smooth, imbricate; digital pads dilated, dilated pad three times the width of non-dilated distal phalanx; distal phalanx narrower than and raised from dilated pad; 30 lamellae under Phalanges II–IV of Toe IV of hind limbs; 9 scales under distal phalanx of Toe IV of hind limbs.

Coloration after 45 years preservation in 70 % ethanol was recorded as follows: Dorsal surfaces of head, body, limbs, and tail Walnut Brown (27); ventral surface of head Clay Color (18) except for Beige (254) dewlap; ventral surface of body Clay Color (18) with a suffusion of Drab (19); ventral surfaces of legs Clay Color (18) with Prout's Brown (47) speckles; ventral surface of tail Clay Color (18).

The completely everted hemipenis (SMF 97873; Fig. 26) is a medium-sized, slightly bilobate organ; sulcus spermaticus bordered by well-developed sulcal lips and opening into a single large apical field void of ornamentation; a low asulcate ridge present; apex strongly calyculate, truncus with transverse folds. The everted hemipenis of another specimen (SMF 97869) agrees well with this description.

Geographic distribution. As currently known, *Audantia ravifaux* is restricted to the extreme southeastern portion of Hispaniola including Isla Saona, all from near sea level (Fig. 18).

Natural history notes. Henderson & Powell (2009) provided a summary of the natural history of "*Anolis cybotes*" which under our concept is represented by several species.

Conservation. More field and lab work is needed to evaluate the geographic area of distribution of *Audantia ravifaux* in order to understand the status of conservation of this species.

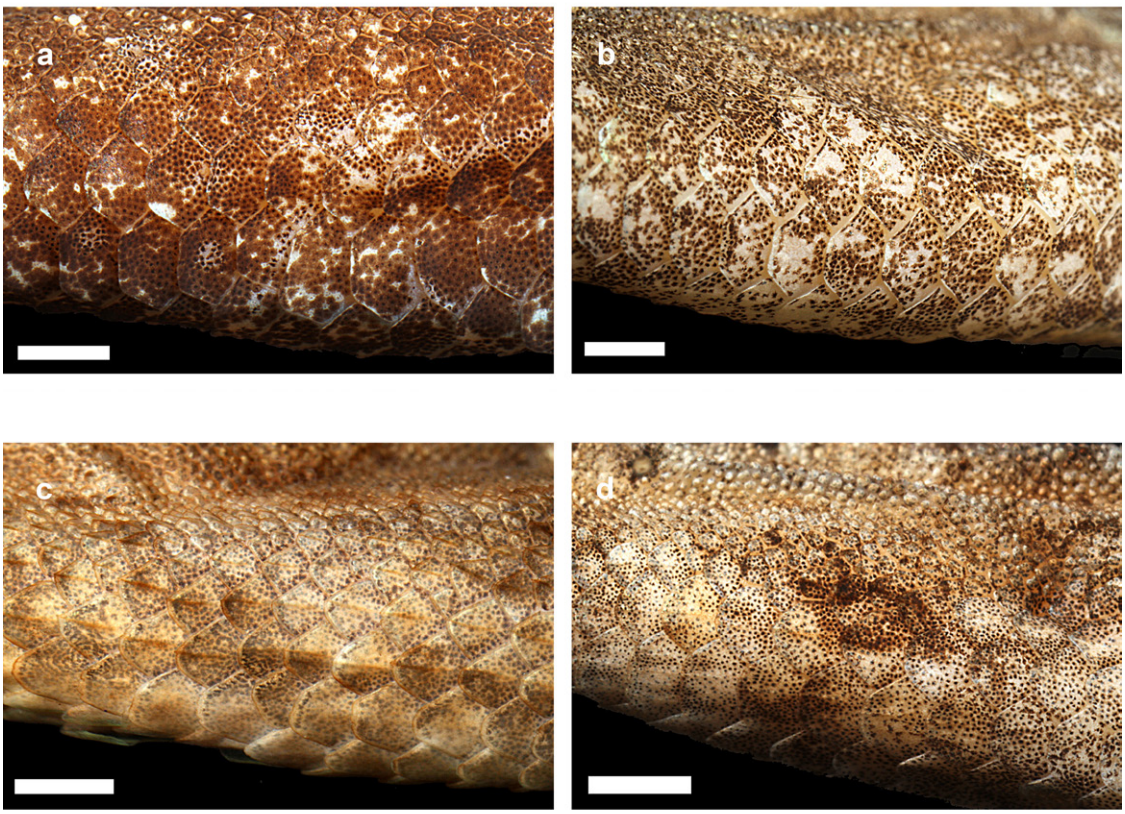

Figure 23. Anterior surface of thigh in (a) *Audantia ravifaux* (MCZ 187416); (b) *A. ravifaux* (MCZ 187412); (c) *A. hispaniolae* (SMF 104237); (d) *A. hispaniolae* (SMF 104236). Scale bars equal 1.0 mm. Photos by Gunther Köhler.

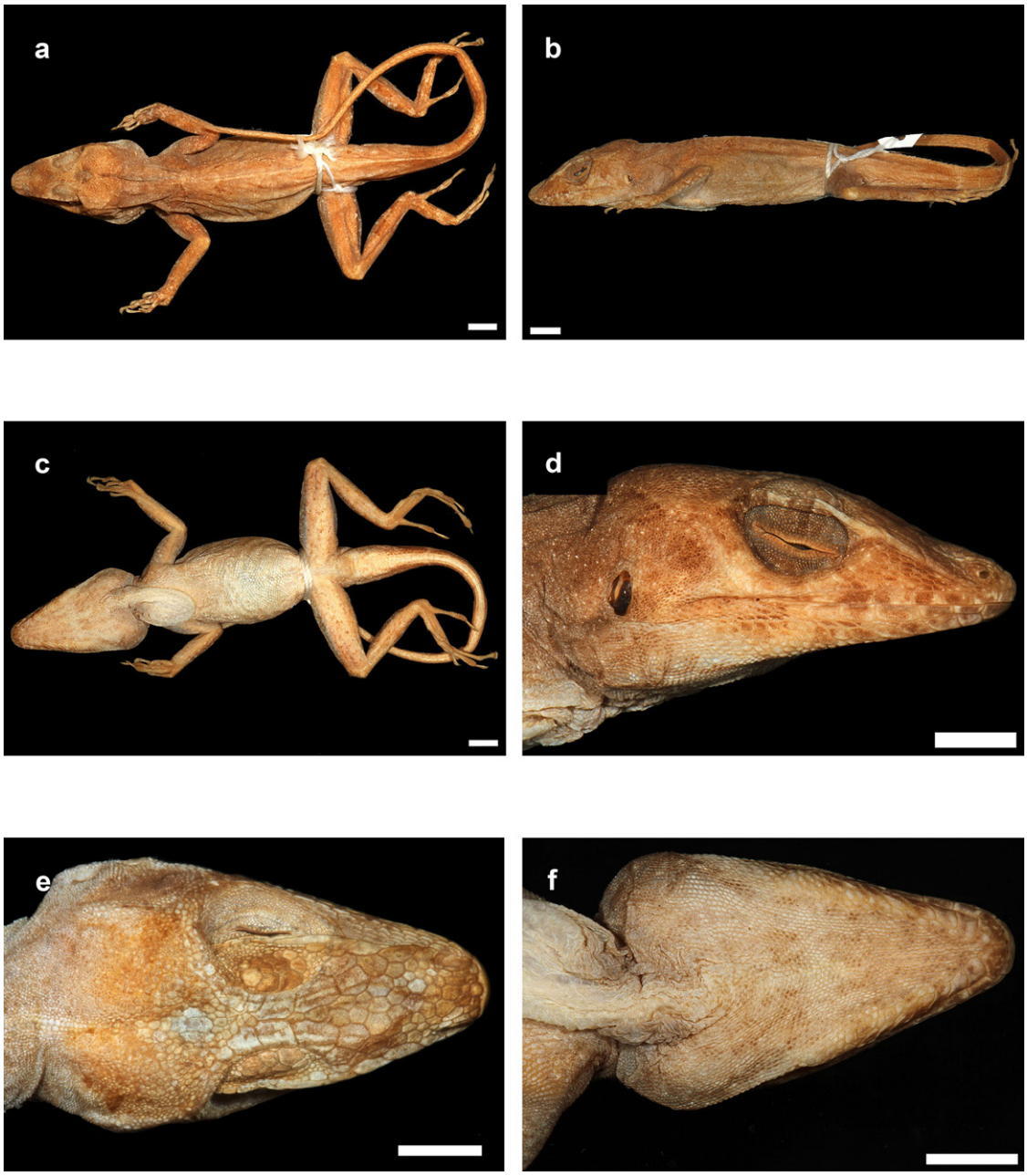

Figure 24. Holotype of *Anolis cybotes ravifaux* Schwartz & Henderson, 1982 (MCZ 156221): (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; (f) ventral view of head. Scale bars equal 10.0 mm in (a–c) and 5.0 mm in (d–f), respectively. Photos by Gunther Köhler.

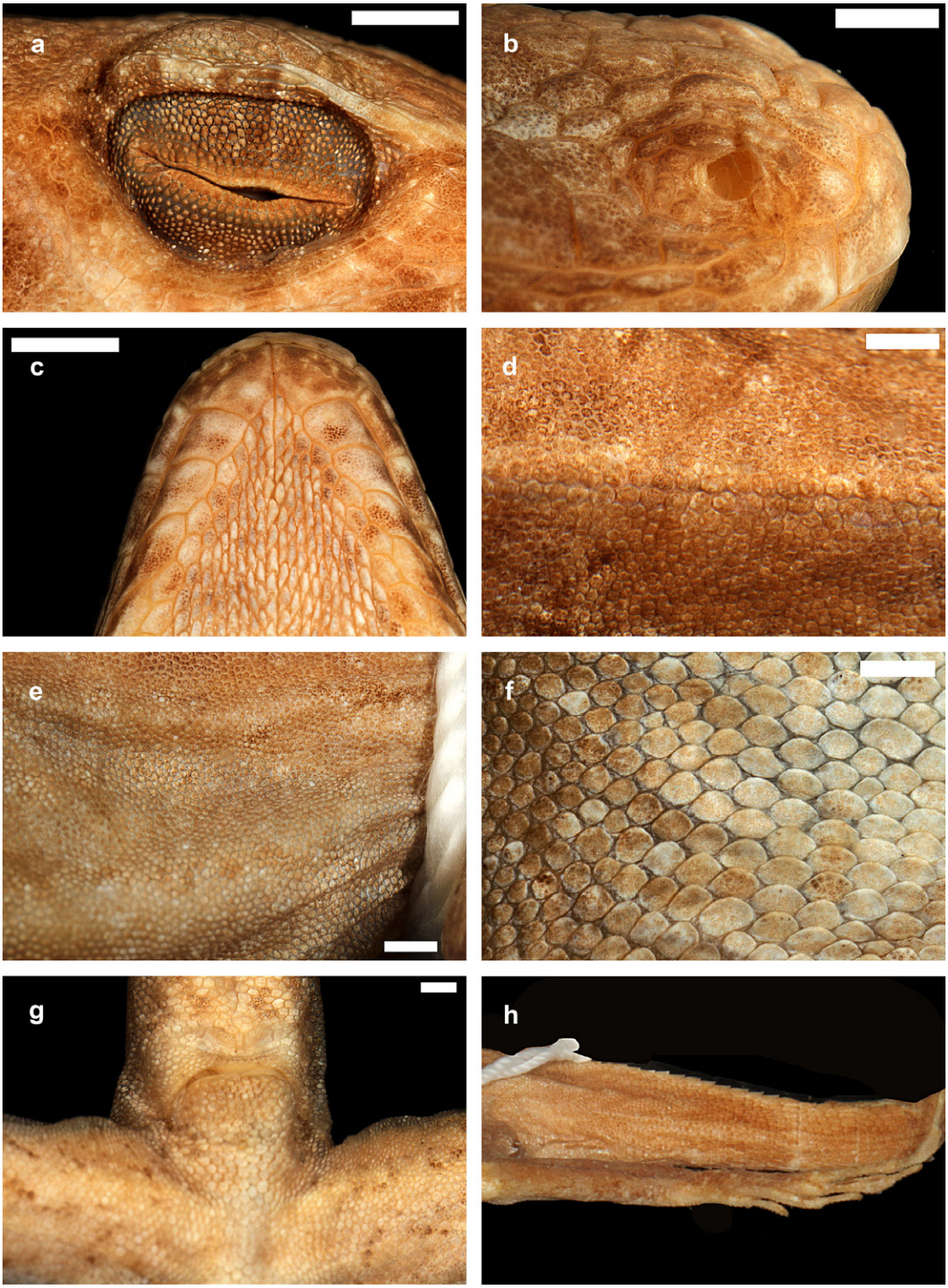

Figure 25. Holotype of *Anolis cybotes ravifaux* Schwartz & Henderson, 1982 (MCZ 156221): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region (e) flank region; (f) midventer; (g) cloacal region; (h) lateral view of tail. Scale bars equal 1.0 mm. Photos by Gunther Köhler.

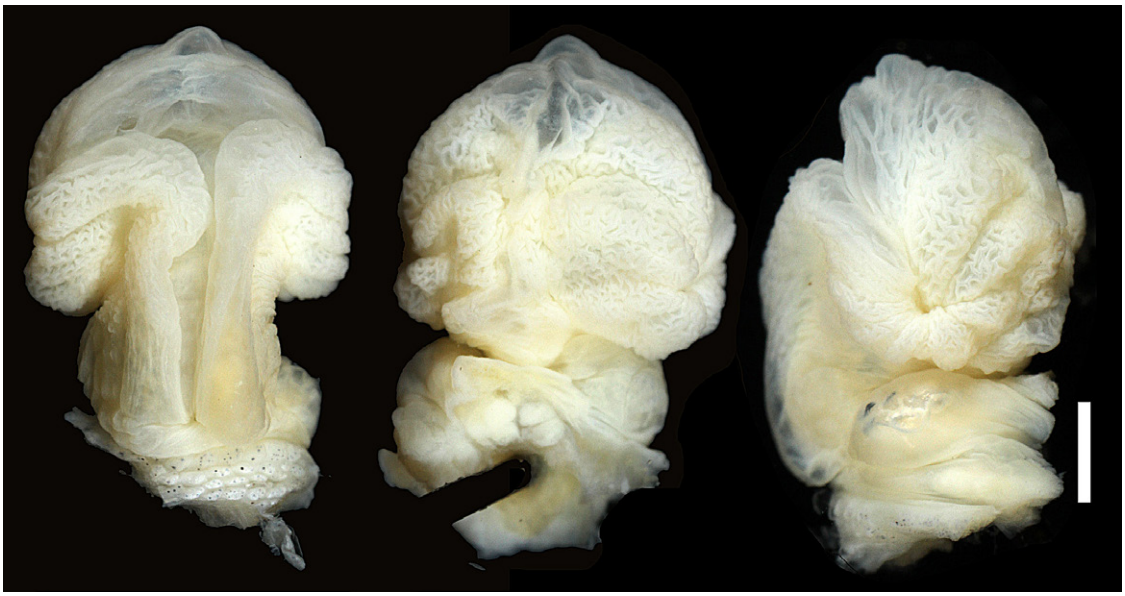

Figure 26. Hemipenis of *Audantia ravifaux* (SMF 97873). Scale bar equals 1.0 mm. Photos by Gunther Köhler.

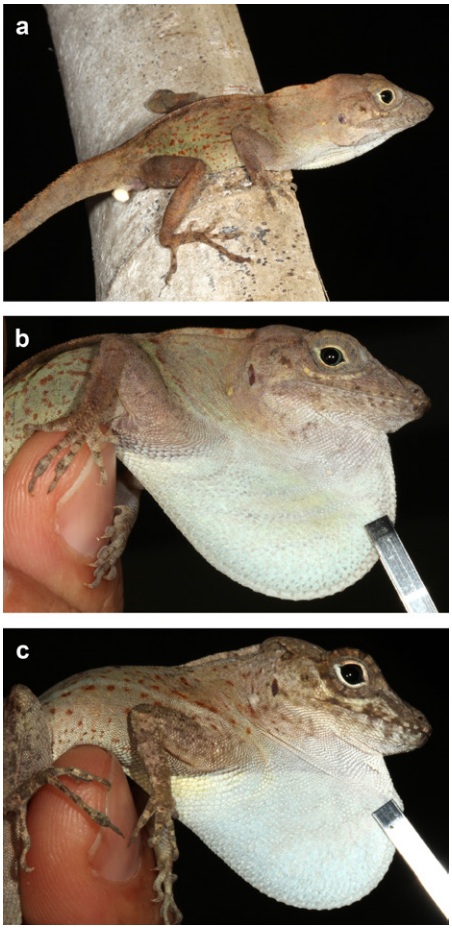

Figure 27. *Audantia ravifaux* in life (all males). (a) SMF 97873; (b) SMF 97873; (c) SMF 97869. Photos by Gunther Köhler.

Figure 28. Habitat of *Audantia ravifaux near* Manatí Park Bávaro, La Altagracia, Dominican Republic (18 October 2013). Photo by Gunther Köhler.

***Audantia hispaniolae* sp. nov.**
Common Stout Anole
ZOOBANK urn: lsid: zoobank.org: act:5FFDB3F3-D7AC-4638-B25F-D493BE1CE80B.
Figs. 29–34

Anolis cybotes: Boulenger, 1885 (in part.); Barbour, 1914 (in part.); Schmidt, 1921 (in part.); Noble, 1923b; Cochran, 1928 (in part.); Barbour & Loveridge, 1929 (in part.); Barbour, 1930a (in part.); Barbour, 1930b (in part.); Rand, 1962 (in part.); Williams, 1963 (in part.); Schwartz & Thomas, 1975 (in part.); Williams, 1975 (in part.); Schwartz, 1979 (in part.); Wyles & Gorman, 1980 (in part.); Schwartz, 1980 (in part.); Schwartz & Henderson, 1982 (in part.); Henderson *et al*., 1984 (in part.); Henderson & Schwartz, 1984 (in part.); (Losos, 1985) (in part.); Case & Williams, 1987; Schwartz, 1989 (in part.); Burnell & Hedges, 1990 (in part.); Powell *et al*., 1996 (in part.); Queiroz *et al.*, 1998 (in part.); Powell *et al.*, 1999 (in part.); Poe, 2004 (in part.); Nicholson *et al.*, 2005 (in part.); Henderson & Powell, 2009 (in part.); Boistel *et al.*, 2011 (in part.); Kolbe *et al*., 2011 (in part.); Poe, 2013 (in part.); Wollenberg *et al.*, 2013 (in part.); Köhler, 2014 (in part.); Muñoz *et al*., 2014a (in part.); Muñoz *et al.,* 2014b (in part.); Klaczko *et al.*, 2015 (in part.); Giovannotti *et al.,* 2017 (in part.); Poe *et al.*, 2017 (in part.); Boronow *et al.*, 2018 (in part.); Muñoz & Losos, 2018 (in part.).

Anolis cybotes cybotes: Cochran, 1934 (in part.); Barbour, 1935 (in part.); Barbour, 1937 (in part.); Mertens, 1938 (in part.); Mertens, 1939 (in part.); Cochran, 1941 (in part.); Schwartz & Thomas, 1975 (in part.); MacLean *et al*., 1977 (in part.); Schwartz & Henderson, 1991 (in part.); Fobes *et al.*, 1993 (in part.); Powell *et al.*, 1999 (in part.); Powell & Henderson, 2012 (in part.).

Audantia cybotes: Nicholson *et al.*, 2014 (in part.); Nicholson *et al.*, 2012 (in part.); Nicholson *et al.*, 2018 (in part.).

Ctenonotus cybotes: Savage & Guyer, 1989 (in part.).

Holotype. SMF 97884, an adult male from El Limón, Peninsula Samaná (19.28929, -69.43118), 30 m, Province Samaná, Dominican Republic; collected 21 October 2013 by Gunther Köhler. Field tag number GK-4721.

Paratypes. MNHNSD 23.3602–03, SMF 97878–83, 97885, same collecting data as holotype. All paratypes are adult males except MNHNSD 23.3602, SMF 97878, 97881, 97885 that are adult females.

Diagnosis. A species of the genus *Audantia* (our Species 1 "*hispaniolae*") that differs from all congeners by the combination of having (1) smooth ventral scales; (2) male dewlap creme white with yellowish, greenish or orange suffusions, and with heterogeneously distributed, moderately spaced gorgetal scales, that are clutterd in groups, and reduced in size in central portion; (3) dark gular streaks in males present; (4) no patch of enlarged scales in nuchal region; (5) a double row of enlarged, keeled and non-mucronate vertebral scales; (6) usually two sublabial scales in contact with infralabials; (7) 214–244 scales around midbody in males; and (8) keeled scales on dorsal surfaces of upper forelimb and anterior surface of thigh.

Audantia hispaniolae differs from *A. breslini, A. shrevei,* and *A. saxatilis* by having smooth ventrals (vs. keeled, some individuals of *A. breslini* with smooth ventrals); by having one or two well-defined pale longitudinal lateral stripes, usually edged with orange or olive-green (vs. such stripes absent); by having heterogeneously distributed gorgetals with groups of cluttered scales (vs. homogeneously distributed gorgetals); and by having dark gular streaks on male dewlap (vs. usually absent). *Audantia hispaniolae* differs further from *A. shrevei* by lacking a patch of greatly enlarged scales in nuchal region (vs. such a patch present). *Audantia hispaniolae* differs from *A. armouri* by having dark gular streaks on the male dewlap (vs. usually absent); by having heterogeneously distributed gorgetals with groups of cluttered scales (vs. homogeneously distributed gorgetals); and by having 214–240 scales around midbody in males (vs. 118–172). *Audantia hispaniolae* differs from *A. cybotes* by having smooth ventrals (vs. keeled, smooth in some individuals); by having non-mucronate vertebral scales (vs. vertebral scales mucronate); by having heterogeneously distributed gorgetals with groups of cluttered scales (vs. homogeneously distributed gorgetals); by having moderately spaced gorgetals and scales reduced in size in central portion of dewlap (vs. all scales narrowly spaced and large on posterior half of dewlap); and males having a dirty white dewlap with yellowish, greenish or orange suffusions (vs. those suffusions absent). *Audantia hispaniolae* differs from *A. doris* by having dark gular streaks (vs. absent); by having yellowish, greenish or orange suffusions on male dewlap (vs. no suffusions, but with an orange blotch in center of dewlap); and by having 214–244 scales around midbody in males (vs. 166184). *Audantia hispaniolae* differs from *A. marcanoi* and *A. strahmi* by having a dirty white male dewlap (vs. rose-red at the edge, more orangish anteriorly and posteriorly, but purplish or even bluish toward the center in *A. marcanoi*, and orange with paler center in *A. strahmi*). *Audantia hispaniolae* differs further from *A. marcanoi* by having a double row of abruptly enlarged vertebral scales (vs. vertebral scales gradually enlarged, not forming a regular double row). *Audantia hispaniolae* differs from *A. longitibialis* by having dark gular streaks on male dewlap (vs. absent); and by having moderately spaced gorgetals and scales reduced in size in central portion of dewlap (vs. all scales widely spaced and small on posterior half of dewlap). *Audantia hispaniolae* differs from *A. ravifaux* by having keeled scales on dorsal surface of upper forelimb and anterior surface of thigh (vs. smooth); by having one or two well-defined pale longitudinal lateral stripes,

usually edged with orange or olive-green (vs. such stripes absent); and by having moderately spaced gorgetals (vs. all scales widely spaced). For differences between *A. hispaniolae* and the species described below, see the respective accounts of the new species.

Description of the holotype. Adult male (Figs. 29 and 30), as indicated by everted hemipenes, well-developed dewlap, and presence of a pair of greatly enlarged postcloacal scales; SVL 62.0 mm; tail length 52.0 mm (incomplete); tail distinctly compressed in cross section, tail height 3.9 mm and width 2.5 mm; axilla to groin distance 22.7 mm; head length 18.6 mm, head length/SVL ratio 0.30; snout length 8.2 mm; head width 10.7 mm; longest toe of adpressed hind limb reaching to anterior margin of eye; shank length 19.1 mm, shank length/head length ratio 1.03; longest finger of extended forelimb reaching to nostril; longest finger of adpressed forelimb reaching to level of anterior insertion of hind limbs. Dorsal head scales smooth or rugose, except weakly keeled scales on snout and supraoculars; 6 postrostrals; 7 scales between nasals; 1 elongate prenasal scale on each side, distinct from circumnasal and in contact with both rostral and first supralabial; circumnasal separated from first supralabial by one scale; scales in deep prefrontal depression smooth or rugose; supraorbital semicircles well-developed, separated medially by one scale row at narrowest point; supraorbital disc composed of 3 moderately enlarged, keeled scales arranged in three rows; circumorbital row complete, therefore, enlarged supraorbital scales separated from supraorbital semicircles; a very large elongated superciliary, followed posteriorly by a much smaller, overlapping one and by several small, keeled scales; three rows of small keeled scales extending between enlarged supraorbitals and large superciliary; a deep parietal depression present; interparietal scale well-developed, 2.5 x 1.4 mm (length x width), surrounded by scales of moderate size; 2 to 3 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 3 large and 2 small anterior canthal scales; 9 scales present between second canthals; 11 scales present between posterior canthals; 73 (right) – 62 (left) mostly keeled loreal scales in a maximum of 8 horizontal rows; 7 to 8 keeled subocular scales arranged in a single row; 7 supralabials to level below center of eye; suboculars separated from supralabials by a complete scale row; ear opening 1.3 x 2.5 mm (length x height); mental distinctly wider than long, almost completely divided medially, bordered posteriorly by 5 postmentals, outer ones much larger than median ones; 7 infralabials to level below center of eye; sublabials greatly enlarged (< four times the size of medial postmental scales), two in contact with infralabials; scales in sublabial row much larger than scales medially adjacent to this row; pointed granular scales present on chin and throat; dewlap large, extending from level below anterior margin of eye onto chest; gorgetals heterogeneously distributed with groups of cluttered scales, those in central portion reduced in size; a nuchal crest and a dorsal ridge present; dorsum of body with keeled, granular scales; 2 medial rows distinctly enlarged, mostly more than twice the size of adjacent body scales; largest dorsal scales about 0.35 x 0.30 mm (length x width); about 56 medial dorsal scales in one head length; about 77 medial dorsal scales between levels of axilla and groin; lateral scales keeled, granular and more or less homogeneous in size, average size 0.12 mm in diameter; ventrals at midbody smooth, flat, almost cycloid, imbricate, about 0.65 x 0.75 mm (length x width); about 36 medial ventral scales in one head length; about 42 medial ventral scales between levels of axilla and groin; 236 scales around midbody; all caudal scales keeled; middorsal caudal scales distinctly enlarged, forming a low crest; lateral caudal scales with whorls of enlarged scales; a pair of greatly enlarged postcloacal scales present, about 1.2 mm wide; no tube-like axillary pocket present; scales on dorsal surface of upper forelimb strongly keeled, mucronate, imbricate; scales on anterior surface of thigh strongly keeled, mucronate, imbricate;

digital pads dilated, dilated pad three times the width of non-dilated distal phalanx; distal phalanx narrower than and raised from dilated pad; 28 lamellae under Phalanges II-IV of Toe IV of hind limbs; 11 scales under distal phalanx of Toe IV of hind limbs.

Coloration after 5 years preservation in 70% ethanol was recorded as follows: Dorsal ground color Smoke Gray (267) with Vandyke Brown (281) diffuse blotches; ventral surface of head Light Buff (2) with Hair Brown (277) streaks; ventral surface of body Cream White (52); ventral surfaces of legs Pale Pinkish Buff (3) with Hair Brown (277) stipples; ventral surface of fingers and toes Hair Brown (277); dorsal, lateral and ventral surfaces of tail Hair Brown (277).

Variation. The paratypes agree well with the holotype in general appearance; morphometrics and scalation (Table II). In most individuals the longest toe of adpressed hind leg reaching to a point between anterior and posterior level of eye, exceptionally to a point between eye and nostril or between ear and eye.

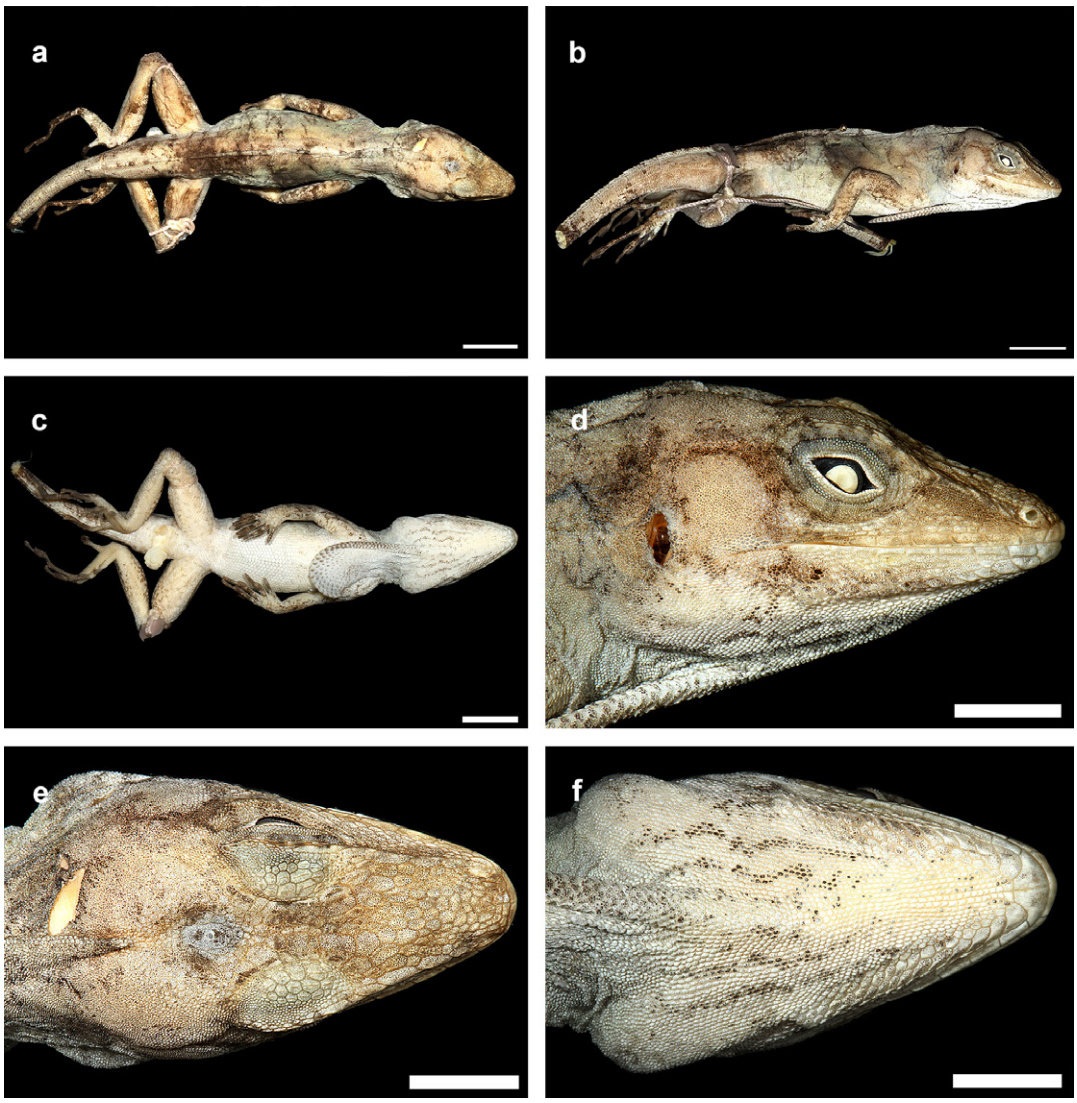

Figure 29. Holotype of *Audantia hispaniolae* (SMF 97884): (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; (f) ventral view of head. Scale bars equal 10.0 mm in (a–c) and 5.0 mm in (d–f), respectively. Photos by Gunther Köhler.

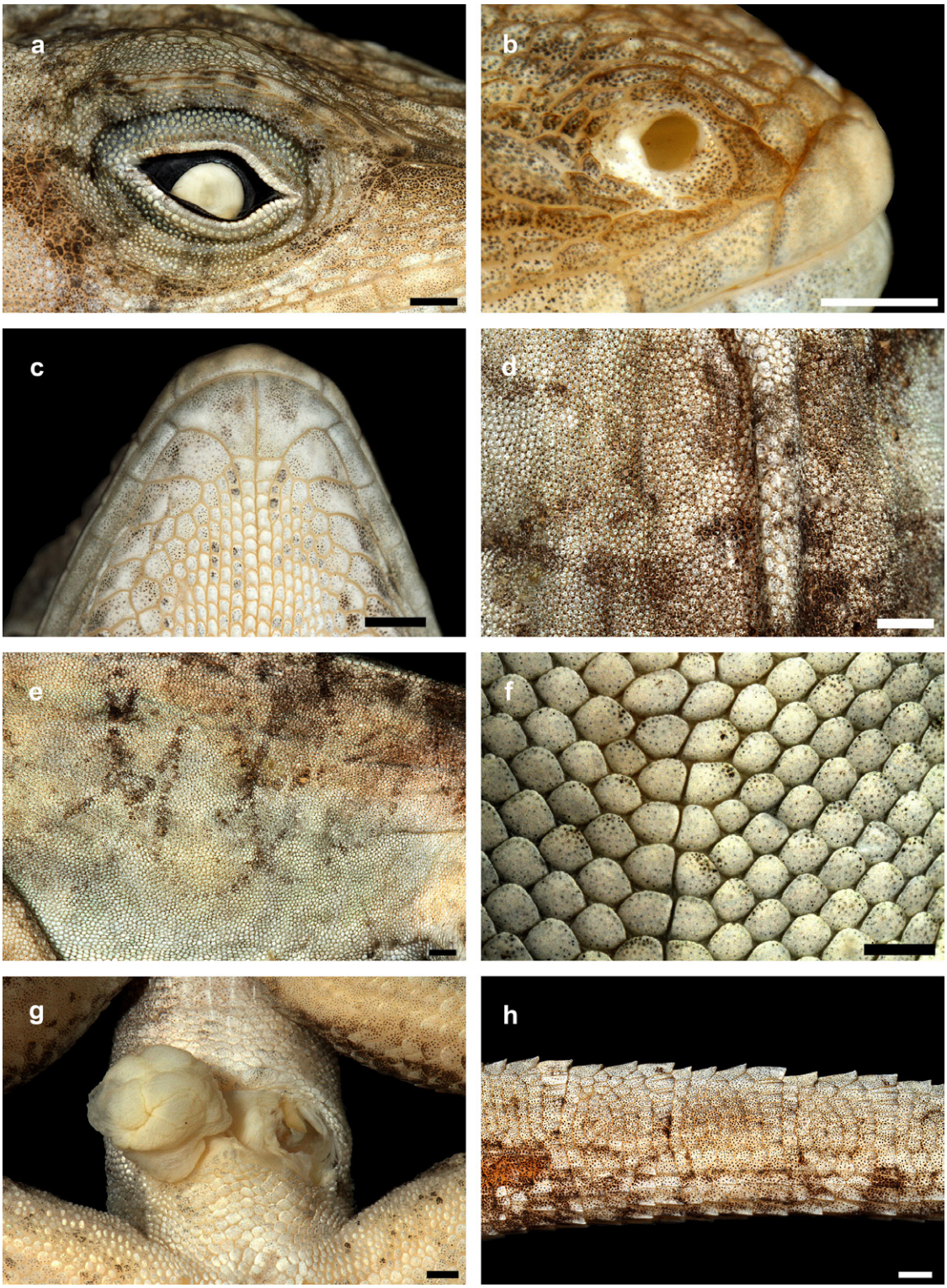

Figure 30. Holotype of *Audantia hispaniolae* (SMF 97884): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region (e) flank region; (f) midventer; (g) cloacal region; (h) lateral view of tail. Scale bars equal 1.0 mm. Photos by Gunther Köhler.

Figure 31. Hemipenis of *Audantia hispaniolae* (SMF 104760). Scale bar equals 1.0 mm. Photos by Gunther Köhler.

Figure 32. *Audantia hispaniolae* in life. (a) MNHNSD 23.3588; (b) SMF 97864; (c) MNHNSD 23.3632; (d) MNHNSD 23.3664. (a–c) are males, (d) is a female. Photos by Gunther Köhler.

Figure 33. Dewlaps of *Audantia hispaniolae* in life. (a) SMF 97863; (b) SMF 97864; (c) SMF 97865; (d) SMF MNHNSD 23.3632; (e) SMF MNHNSD 23.3664; (f) SMF 97866. (a–d) are males, (e–f) are females. Photos by Gunther Köhler.

The coloration in life of an adult male (SMF 97863) was recorded as follows: Dorsum of head Ground Cinnamon (270); dorsum of body and limbs Ground Cinnamon (270), with a Light Smoke Grey (263) stripe edged by True Cinnamon (260); dewlap Whitish Lime Green (111), centrally suffused with Cinnamon (255); underside of head Beige (254) with Dark Drab (45) irregular lines; circum orbitale region Dark Greyish Olive (275) with a Pale Horn Color (11) inner ring; iris Maroon (39); ventral side of body and tail Pale Buff (1); ventral surface of limbs Cinnamon-Drab (50) with Prout's Brown (47) speckles. The coloration in life of an adult female (SMF 97866) was recorded as follows: Dorsum of head Drab (19); dorsal surface of body Drab (19) with Tawny Olive (17) vertebral stripes and diamonds; lateral side of body with a Sayal Brown (41) longitudinal stripe; dorsal surface of limbs Verona Brown (37) with indistinct Drab (19) bands; tail Drab (19) with Clay Color (18) diamonds; iris Raw Umber (22); a Pale Horn Color (1) inner eye ring; ventral surface of head Smokey White (261) with Sepia (279) streaks; ventral suface of body and limbs Light Buff (2); ventral surface of tail Pale Pinkish Buff (3), grading into Cinnamon-Drab (50) distally.

Figure 34. Habitat of *Audantia hispaniolae*. (a) Reserva Científica Ébano Verde, Arroyazo, La Vega, Dominican Republic, 1080 m a.s.l. (3 November 2013); (b) El Limón, Peninsula Samaná, Samaná, Dominican Republic, 30 masl (21 October 2013); (c) El Seibo, El Seibo, Dominican Republic, 110 masl (14 October 2013); (d) 27 Cascadas, ca. 13 km airline WSW Puerto Plata, Puerto Plata; Dominican Republic, 20 m a.s.l. (1 August 2014). Photos by Gunther Köhler.

The completely everted hemipenis (SMF 104760; Fig. 31) is a medium-sized, slightly bilobate organ; sulcus spermaticus bordered by well-developed sulcal lips and opening into a single large apical field void of ornamentation; an asulcate finger-like processus present; apex strongly calyculate, truncus with transverse folds. The everted hemipenis of 19 other specimens (SMF 90421, 97863–65, 97868, 97875–76, 97882–84, 97888, 97900, 97903, 104758–62, 104764) agree well with this description. However, the shape of the asulcal processus varies from ridge-like to finger-like.

Etymology. The species name (*hispaniolae*) is a feminine genitive singular noun, referring to the broad distribution of the species on the island of Hispaniola.

Geographic distribution. As currently known, *Audantia hispaniolae* is widely distributed across the North Island of Hispaniola north of the Sierra de Bahoruco, except for the extreme northwestern portion, from near sea level to 1800 m a.s.l. (Fig. 18).

Natural history notes. We observed this species in a wide range of habitats, ranging from wet cloud forest to degraded, rocky, dry forest, and also very often within human settlements as long as trees were present (Fig. 34). Individuals were collected on rocks, under rocks, low on tree trucks and bush stems, and under among dead agaves during the day. Especially in the morning hours, individuals were seen perching head-down on bushes and trees. At night we saw these lizards sleeping on leaves and twigs of palms, bushes and trees up to 2 m above the ground. In some instances, the same individual was observed on exactly the same sleeping place on several successive nights. The flight distance was usually in the range of 1–2 m. Both males and females often emitted a high-pitched distress call when caught. Henderson & Powell (2009) provided a summary of the natural history of "*Anolis cybotes*" which under our concept is represented by several species.

Conservation. Given its broad range and usual abundance wherever this species occurs, we consider the conservation status of *Audantia hispaniolae* as Least Concern based on the IUCN Red List Categories and Criteria (IUCN, 2012).

***Audantia higuey* sp. nov.**
Cordillera Oriental Stout Anole
ZOOBANK urn:lsid:zoobank.org: act:F025F86B-79C4-41C2-A828-78C89317DFCC.
Figs. 35–39

Anolis cybotes: Boulenger, 1885 (in part.); Schmidt, 1921 (in part.); Barbour & Loveridge, 1929 (in part.); Barbour, 1930a (in part.); Barbour, 1930b (in part.); Rand, 1962 (in part.); Schwartz & Thomas, 1975 (in part.); Schwartz, 1979 (in part.); Wyles & Gorman, 1980 (in part.); Schwartz, 1980 (in part.); Schwartz & Henderson, 1982 (in part.); Henderson *et al.,* 1984 (in part.); Henderson & Schwartz, 1984 (in part.); Schwartz, 1989 (in part.); Burnell & Hedges, 1990 (in part.); Powell *et al*., 1996 (in part.); Queiroz *et al.*, 1998 (in part.); Powell *et al.*, 1999 (in part.); Poe, 2004 (in part.); Nicholson *et al.*, 2005 (in part.); Henderson & Powell, 2009 (in part.); Boistel *et al.,* 2011 (in part.); Kolbe *et al*., 2011 (in part.); Poe, 2013 (in part.); Köhler, 2014 (in part.); Muñoz *et al.*, 2014 (in part.); Klaczko *et al.*, 2015 (in part.); Giovannotti *et al.,* 2017 (in part.); Poe *et al.*, 2017 (in part.).

Anolis cybotes cybotes: Cochran, 1934 (in part.); Barbour, 1935 (in part.); Barbour, 1937 (in part.); Mertens, 1938 (in part.); Mertens, 1939 (in part.); Cochran, 1941 (in part.); Schwartz & Thomas, 1975 (in part.); MacLean *et al*., 1977 (in part.); Schwartz & Henderson, 1991 (in part.); Fobes *et al.*, 1993 (in part.); Powell *et al.*, 1999 (in part.); Powell & Henderson, 2012 (in part.).

Audantia cybotes: Nicholson *et al.*, 2014 (in part.); Nicholson *et al.*, 2012 (in part.); Nicholson *et al.*, 2018 (in part.).

Ctenonotus cybotes: *S*avage & Guyer, 1989 (in part.).

Holotype. SMF 97872, an adult male from Manatí Park Bávaro (18.64735, -68.42858), 20 m, Province La Altagracia, Dominican Republic; collected 19 October 2013 by Gunther Köhler. Field tag number GK-4693.

Paratypes. SMF 97870 (adult male), 97874 (adult female), same collecting data as holotype.

Diagnosis. A species of the genus *Audantia* (our Species 2 "*higuey*") that differs from all congeners by the combination of having (1) smooth ventral scales; (2) male dewlap dirty white with yellowish, greenish or orange suffusions, and with homogeneously distributed, upper portion of dewlap mostly covered by gorgetals with little free skin, and gorgetals reduced in size in central portion; (3) no dark gular streaks in males; (4) no patch of enlarged scales in nuchal region; (5) a double row of enlarged, keeled and non-mucronate vertebral scales; (6) usually two sublabial scales in contact with infralabials; (7) 166–212 scales around midbody in males; and (8) keeled scales on dorsal surfaces of upper forelimb and anterior surface of thigh.

Audantia higuey differs from *A. armouri* by having the upper portion of dewlap mostly covered by gorgetals with little free skin and gorgetals reduced in size in central portion (vs. moderately spaced gorgetals, and all scales medium-sized on posterior half of dewlap); and by having 166–212 scales around midbody in males (vs. 118–172). *Audantia higuey* differs from

A. breslini and *A. cybotes* by having smooth ventrals (vs. keeled, some individuals of *A. breslini* and *A. cybotes* with smooth ventrals); and by having gorgetals reduced in size in central portion (vs. all scales large on posterior half of dewlap). *Audantia higuey* differs further from *A. cybotes* by lacking dark gular streaks (vs. present); and by having moderately enlarged, non-mucronate vertebral scales (vs. greatly enlarged, at least three times the size of adjacent scales, mucronate vertebral scales). *Audantia higuey* differs from *A. doris* by having yellowish or orange suffusions on male dewlap (vs. no suffusions, but with an orange blotch in center of dewlap); by having enlarged, non-mucronate vertebral scales (vs. greatly enlarged, at least three times the size of adjacent scales, mucronate vertebral scales); by having one or two well-defined pale longitudinal lateral stripes, usually edged with orange or olive-green (vs. such stripes absent); and by having homogeneously distributed gorgetals (vs. heterogeneously distributed gorgetals with groups of cluttered scales). *Audantia higuey* differs from *A. longitibialis* by having yellowish or orange suffusions on male dewlap (vs. no suffusions); and by only having the upper portion of dewlap mostly covered by gorgetals with little free skin, and scales reduced in size in central portion of dewlap (vs. all scales widely spaced and small on posterior half of dewlap). *Audantia higuey* differs from *A. marcanoi* and *A. strahmi* by having a dirty white male dewlap with yellowish or orange suffusions (vs. rose-red at the edge, more orangish anteriorly and posteriorly, but purplish or even bluish toward the center in *A. marcanoi*, and orange with paler center in *A. strahmi*). *Audantia higuey* differs further from *A. marcanoi* by having a double row of abruptly enlarged vertebral scales (vs. vertebral scales gradually enlarged, not forming a regular double row). *Audantia higuey* differs from *A. hispaniolae* by lacking dark gular streaks (vs. present); and by having homogeneously distributed gorgetals (vs. heterogeneously distributed with groups of cluttered scales). *Audantia higuey* differs from *A. ravifaux* by having keeled scales on dorsal surface of upper forelimb and anterior surface of thigh (vs. smooth); by having homogeneously distributed gorgetals and the upper portion of dewlap mostly covered by scales with little free skin (vs. heterogeneously distributed gorgetals with groups of cluttered scales, widely spaced); and by having one or two well-defined pale longitudinal lateral stripes, usually edged with orange or olive-green (vs. such stripes absent). *Audantia higuey* differs from *A. shrevei* and *A. saxatilis* by having smooth ventrals (vs. keeled); and by having one or two well-defined pale longitudinal lateral stripes, usually edged with orange or olive-green (vs. such stripes absent). *Audantia higuey* differs further from *A. shrevei* by lacking a patch of greatly enlarged scales in nuchal region (vs. such a patch present). *Audantia higuey* differs further from *A. saxatilis* by having the upper portion of dewlap mostly covered by gorgetals with little free skin and gorgetals reduced in size in central portion (vs. widely spaced, more scales uncovered than covered by gorgetals; aall scales small on posterior half of dewlap). For differences between *A. higuey* and the species described below, see the respective accounts of the new species.

Description of the holotype. Adult male (Figs. 35–36), as indicated by well-developed dewlap, and presence of a pair of greatly enlarged postcloacal scales; SVL 53.5 mm; tail length 51.0 mm (incomplete); tail distinctly compressed in cross section, tail height 3.7 mm and width 2.3 mm; axilla to groin distance 18.0 mm; head length 16.8 mm, head length/SVL ratio 0.31; snout length 7.4 mm; head width 9.7 mm; longest toe of adpressed hind limb reaching to level of anterior margin of eye; shank length 17.1 mm, shank length/head length ratio 1.02; longest finger of extended forelimb reaching to tip of snout; longest finger of adpressed forelimb reaching to 5 mm past anterior insertion of hind limbs. Dorsal head scales smooth or rugose, except weakly keeled scales on snout and supraoculars; 7 postrostrals; 6 scales between nasals; 1 elongate prenasal scale on each side, distinct from circumnasal and in contact with both rostral and first supralabial; circumnasal separated from first supralabial by one scale; scales in deep prefrontal

depression smooth or rugose; supraorbital semicircles well-developed, broadly in contact medially; supraorbital disc composed of 4 to 5 moderately enlarged, keeled scales arranged in three rows; circumorbital row complete, therefore, enlarged supraorbital scales separated from supraorbital semicircles; a very large elongated superciliary, followed posteriorly by a much smaller, overlapping one and by several small, keeled scales; 2–4 rows of small keeled scales extending between enlarged supraorbitals and large superciliary; a deep parietal depression present; interparietal scale well-developed, 2.5 x 1.6 mm (length x width), surrounded by scales of moderate size; 2 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 3 large and 1 small anterior canthal scales; 8 scales present between second canthals; 8 scales present between posterior canthals; 49 (right)–48 (left) mostly keeled loreal scales in a maximum of 7 (right)–8 (left) horizontal rows; 8 keeled subocular scales arranged in a single row; 6 supralabials to level below center of eye; suboculars separated from supralabials by a complete scale row; ear opening 1.4 x 2.0 mm (length x height); mental distinctly wider than long, almost completely divided medially, bordered posteriorly by 7 postmentals, outer ones much larger than median ones; 6 infralabials to level below center of eye; sublabials greatly enlarged (< four times the size of medial postmental scales), one in contact with infralabials; scales in sublabial row much larger than scales medially adjacent to this row; pointed granular scales present on chin and throat; dewlap large, extending from level below anterior margin of eye onto chest; gorgetals homogeneously, those in central portion reduced in size; a nuchal crest and a dorsal ridge present; dorsum of body with keeled, granular scales; 2 medial rows distinctly enlarged, mostly more than twice the size of adjacent body scales; largest dorsal scales about 0.35 x 0.30 mm (length x width); about 50 medial dorsal scales in one head length; about 67 medial dorsal scales between levels of axilla and groin; lateral scales keeled, granular and more or less homogeneous in size, average size 0.12 mm in diameter; ventrals at midbody smooth, flat, almost cycloid, imbricate, about 0.65 x 0.75 mm (length x width); about 40 medial ventral scales in one head length; about 43 medial ventral scales between levels of axilla and groin; 212 scales around midbody; all caudal scales keeled; middorsal caudal scales distinctly enlarged, forming a low crest; lateral caudal scales without whorls of enlarged scales, although an indistinct division in segments is discernible; a pair of greatly enlarged postcloacal scales present, about 1.6 mm wide; no tube-like axillary pocket present; scales on dorsal surface of upper forelimb strongly keeled, mucronate, imbricate; scales on anterior surface of thigh strongly keeled, mucronate, imbricate; digital pads dilated, dilated pad three times the width of non-dilated distal phalanx; distal phalanx narrower than and raised from dilated pad; 31 lamellae under Phalanges II–IV of Toe IV of hind limbs; 10 scales under distal phalanx of Toe IV of hind limbs.

The completely everted hemipenis (Fig. 37) is a medium-sized, slightly bilobate organ; sulcus spermaticus bordered by well-developed sulcal lips and opening into a single large apical field void of ornamentation; an asulcate finger-like processus present; apex strongly calyculate, truncus with transverse folds.

The coloration in life was recorded as follows: dorsal surface Beige (254) with Warm Sepia (40) chevrons on dorsal body; lateral side of body Drab-Gray (256) with a Cyan White (156) longitudinal stripe bordered by Mahogany Red (34) flecks; dorsal surface of limbs Verona Brown (37) with ill-defined Medium Neutral Gray (298) bands; edge of eye lid Pale Horn Color (11); iris Parrot Green (121); dewlap Pale Greenish White (97) with Light Yellow Ocher (13) suffusions; ventral surface of head Smoky White (261); ventral surface of body Pale Buff (1).

Coloration after almost five years preservation in 70 % ethanol was recorded as follows: Dorsal ground color Smoke Gray (267) with Vandyke Brown (281) chevrons; ventral surface of head Cream White (52) with Pale Neutral Gray (296) stipples; ventral surface of body Smoky White (261); ventral surfaces of legs Light Buff (2); ventral surfaces of fingers and toes Dark Brownish Olive (127); surfaces of tail Pale Buff (1) ventrally and Pale Neutral Gray (296) dorsally.

Variation. The paratypes agree well with the holotype in general appearance; morphometrics and scalation (see Table II). In most individuals the longest toe of adpressed hind leg reaching to a point between anterior and posterior level of eye, exceptionally to a point between eye and nostril.

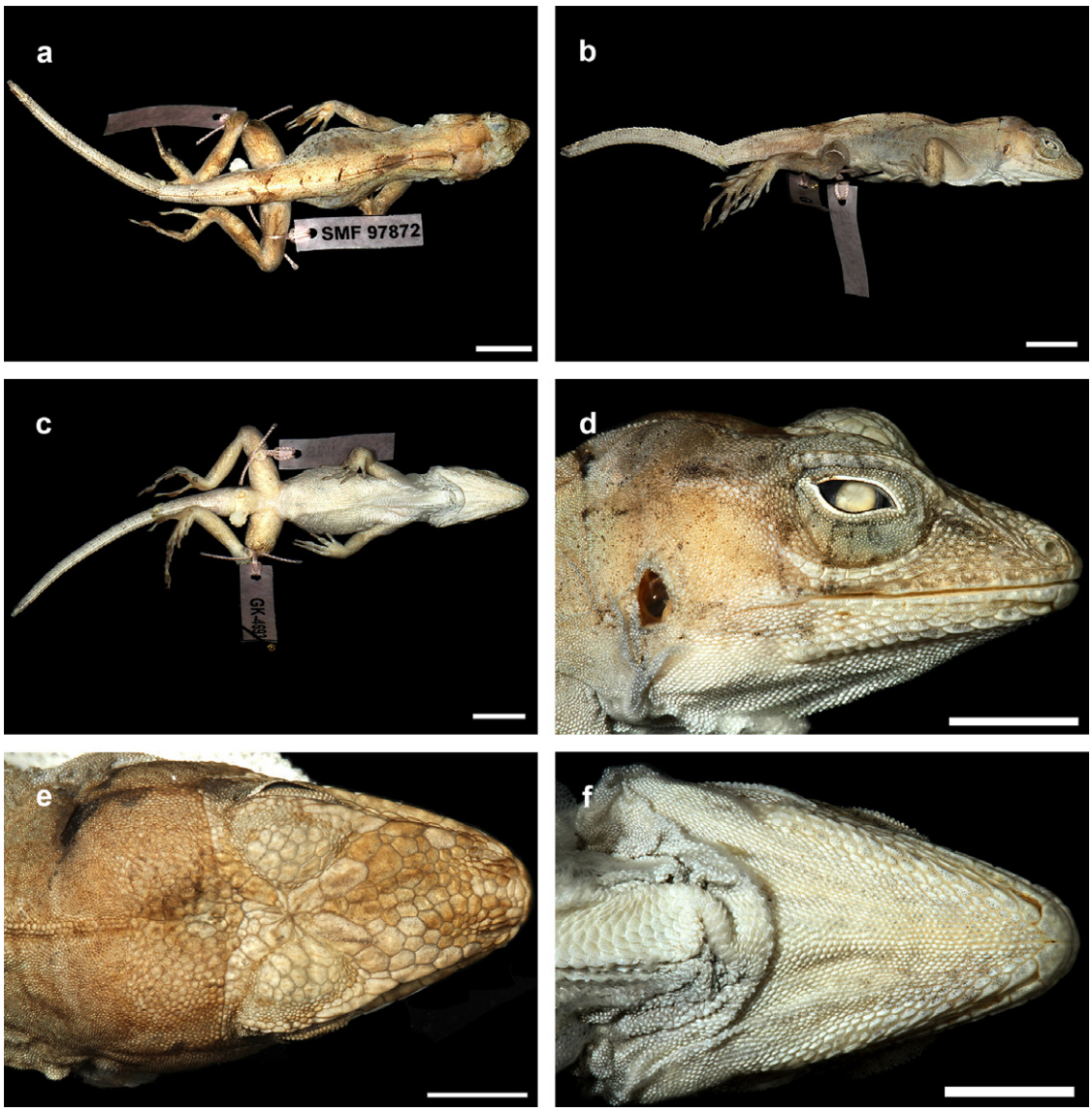

Figure 35. Holotype of *Audantia higuey* (SMF 97872): (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; (f) ventral view of head. Scale bars equal 10.0 mm in (a–c) and 5.0 mm in (d–f), respectively. Photos by Gunther Köhler.

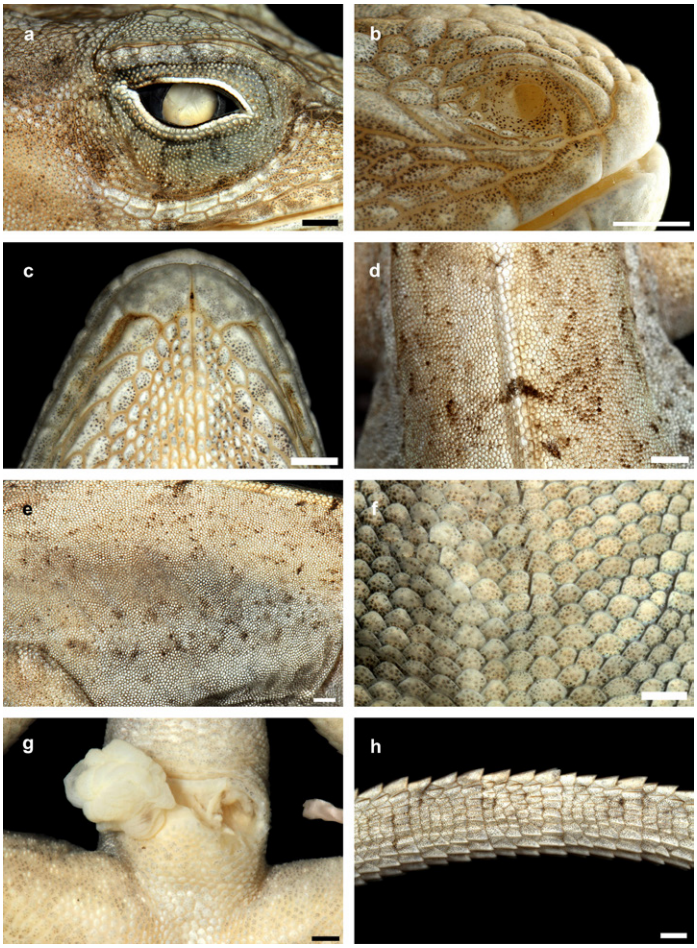

Figure 36. Holotype of *Audantia higuey* (SMF 97872): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region; (e) flank region; (f) midventer; (g) cloacal region; (h) lateral view of tail. Scale bars equal 1.0 mm. Photos by Gunther Köhler.

Figure 37. Hemipenis of *Audantia higuey* (SMF 97872). Scale bar equals 1.0 mm. Photos by Gunther Köhler.

Figure 38. *Audantia higuey* in life. (a) GK-4694, uncatalogued specimen from Manatí Park Bávaro, La Altagracia, Dominican Republic; (b) SMF 97872; (c) MNHNSD 23.3599; (d) SMF 97874. (a) and (b) are males, (c) and (d) are females. Photos by Gunther Köhler.

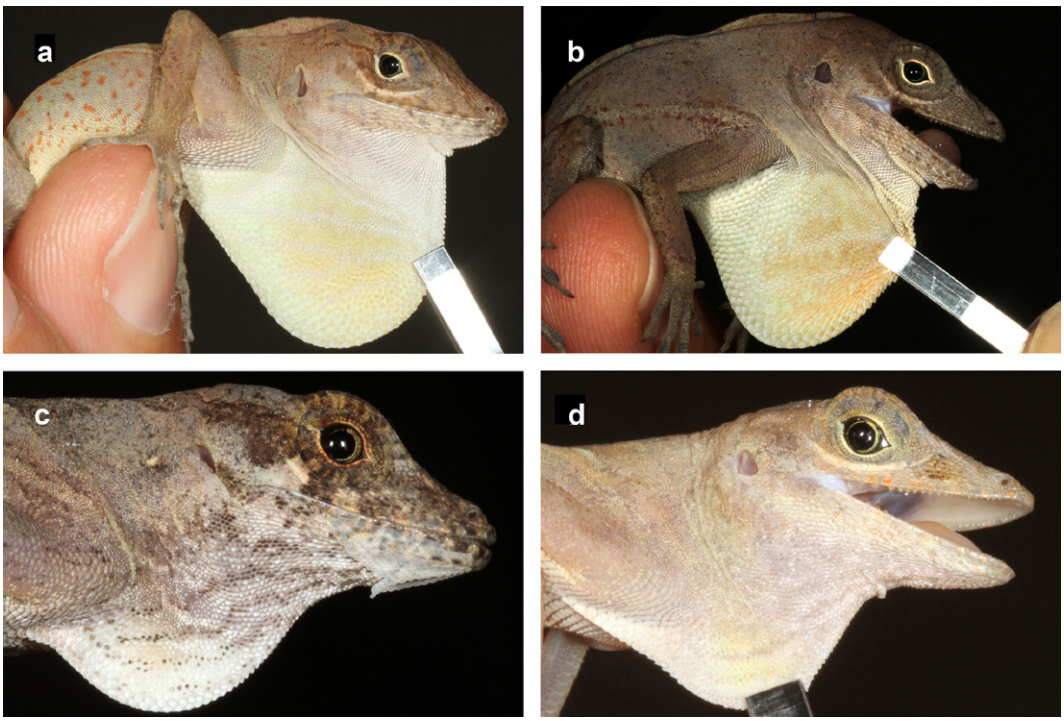

Figure 39. Dewlaps of *Audantia higuey* in life. (a) GK-4694, uncatalogued specimen from Manatí Park Bávaro, La Altagracia, Dominican Republic; (b) SMF 97872; (c) MNHNSD 23.3599; (d) SMF 97874. (a) and (b) are males, (c) and (d) are females. Photos by Gunther Köhler.

Figure 40. Habitat of *Audantia higuey* at 22 km WNW Valle (16 km to Trepada Alta, ca. 6 km by trail to Montebonito), Hato Mayor, Dominican Republic, 75 m a.s.l. (29 June 1985). Photo by S. Blair Hedges.

The coloration in life of an adult female (MNHNSD 23.3599) was recorded as follows: dorsum of head Drab (19); lateral side of body Beige (254) with Medium Plumbeous (294) suffusions posteriorly, and with a Tawny Olive (17) longitudinal stripe and an ill-defined Pratt's Payne's Gray (293) stripe edged by Sepia (279) flecks; dorsal surface of limbs Walnut Brown (27) with indistinct Maroon (39) crossbars; edge of eye lid Light Chrome Orange (76); iris Olive-Green (124); Sepia (279) streaks radiating out from eye; ventral surface of head Smoky White (261) with irregular Olive-Brown (278) streaks; ventral surface of body Light Buff (2).

Etymology. The species name (*higuey*) is a noun in apposition referring to the distribution of the species in eastern Hispaniola, the region of the former Taino kingdom of Higüey.

Geographic distribution. As currently known, *Audantia higuey* is distributed across the eastern portion of the Dominican Republic, from near sea level to 290 m a. s. l. (Fig. 18).

Natural history notes. As typical for most species of this genus, *Audantia higuey* is found in a wide range of environments, and often in disturbed habitats (Fig. 40). There these lizards can be observed perching head-down on bushes and trees. Sleeps at night on leafs of bushes. Henderson & Powell (2009) provided a summary of the natural history of "*Anolis cybotes*" which under our concept is represented by several species.

Conservation. Given its geographic range and capability to live in anthropogenically disturbed habitats, we consider the conservation status of *Audantia higuey* to be Least Concern based on the IUCN Red List Categories and Criteria (IUCN, 2012).

***Audantia australis* sp. nov.**
Southern Stout Anole
ZOOBANK urn:lsid:zoobank.org: act:95668B57-FEB7-465F-A34E-9465545C5362.
Figs. 41–43

Anolis cybotes: Boulenger, 1885 (in part.); Schmidt, 1921 (in part.); Cochran, 1928 (in part.); Barbour & Loveridge, 1929 (in part.); Barbour, 1930a (in part.); Barbour, 1930b (in part.); Schwartz & Thomas, 1975 (in part.); Schwartz, 1979 (in part.); Wyles & Gorman, 1980 (in part.); Schwartz, 1980 (in part.); Henderson *et al.,* 1984 (in part.); Henderson & Schwartz, 1984 (in part.); Schwartz, 1989 (in part.); Burnell & Hedges, 1990 (in part.); Powell *et al*., 1996 (in part.); Queiroz *et al.*, 1998 (in part.); Powell *et al.*, 1999 (in part.); Poe, 2004 (in part.); Nicholson *et al.*, 2005 (in part.); Henderson & Powell, 2009 (in part.); Boistel *et al.*, 2011 (in part.); Kolbe *et al*., 2011 (in part.); Poe, 2013 (in part.); Köhler, 2014 (in part.); Muñoz *et al*., 2014a (in part.); Klaczko *et al.*, 2015 (in part.); Giovannotti *et al.,* 2017 (in part.); Poe *et al.*, 2017 (in part.).

Anolis cybotes cybotes: Cochran, 1934 (in part.); Barbour, 1935 (in part.); Barbour, 1937 (in part.); Cochran, 1941 (in part.); Schwartz & Thomas, 1975 (in part.); MacLean *et al*., 1977 (in part.); Schwartz & Henderson, 1991 (in part.); Fobes *et al*., 1993 (in part.); Powell *et al*., 1999 (in part.); Powell & Henderson, 2012 (in part.).

Audantia cybotes: Nicholson *et al.*, 2014 (in part.); Nicholson *et al.*, 2012 (in part.); Nicholson *et al.*, 2018 (in part.).

Ctenonotus cybotes: Savage & Guyer, 1989 (in part.).

Holotype. SMF 104272, an adult male from 9.4 km S of Aceitillar (26.6 km N of Cabo Rojo) (18.1083, -71.6200), 710 m, Province Pedernales, Dominican Republic; collected 26 July 1991 by S. Blair Hedges, Nicholas Plummer, and Richard Thomas. Field tag number SBH-192576.

Paratypes. SMF 104273, USNM 575285–86, same collecting data as holotype; SMF 104274-75, USNM 575287, from 18.2 km N. Pedernales at stream (Los Arroyos border road) (18.155; -71.75), 200 m, Province Pedernales, Dominican Republic; collected 20 August 2015 by S. Blair Hedges, Matthew Heinicke, and Nicolás Corona; SMF 104276, near Altagracia (18.19389; -71.73306), 670 m, Province Pedernales, Dominican Republic; collected 20 August 2015 by S. Blair Hedges, Matthew Heinicke, and Nicolás Corona; SMF 104277, Mencía-Altagracia road, 1 km S Altagracia (18.1781; -71.72965), 700 m, collected 20 August 2015 by S. Blair Hedges, Matthew Heinicke, and Nicolás Corona. All paratypes are adult males except SMF 104274–75, USNM 575287, 575285 that are adult females, and USNM 575286 in which the sex was not determined.

Diagnosis. A species of the genus *Audantia* (our Species 3 "*australis*") that differs from all congeners by the combination of having (1) smooth ventral scales; (2) male dewlap dirty white with yellowish or orange suffusions, and with homogeneously distributed gorgetal scales, reduced in size in central portion of dewlap; (3) dark gular streaks present in males; (4) no patch of enlarged scales in nuchal region; (5) a double row of weakly enlarged, usually less than twice the size of adjacent scales, non-mucronate vertebral scales; (6) usually one sublabial scale in contact with infralabials; (7) 206–240 scales around midbody in males; and (8) keeled scales on dorsal surfaces of upper forelimb and anterior surface of thigh.

Audantia australis differs from *A. armouri, A. breslini, A. shrevei,* and *A. saxatilis* by having dark gular streaks (usually absent); and by having one or two well-defined pale longitudinal lateral stripes, usually edged with orange or olive-green (vs. such stripes absent).

Audantia australis differs further from *A. armouri* by having 206–240 scales around midbody in males (vs. 118–172). *Audantia australis* differs further from *A. shrevei* by lacking a patch of greatly enlarged scales in nuchal region (vs. such a patch present). *Audantia australis* differs from *A. cybotes* by having smooth ventral scales (vs. keeled, smooth in some individuals); by having a double row of only weakly enlarged, usually less than twice the size of adjacent scales, non-mucronate vertebral scales (vs. greatly enlarged, at least three times the size of adjacent scales, and mucronate); by having a dirty white male dewlap with yellowish or orange suffusions (vs. suffusions absent); and by having smaller gorgetal scales in central region of dewlap (vs. all large). *Audantia australis* differs from *A. doris* by having dark gular streaks (usually absent); by having a male dewlap with homogeneously distributed, narrowly spaced gorgetal scales (vs. heterogeneously distributed with groups of cluttered scales); and by having 206–240 scales around midbody in males (vs. 166–184). *Audantia australis* differs from *A. marcanoi* and *A. strahmi* by having a dirty white male dewlap with yellowish or orange suffusions (vs. rose-red at the edge, more orangish anteriorly and posteriorly, but purplish or even bluish toward the center in *A. marcanoi*, and orange with paler center in *A. strahmi*). *Audantia australis* differs further from *A. marcanoi* by having a well-defined double row of enlarged vertebral scales (vs. vertebral scales gradually enlarged, not forming a regular double row). *Audantia australis* differs from *A. hispaniolae* and *A. longitibialis* by having a male dewlap with homogeneously distributed gorgetal scales, all large on posterior half of dewlap (vs. heterogeneously distributed, somewhat spaced, and with groups of cluttered scales, scales smaller in central region of dewlap or all gorgetals small). *Audantia australis* differs further from *A. hispaniolae* by having 180–222 scales around midbody in males (vs. 214–244); and by lacking yellowish or orange suffusions on male dewlap (vs. often present). *Audantia australis* differs from *A. higuey* by having dark gular streaks (vs. absent); by having a weakly keeled double row of only weakly enlarged, usually less than twice the size of adjacent scales vertebrals scales (vs. strongly keeled and greatly enlarged, at least three times the size of adjacent scales); and by having 206–240 scales around midbody in males (vs. 166–212). *Audantia australis* differs from *A. ravifaux* by having keeled scales on dorsal surface of upper forelimb and anterior surface of thigh (vs. smooth); by having homogeneously distributed gorgetals and the upper portion of dewlap mostly covered by scales with little free skin (vs. heterogeneously distributed gorgetals with groups of cluttered scales, widely spaced); and by having one or two well-defined pale longitudinal lateral stripes, usually edged with orange or olive-green (vs. such stripes absent). For differences between *A. australis* and the species described below, see the respective accounts of the new species.

Description of the holotype. Adult male (Figs. 41–42), as indicated by well-developed dewlap, and presence of a pair of greatly enlarged postcloacal scales; SVL 69.0 mm; tail length 128.0 mm (complete); tail distinctly compressed in cross section, tail height 4.2 mm and width 2.5 mm; axilla to groin distance 26.6 mm; head length 21.3 mm, head length/SVL ratio 0.31; snout length 9.2 mm; head width 12.3 mm; longest toe of adpressed hind limb reaching to level of anterior margin of eye; shank length 20.2 mm, shank length/head length ratio 0.95; longest finger of extended forelimb reaching to tip of snout; longest finger of adpressed forelimb reaching to 5 mm past anterior insertion of hind limbs. Dorsal head scales smooth or rugose, except weakly keeled scales on snout and supraoculars; 7 postrostrals; 6 scales between nasals; 1 elongate prenasal scale on each side, distinct from circumnasal and in contact with both rostral and first supralabial; circumnasal separated from first supralabial by one scale; scales in deep prefrontal depression smooth or rugose; supraorbital semicircles well-developed, narrowly in contact medially; supraorbital disc composed of 2 to 3 moderately enlarged, keeled scales arranged in three rows; circumorbital row complete, therefore, enlarged supraorbital scales separated from supraorbital semicircles; a very large elongated superciliary,

followed posteriorly by a much smaller, overlapping one and by several small, keeled scales; three rows of small keeled scales extending between enlarged supraorbitals and large superciliary; a deep parietal depression present; interparietal scale well-developed, 2.9 x 1.4 mm (length x width), surrounded by scales of moderate size; 2 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 3 large and 3 small anterior canthal scales; 8 scales present between second canthals; 12 scales present between posterior canthals; 53 (right)–57 (left) mostly keeled loreal scales in a maximum of 7(right)–8 (left) horizontal rows; 7 to 8 keeled subocular scales arranged in a single row; 6 supralabials to level below center of eye; suboculars separated from supralabials by a complete scale row; ear opening 2.0 x 2.6 mm (length x height); mental distinctly wider than long, almost completely divided medially, bordered posteriorly by 6 postmentals, outer ones much larger than median ones; 6 infralabials to level below center of eye; sublabials greatly enlarged (< four times the size of medial postmental scales), one in contact with infralabials; scales in sublabial row much larger than scales medially adjacent to this row; pointed granular scales present on chin and throat; dewlap large, extending from level below anterior margin of eye onto chest; gorgetals heterogeneously distributed with groups of cluttered scales, those in central portion reduced in size; a nuchal crest and a dorsal ridge present; dorsum of body with keeled, granular scales; 2 medial rows distinctly enlarged, mostly more than twice the size of adjacent body scales; largest dorsal scales about 0.35 x 0.30 mm (length x width); about 52 medial dorsal scales in one head length; about 81 medial dorsal scales between levels of axilla and groin; lateral scales keeled, granular and more or less homogeneous in size, average size 0.12 mm in diameter; ventrals at midbody smooth, flat, almost cycloid, imbricate, about 0.65 x 0.75 mm (length x width); about 42 medial ventral scales in one head length; about 56 medial ventral scales between levels of axilla and groin; 240 scales around midbody; ventral basal caudal scales smooth, all other caudal scales keeled; middorsal caudal scales distinctly enlarged, forming a low crest; lateral caudal scales with whorls of enlarged scales; a pair of greatly enlarged postcloacal scales present, about 1.7 mm wide; no tube-like axillary pocket present; scales on dorsal surface of upper forelimb strongly keeled, mucronate, imbricate; scales on anterior surface of thigh strongly keeled, mucronate, imbricate; digital pads dilated, dilated pad three times the width of non-dilated distal phalanx; distal phalanx narrower than and raised from dilated pad; 32 lamellae under Phalanges II–IV of Toe IV of hind limbs; 9 scales under distal phalanx of Toe IV of hind limbs.

The coloration in life was recorded as follows: dorsum of head Cinnamon Drab (259); lateral side of body Cinnamon Drab (50) with a Pale Emerald Green (141) longitudinal stripe bordered by Mahogany Red (34) lines, and an indistinct dorsolateral Yellowish Olive-Green (118) stripe; dorsal surface of limbs Verona Brown (37) with indistinct Maroon (39) crossbars on hind limbs; edge of eye lid Whitish Lime Green (111); iris Hooker's Green; dewlap Light Flesh Color (250) with weak Sepia (279) streaks; ventral surface of head Smoky White (261) with irregular, weak Sepia (279) streaks; ventral surface of body Light Flesh Color (250).

Coloration after 27 years preservation in 70 % ethanol was recorded as follows: Dorsal ground color Hair Brown (277) with a Fuscous (283) vertebral line; ventral surface of head Smoke Gray (266); ventral surface of body Glaucous (289) with Brownish Olive (276) speckles; ventral surfaces of legs Cinnamon-Drab (50) with Prout`s Brown (47) speckles; ventral surfaces of fingers and toes Grayish Horn Color (268); dorsal, lateral and ventral surfaces of tail Raw Umber (280).

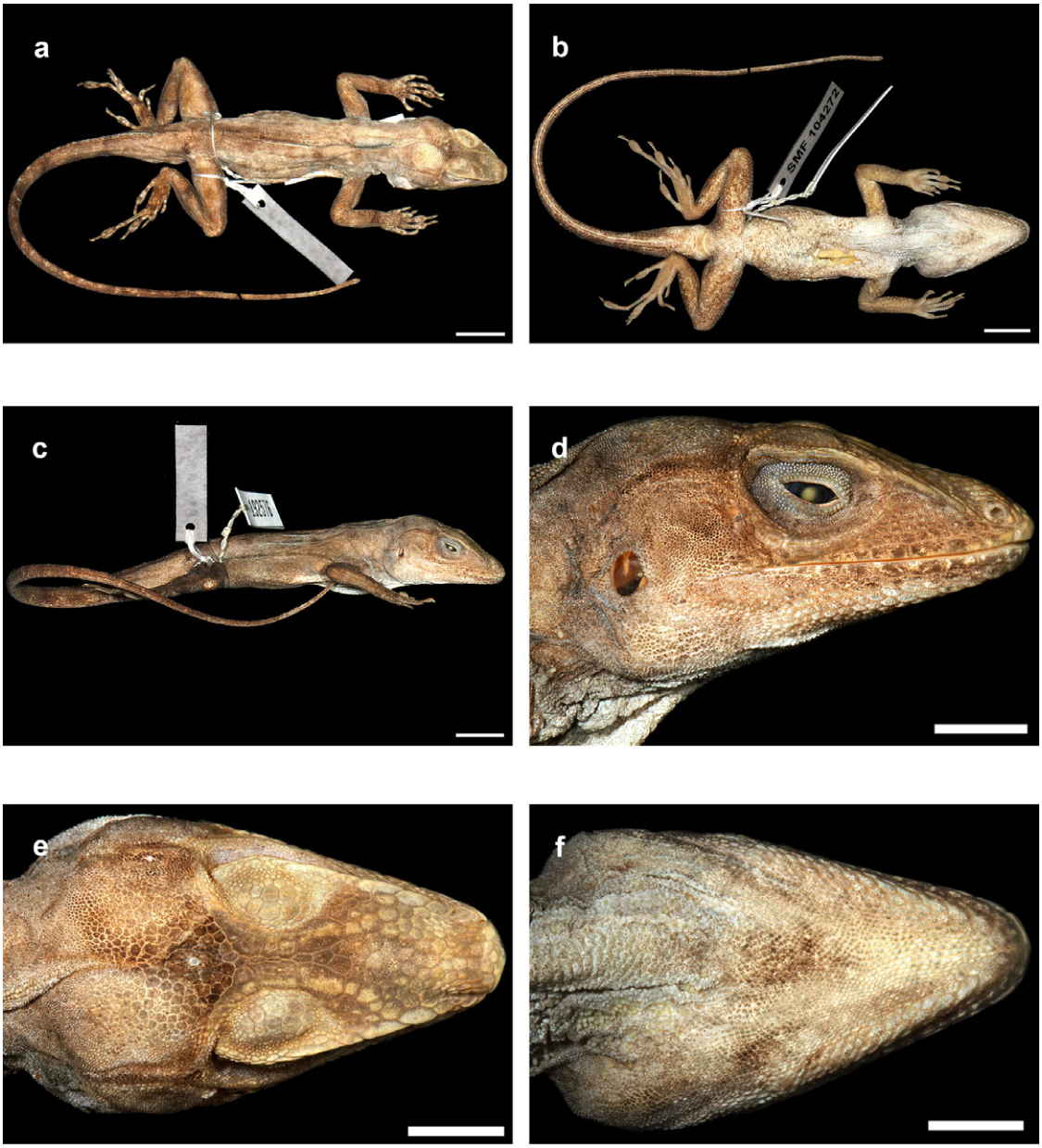

Figure 41. Holotype of *Audantia australis* (SMF 104272): (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; (f) ventral view of head. Scale bars equal 10.0 mm in (a–c) and 5.0 mm in (d–f), respectively. Photos by Gunther Köhler.

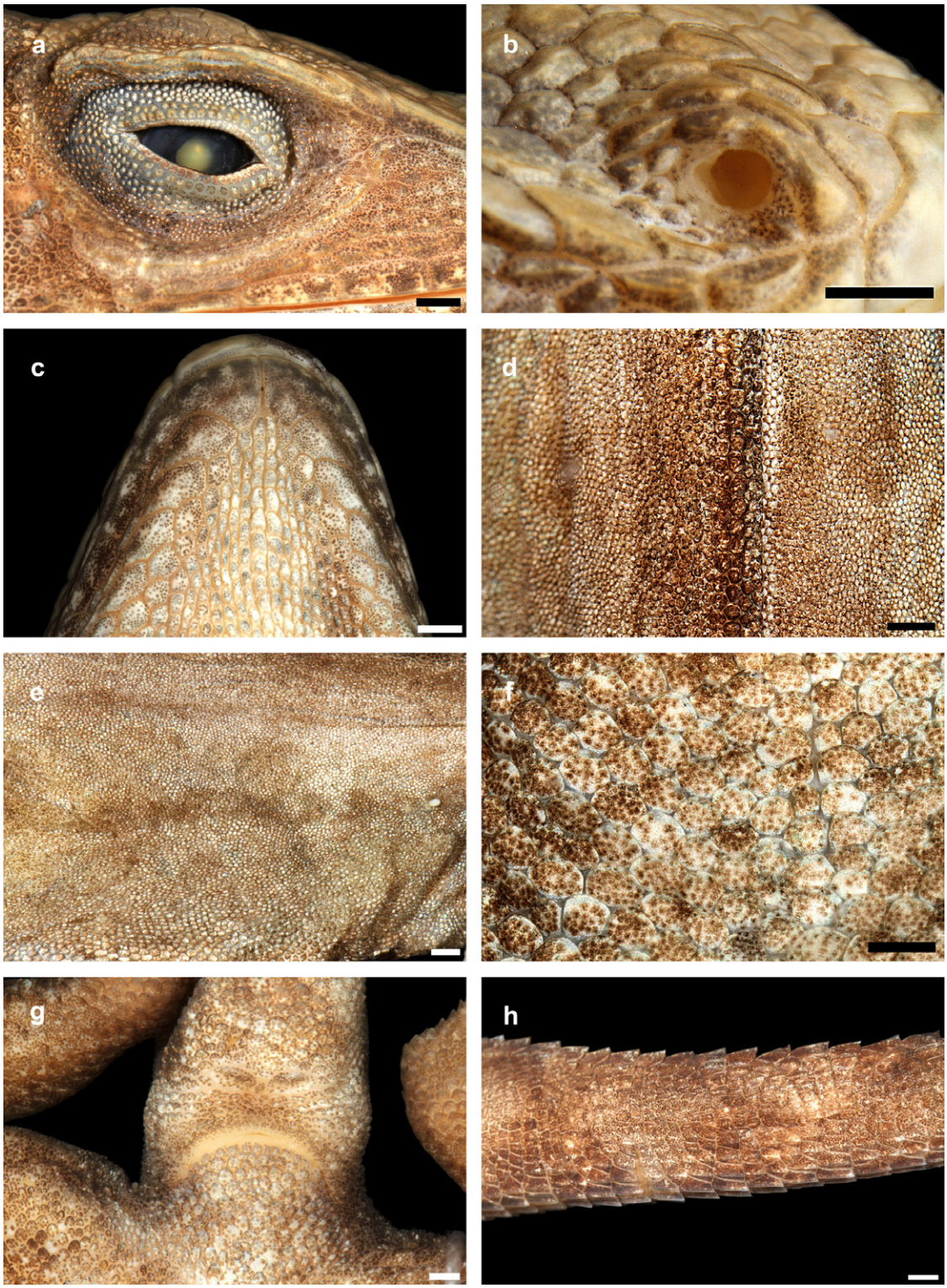

Figure 42. Holotype of *Audantia australis* (SMF 104272): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region; (e) flank region; (f) midventer; (g) cloacal region; (h) lateral view of tail. Scale bars equal 1.0 mm. Photos by Gunther Köhler.

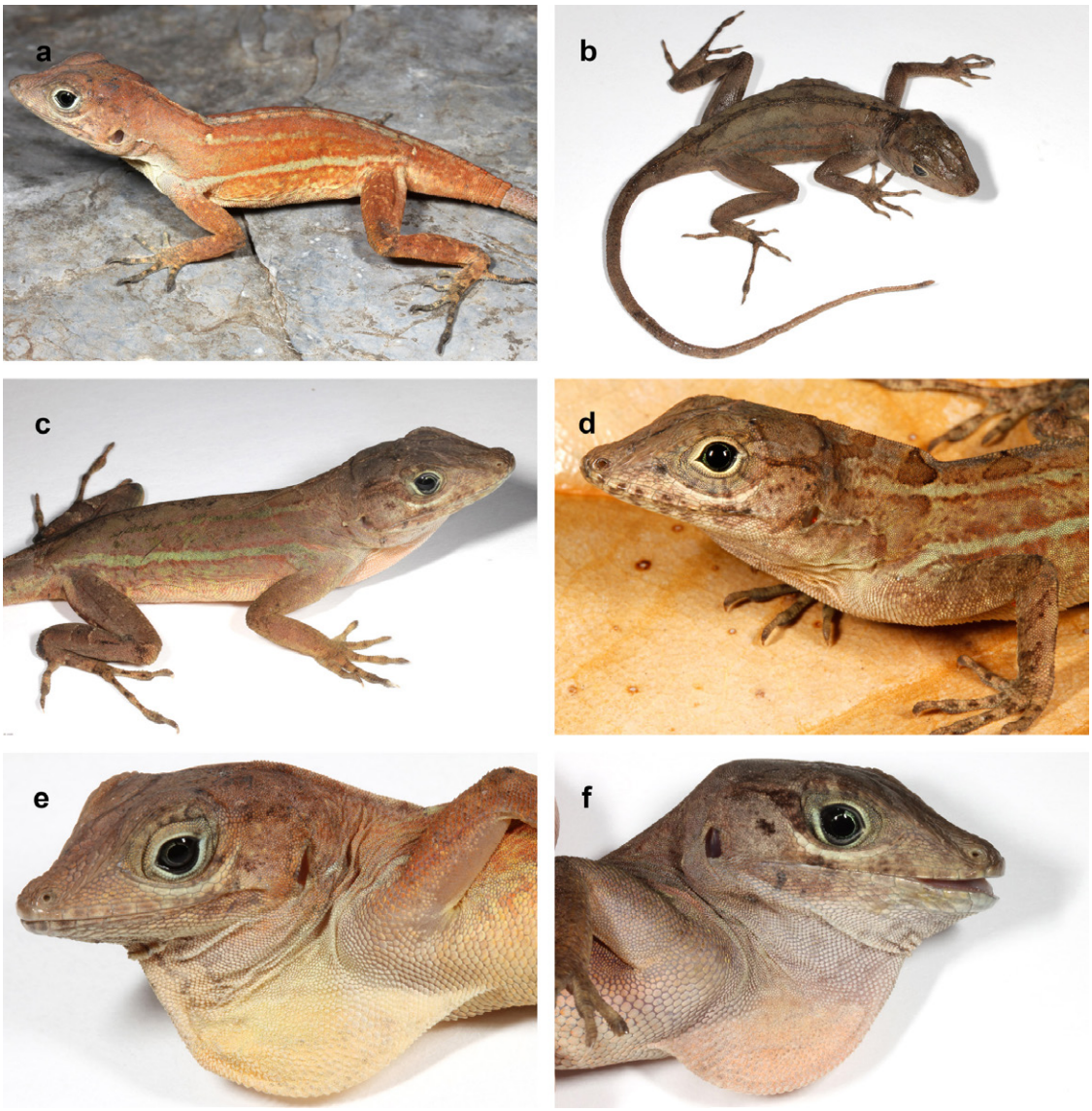

Figure 43. *Audantia australis* in life (all males). (a) SMF 104285; (b) SMF 104287; (c) SMF 104291; (d) SMF 104293; (e) SMF 104285; (f) SMF 104291. Photos by S. Blair Hedges.

Figure 44. Habitat of *Audantia australis.* (a, b) Los Arroyos, Pedernales, Dominican Republic, 1 265 m a.s.l. (31 October 2013); (c, d) road to Pelempito, Pedernales, Dominican Republic, 755 m a.s.l. (27 October 2013). Photos by Gunther Köhler.

Variation. The paratypes agree well with the holotype in general appearance (see also Fig. 43); morphometrics and scalation (see Table II). In most individuals the longest toe of adpressed hind leg reaching to a point between anterior and posterior level of eye, exceptionally to a point between eye and nostril or ear and eye.

Etymology. The species name (*australis*) is an adjective meaning "southern," referring to the distribution of the species on the southern paleo-island of Hispaniola.

Geographic distribution. As currently known, *Audantia australis* is restricted to the central and eastern portions of the Tiburón Peninsula, Haiti and adjacent areas in the Dominican Republic south of the Sierra de Bahoruco from near sea level to 1630 m a. s. l. (Fig. 18).

Natural history notes. As typical for the species in this genus, *Audantia australis* occurs in a wide array of habitats including secondary forest and within villages (Fig. 44). It was found sleeping at night on leaves of bushes about 1 m above ground.

Conservation. Given its geographic range and capability to live in anthropogenically disturbed habitats, we consider the conservation status of *Audantia australis* to be Least Concern based on the IUCN Red List Categories and Criteria (IUCN, 2012).

***Audantia aridius* sp. nov.**
Desert Stout Anole
ZOOBANK urn:lsid:zoobank.org: act:D83E799C-483C-4A66-8F9E-AC83A9A40743.
Figs. 46–48

Anolis cybotes: Boulenger, 1885 (in part.); Schmidt, 1921 (in part.); Barbour & Loveridge, 1929 (in part.); Barbour, 1930a (in part.); Barbour, 1930b (in part.); Schwartz & Thomas, 1975 (in part.); Schwartz, 1979 (in part.); Wyles & Gorman, 1980 (in part.); Schwartz, 1980 (in part.); Henderson *et al*., 1984 (in part.); Henderson & Schwartz, 1984 (in part.); Schwartz, 1989 (in part.); Burnell & Hedges, 1990 (in part.); Powell *et al*., 1996 (in part.); Queiroz *et al.*, 1998 (in part.); Cast *et al.,* 2000; Sifers *et al.,* 2001 (in part.); Poe, 2004 (in part.); Nicholson *et al.*, 2005 (in part.); Henderson & Powell, 2009 (in part.); Boistel *et al.*, 2011 (in part.); Kolbe *et al*., 2011 (in part.); Poe, 2013 (in part.); Wollenberg *et al.,* 2013 (in part.); Köhler, 2014 (in part.); Muñoz *et al*.,2014a (in part.); Muñoz *et al*., 2014b (in part.); Klaczko *et al.*, 2015 (in part.); Conover *et al.,* 2015 (in part.); Giovannotti *et al*., 2017 (in part.); Poe *et al.*, 2017 (in part.); Boronow *et al.*, 2018 (in part.); Kahrl *et al.,* 2018 (in part.).

Anolis cybotes cybotes: Cochran, 1934 (in part.); Barbour, 1935 (in part.); Barbour, 1937 (in part.); Mertens, 1938 (in part.); Mertens, 1939 (in part.); Cochran, 1941 (in part.); Schwartz & Thomas, 1975 (in part.); MacLean *et al*., 1977 (in part.); Schwartz & Henderson, 1991 (in part.); Fobes *et al.*, 1993 (in part.); Powell & Henderson, 2012 (in part.).

Audantia cybotes: Nicholson *et al.*, 2014 (in part.); Nicholson *et al.*, 2012 (in part.); Nicholson *et al.*, 2018 (in part.).

Ctenonotus cybotes: Savage & Guyer, 1989 (in part.)

Holotype. SMF 97896, an adult male from near Cortico (18.11163, -71.22293), 1340 m, Province Barahona, Dominican Republic; collected 31 October 2013 by Gunther Köhler. Field tag number GK-4823.

Paratypes. All from Barahona Province, Dominican Republic: SMF 97895, Barahona, Hotel Costa Larimar (18.199622; -71.086953), 10 m, collected 29 October 2013 by Gunther Köhler; SMF 97892–94, Los Lirios (18.11345; -71.2617), 1110 m, collected 29 October 2013 by Gunther Köhler; MNHNSD 23.3620, near Polo (18.1135; -71.26964), 855 m, collected 31 October 2013 by Gunther Köhler; SMF 104162-63, 2.9 miles NW La Ciénaga (18.07022; -71.12332), 355 m, collected 30 July 1999 by locals; USNM 329093 11.3 km S Barahona (measured from Hotel Caribe) (18.1172;-71.0717), 20 m, collected 20 August 1984 by S. Blair Hedges and Richard Thomas; USNM 329090-92, 20.8 km S Cabral (18.0964; -71.2819), 975 m, collected 19 August 1984 by S. Blair Hedges and Richard Thomas; USNM 329089, ca. 6–7 km NW Paraíso (18.0274; -71.1920), 180 m, collected 13 August 1983 by S. Blair Hedges. All paratypes are adult males except MNHNSD 23.3620 and USNM 329090 which are adult females, and USNM 329089 and 329093 in which the sex was not determined.

Diagnosis. A species of the genus *Audantia* (our Species 4 "*aridius*") that differs from all congeners by the combination of having (1) smooth ventral scales; (2) male dewlap dirty white with yellowish or orange suffusions, and with homogeneously distributed gorgetal scales, reduced in size in central portion of dewlap; (3) no dark gular streaks in males; (4) no patch of enlarged scales in nuchal region; (5) a double row of greatly enlarged, at least three times the size of adjacent scales, non-mucronate vertebral scales; (6) usually two to three sublabial scale in contact with infralabials; (7) 186–234 scales around midbody in males; and (8) keeled scales on dorsal surfaces of upper forelimb and anterior surface of thigh.

Audantia aridius differs from *A. armouri* by having one or two well-defined pale longitudinal lateral stripes, usually edged with orange or olive-green (vs. such stripes absent); by having widley spaced gorgetals (vs. moderately spaced gorgetals); by having a double row of greatly enlarged vertebral scales, at least three times the size of adjacent scales (vs. those scales only weakly enlarged, usually less than twice the size of adjacent scales); and by having 184–234 scales around midbody in males (vs. 118–172).

Audantia aridius differs from *A. breslini* and *A. shrevei* by having smooth ventral scales (vs. usually keeled); by having dark gular streaks (usually absent); by having one or two well-defined pale longitudinal lateral stripes, usually edged with orange or olive-green (vs. such stripes absent); and by having a double row of greatly enlarged vertebral scales, at least three times the size of adjacent scales (vs. those scales only weakly enlarged, usually less than twice the size of adjacent scales). *Audantia aridius* differs further from *A. shrevei* by lacking a patch of greatly enlarged scales in nuchal region (vs. such a patch present). *Audantia aridius* differs from *A. cybotes* by having smooth ventral scales (vs. keeled, some individuals of *A. cybotes* with smooth ventrals); by lacking dark gular streaks on male dewlap (vs. those present); by having yellowish or orange suffusions (vs. absent); by having widely spaced gorgetals and scales reduced in size in central portion of dewlap (vs. all scales narrowly spaced and large on posterior half of dewlap); and by having non-mucronate vertebral scales (vs. mucronate). *Audantia aridius* differs from *A. doris* and *A. hispaniolae* by having homogeneously distributed gorgetals (vs. heterogeneously distributed with groups of cluttered scales). *Audantia aridius* differs further from *A. doris* by having one or two well-defined pale longitudinal lateral stripes, usually edged with orange or olive-green (vs. such stripes absent); by having yellowish or orange suffusions on male dewlap (vs. no suffusions, but with an orange blotch in center of dewlap); by having 186–234 scales around midbody in males (vs. 166–184); and by having non-mucronate vertebral scales (vs. mucronate). *Audantia aridius* differs further from *A. hispaniolae* by lacking dark gular streaks (vs. present). *Audantia aridius* differs from *A. marcanoi* and *A. strahmi* by having a dirty white male dewlap with yellowish or orange suffusions (vs. rose-red at the edge, more orangish anteriorly and posteriorly, but purplish or even bluish toward the center in *A. marcanoi*, and orange with paler center in *A. strahmi*). *Audantia aridius* differs further from *A. marcanoi* by having a well-defined double row of enlarged vertebral scales (vs. vertebral scales gradually enlarged, not forming a regular double row). *Audantia aridius* differs from *A. longitibialis* by having a male dewlap with homogeneously distributed gorgetal scales, that are smaller in central region of dewlap (vs. heterogeneously distributed with groups of cluttered scales, all gorgetals small); and by having yellowish or orange suffusions (vs. absent). *Audantia aridius* differs from *A. ravifaux* by having keeled scales on dorsal surface of upper forelimb and anterior surface of thigh (vs. smooth); by having homogeneously distributed gorgetals (vs. heterogeneously distributed with groups of cluttered scales); by having a double row of greatly enlarged vertebral scales, at least three times the size of adjacent scales (vs. those scales only weakly enlarged, usually less than twice the size of adjacent scales); and by having one or two well-defined pale longitudinal lateral stripes, usually edged with orange or olive-green (vs. such stripes absent). *Audantia aridius* differs from *A. saxatilis* by having smooth ventral scales (vs. keeled); by having yellowish or orange suffusions (vs. absent); and by having a male dewlap with gorgetal scales, that are smaller in central region of dewlap (vs. all gorgetals small). *Audantia aridius* differs from *A. australis* and *A. higuey* by having widely spaced gorgetals, so more skin is more uncovered than covered by gorgetals (vs. upper portion of dewlap mostly covered by gorgetals with little free skin). *Audantia aridius* differs further from *A. australis* by lacking dark gular streaks (vs. present); and by having a double row of greatly enlarged, at least three times the size of adjacent scales, vertebral scales (vs. weakly enlarged, usually less than twice the size of adjacent scales). For differences between *A. aridius* and the species described below, see the respective accounts of the new species.

Description of the holotype. Adult male (Figs. 46–47), as indicated by everted hemipenes, well-developed dewlap, and presence of a pair of greatly enlarged postcloacal scales; SVL 70.0 mm; tail length 78.0 mm (incomplete); tail distinctly compressed in cross section, tail height 4.5 mm and width 3.3 mm; axilla to groin distance 24.3 mm; head length 21.8 mm, head length/SVL ratio 0.31; snout length 9.2 mm; head width 12.6 mm; longest toe of adpressed hind limb reaching to a point between eye and nostril; shank length 22.2 mm, shank length/head length ratio 1.02; longest finger of extended forelimb reaching to a point 1.0 mm in front of tip of snout; longest finger of adpressed forelimb reaching to a point 6.6 mm past level of anterior insertion of hind limbs. Dorsal head scales smooth or rugose, except weakly keeled supraoculars; 6 postrostrals; 6 scales between nasals; 1 elongate prenasal scale on each side, fused with circumnasal and in contact with both rostral and first supralabial; circumnasal separated from first supralabial by one scale; scales in deep prefrontal depression smooth or rugose; supraorbital semicircles well-developed, broadly in contact medially; supraorbital disc composed of 4 to 5 moderately enlarged, keeled scales arranged in three rows; circumorbital row incomplete, therefore, some enlarged supraorbital scales in contact with supraorbital semicircles; a very large elongated superciliary, followed posteriorly by a much smaller, overlapping one and by six small, keeled scales; three rows of small keeled scales extending between enlarged supraorbitals and large superciliary; a deep parietal depression present; interparietal scale well-developed, 2.1 x 1.3 mm (length x width), T-shaped, surrounded by scales of moderate size; 2 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 3 large and 3 small anterior canthal scales; 8 scales present between second canthals; 8 scales present between posterior canthals; 34 (right)–32 (left) mostly keeled loreal scales in a maximum of 6 horizontal rows; 7 to 8 keeled subocular scales arranged in a single row; 7 supralabials to level below center of eye; suboculars separated from supralabials by a complete scale row; ear opening 1.6 x 2.2 mm (length x height); mental distinctly wider than long, almost completely divided medially, bordered posteriorly by 6 postmentals, outer ones much larger than median ones; 6 (right)–7 (left) infralabials to level below center of eye; sublabials greatly enlarged (< four times the size of medial postmental scales), two in contact with infralabials; scales in sublabial row much larger than scales medially adjacent to this row; pointed granular scales present on chin and throat; dewlap large, extending from level below anterior margin of eye onto chest; dewlap more or less homogeneously covered with moderate-sized, widely spaced gorgetal scales, those in central portion reduced in size; a nuchal crest and a dorsal ridge present; dorsum of body with keeled, granular scales; 2 medial rows distinctly enlarged, more than twice the size of adjacent body scales; largest dorsal scales about 0.60 x 0.50 mm (length x width); about 48 medial dorsal scales in one head length; about 62 medial dorsal scales between levels of axilla and groin; lateral scales keeled, granular and more or less homogeneous in size, average size 0.18 mm in diameter; ventrals at midbody smooth, flat, almost cycloid, imbricate, about 0.70 x 0.70 mm (length x width); about 38 medial ventral scales in one head length; about 50 medial ventral scales between levels of axilla and groin; 220 scales around midbody; all caudal scales keeled; middorsal caudal scales distinctly enlarged, forming a low crest; lateral caudal scales with whorls of enlarged scales; a pair of greatly enlarged postcloacal scales present, about 2.0 mm wide; no tube-like axillary pocket present; scales on dorsal surface of upper forelimb strongly keeled, mucronate, imbricate; scales on anterior surface of thigh strongly keeled, mucronate, imbricate; digital pads dilated, dilated pad twice the width of non-dilated distal phalanx; distal phalanx narrower than and raised from dilated pad; 28 lamellae under Phalanges II–IV of Toe IV of hind limbs; 10 (right; missing distal phalanx left) scales under distal phalanx of Toe IV of hind limbs.

Coloration after 5 years preservation in 70 % ethanol was recorded as follows: Dorsal ground color Glaucous (272) with Hair Brown (277) chevrons; ventral surface of head Pale Greenish White (97); dewlap Cream White (52) with Light Neutral Gray (297) stipples; ventral surface of body Paris White (139); ventral surfaces of legs Light Buff (2) with Beige (254) stipples; ventral surfaces of fingers and toes Glaucous (289) with Hair Brown (277) tips; surfaces of tail Pale Buff (1) ventrally and Pale Neutral (296) dorsally.

Variation. The paratypes agree well with the holotype in general appearance; morphometrics and scalation (Table II). In most individuals the longest toe of adpressed hind leg reaching to a level of anterior margin of eye, exceptionally to a point between eye and nostril.

The coloration in life of an adult male (SMF 97894) was recorded as follows: lateral side of body Cinnamon Drab (259) with Vinaceous (247) suffusions edging an Olive Horn Color (16) longitudinal stripe; dorsal surface of limbs Verona Brown (37) with indistinct Mars Brown (25) cross bars; edge of eye lid Cream Color (12); iris Dark Brownish Olive (127); dewlap Smoky White (261) with Light Buff (2) suffusions; ventral surface of head Smoky White (261); ventral surface of body Pale Buff (1).

The completely everted hemipenis (SMF 97896; Fig. 48) is a medium-sized, slightly bilobate organ; sulcus spermaticus bordered by well-developed sulcal lips and opening into a single large apical field void of ornamentation; an asulcate ridge present; apex strongly calyculate, truncus with transverse folds. The everted hemipenis of two other specimens (SMF 97892–93) agree well with this description

Etymology. The species name (*aridius*) is a noun in apposition derived from the Latin adjective *aridus* ("dry"), in allusion to the arid habitats where this species occurs.

Geographic distribution. As currently known, *Audantia aridius* is restricted to the eastern portion of the Barahona Peninsula, Dominican Republic, from near sea level to 1340 m a. s. l. (Fig. 18).

Natural history notes. The habitat near the type locality of *Audantia aridius* is disturbed broadleaf forest (Fig. 49). We observed and collected this species mostly perched on rocks and low vegetation during daytime.

Also, it was commonly found on and under rocks, or on tree trunks low to the ground, during the day. At night these lizards can be found sleeping on branches and on the upper suface of leafs as it is typical for most anoles.

Conservation. Given its geographic range and capability to live in anthropogenically disturbed habitats, we consider the conservation status of *Audantia aridius* to be Least Concern based on the IUCN Red List Categories and Criteria (IUCN, 2012).

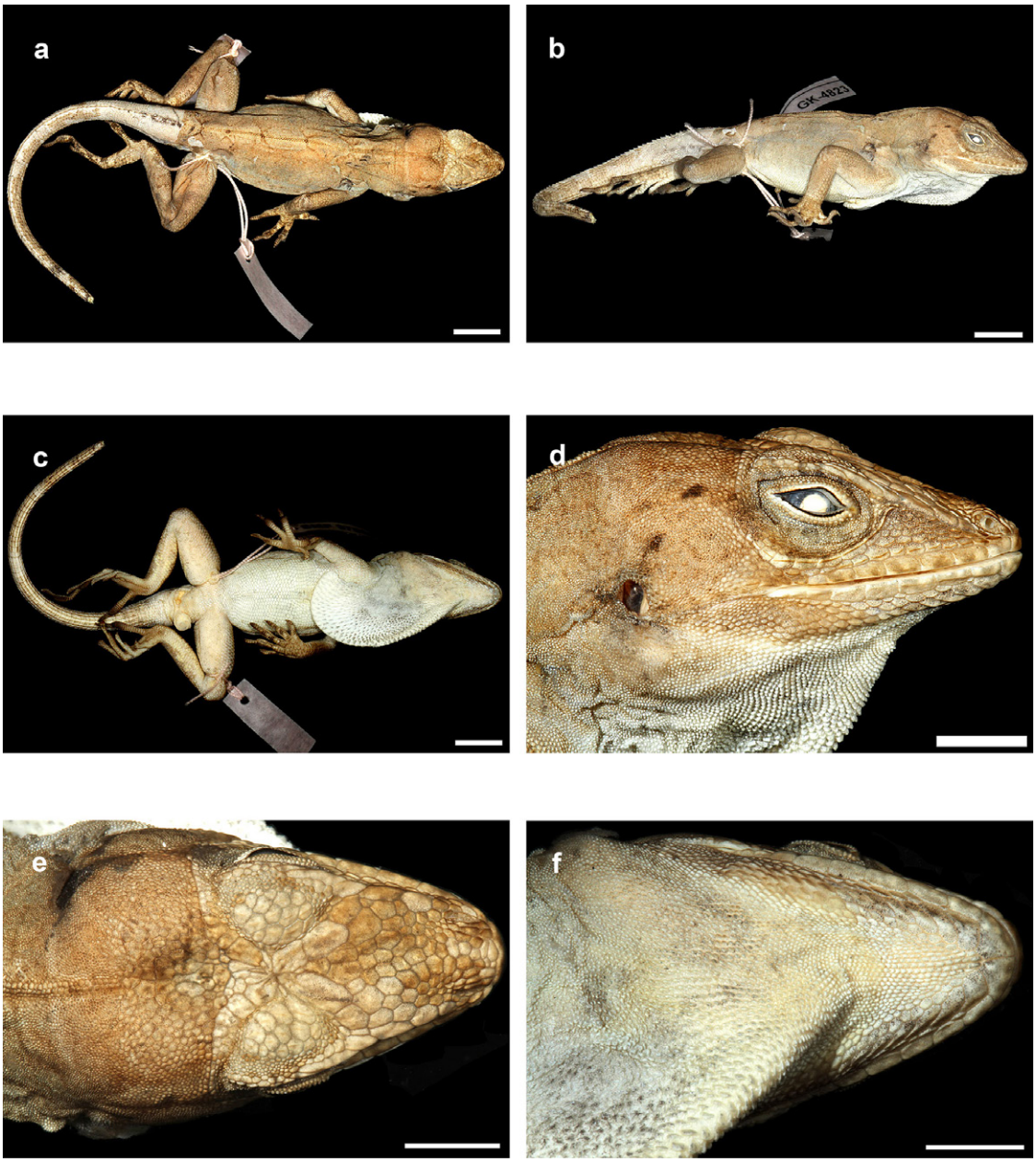

Figure 45. Holotype of *Audantia aridius* (SMF 97896): (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; (f) ventral view of head. Scale bars equal 10.0 mm in (a–c) and 5.0 mm in (d–f), respectively. Photos by Gunther Köhler.

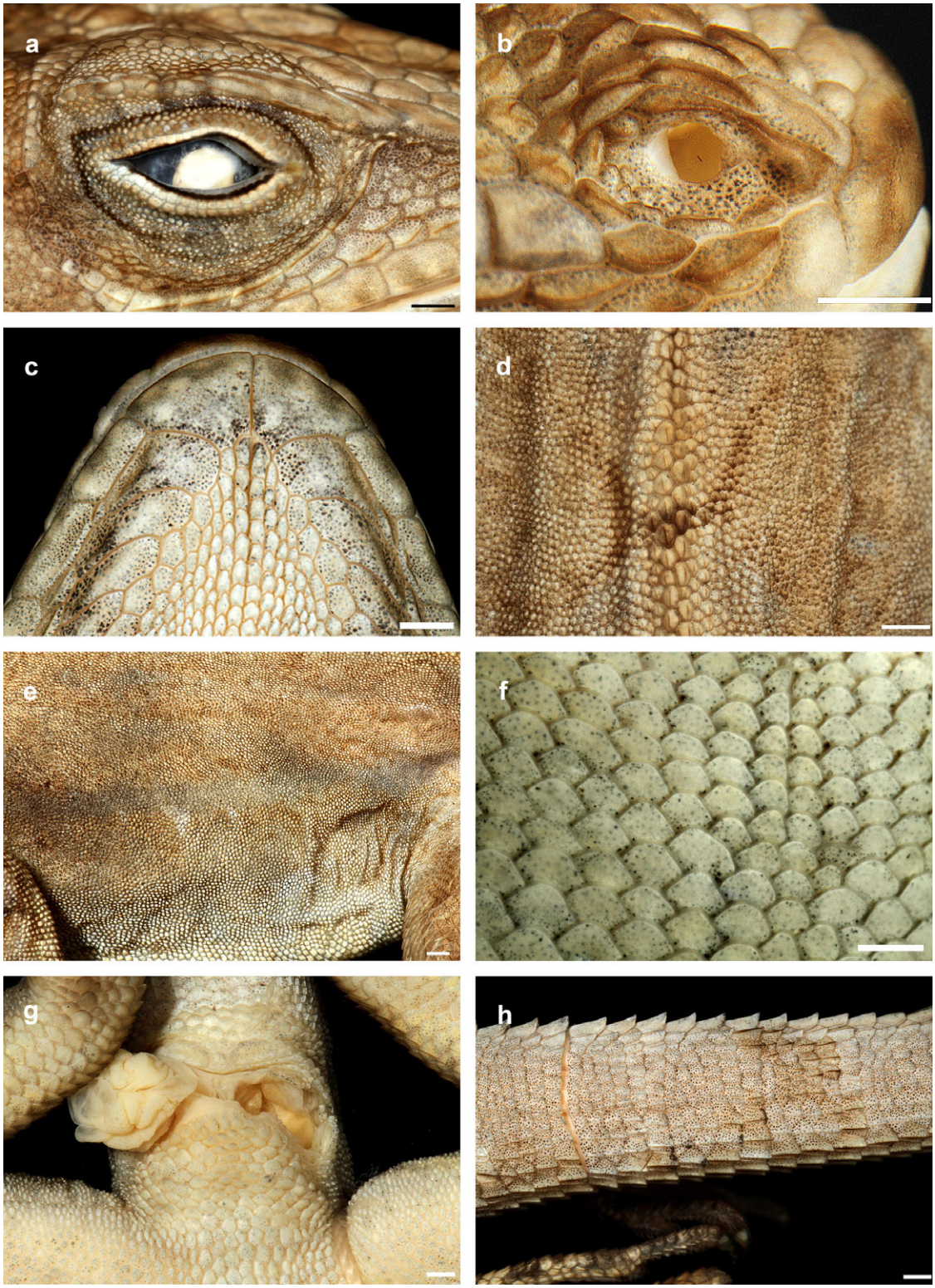

Figure 46. Holotype of *Audantia aridius* (SMF 97896): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region; (e) flank region; (f) midventer; (g) cloacal region; (h) lateral view of tail. Scale bars equal 1.0 mm. Photos by Gunther Köhler.

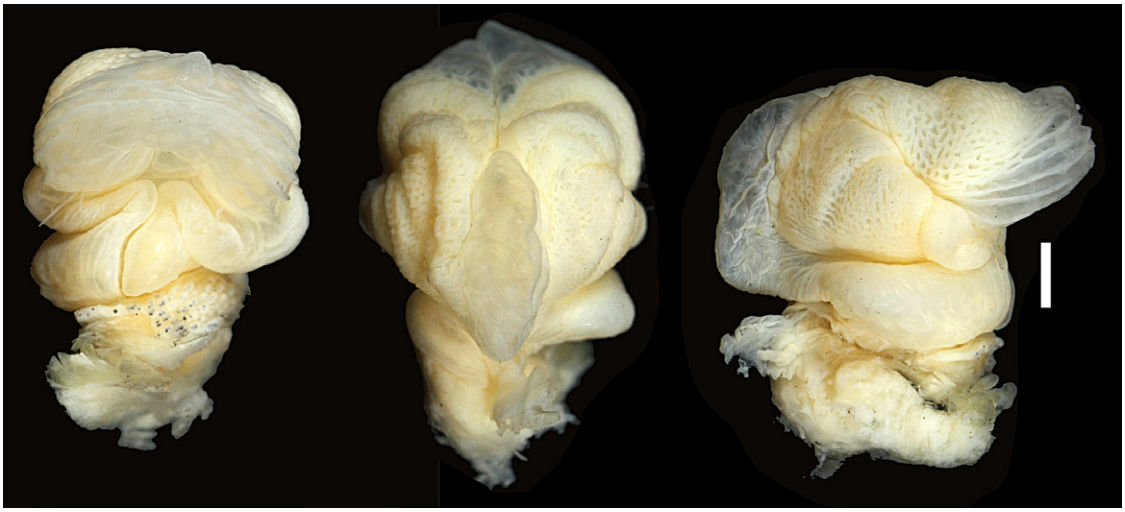

Figure 47. Hemipenis of *Audantia aridius* (SMF 97896). Scale bar equals 1.0 mm. Photos by Gunther Köhler.

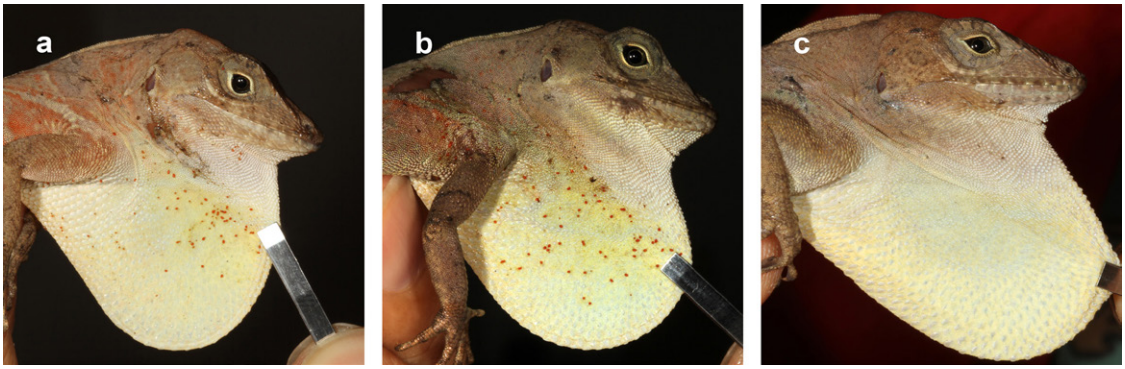

Figure 48. Dewlaps of adult males of *Audantia aridius* in life. (a) SMF 97894; (b) SMF 97893; (c) SMF 97896. Photos by Gunther Köhler.

Figure 49. Habitat o*f Audantia aridius* near Cortico, Laguna, Barahona, Dominican Republic, 1340 m a.s.l. (31 October 2013). Photo by Gunther Köhler.

Table IV. Overview of the taxonomic revision of the genus *Audantia*

Original name	**Old taxonomy**	**New taxonomy**
Anolis whitemani breslini Schwartz, 1980	*Anolis breslini*	*Audantia breslini*
Anolis citrinellus Cope, 1864	*Anolis cybotes*	*Audantia distichus*
Anolis cybotes Cope, 1862	*Anolis cybotes*	*Audantia cybotes*
Anolis cybotes ravifaux Schwartz & Henderson,1982	*Anolis cybotes ravifaux*	*Audantia ravifaux*
Anolis cybotes saxatilis Mertens, 1938	*Anolis cybotes*	*Audantia saxatilis*
Anolis doris Barbour, 1925	*Anolis cybotes doris*	*Audantia doris*
Anolis heatianus Garman, 1887	*Anolis heatianus*	*Audantia cybotes*
Anolis longitibialis Noble, 1923	*Anolis longitibialis*	*Audantia longitibialis*
Anolis marcanoi Williams, 1975	*Anolis marcanoi*	*Audantia marcanoi*
Anolis riisei Reinhardt & Lütken, 1862	*Anolis cybotes*	*Audantia cybotes*
Anolis strahmi Schwartz, 1979	*Anolis strahmi*	*Audantia strahmi*
Anolis whitemani Williams, 1963	*Anolis whitemani*	*Audantia saxatilis*
Audantia armouri Cochran, 1934	*Anolis armouri*	*Audantia armouri*
Audantia shrevei Cochran, 1939	*Anolis shrevei*	*Audantia shrevei*
Audantia aridius in this study	*Anolis cybotes* in part.	*Audantia aridius*
Audantia australis in this study	*Anolis cybotes* in part.	*Audantia australis*
Audantia higuey in this study	*Anolis cybotes* in part.	*Audantia higuey*
Audantia hispaniolae in this study	*Anolis cybotes* in part.	*Audantia hispaniolae*

KEY TO THE SPECIES OF THE GENUS AUDANTIA

1a. Ventral scales keeled…….. 2

1b. Ventral scales smooth…….....5

2a. Several rows of scales in nuchal region much enlarged, same size or larger than those in vertebral double row…… . *Audantia shrevei*

2b. Only two rows of scales in nuchal region slightly enlarged, larger than adjacent scales…... 3

3a. All gorgetals on posterior portion of male dewlap large, only slightly reduced towards base, all narrowly spaced…….. *Audantia cybotes* (in part)

3b. All gorgetals on male dewlap small and widely spaced…….. 4

4a. Neck and dorsum with clearly defined blackish, very dark gray, or dark brown crossbands; SVL in males to 67 mm, in females to 54 mm…….*Audantia saxatilis*

4b. Dorsal crossbands blurred to absent, never clearly delineated, usually no dark band on neck; SVL in males to 60 mm, in females to 45 mm……*Audantia breslini*

5a. Male dewlap red or orange in life……6

5b. Male dewlap white or pale gray in life, with or without suffusions of yellow, green, or orange…….....7

6a. A double row of distinctly and abruply enlarged vertebral scales…….. *Audantia strahmi*

6b. Scales in vertebral area gradually and slightly enlarged, not forming a distinct double row……*Audantia marcanoi*

7a. Habitus very stout; usually <170 scales around midbody; restricted to the highlands of the Sierra de Bahoruco, Dominican Republic, and Massif de La Selle, Haiti……*Audantia armouri*

7b. Habitus not particularly stout; usually >170 scales around midbody; distributed in the lowlands of Hispaniola…… 8

8a. Scales on anterior surface of thigh greatly enlarged and smooth……*Audantia ravifaux*

8b. Scales on anterior surface of thigh only slightly enlarged and usually keeled…… 9

9a. All gorgetals on posterior portion of male dewlap large, only slightly reduced towards base, all narrowly spaced…… . .*Audantia cybotes* (in part)

9b. Gorgetals in central portion of male dewlap much reduced in size and widely spaced, or all gorgetals small and widely spaced……10

10a. Gorgetals on male dewlap heterogeneously distributed with groups of cluttered scales…… 11

10b. Gorgetals on male dewlap more or less homogeneously distributed……..12

11a. Gorgetals on male dewlap in central portion of male dewlap much reduced in size; dark streaks present on anterior base of male dewlap……*Audantia hispaniolae*

11b. All gorgetals on male dewlap small and widely spaced; no dark streaks on anterior base of male dewlap……*Audantia longitibialis*

12a. Male dewlap with a central orange blotch in life; usually <185 scales around midbody; restricted to Île de la Gonâve, Haiti…….....*Audantia doris*

12b. Male dewlap without a central orange blotch in life; usually >185 scales around midbody; distributed on the main island of Hispaniola……13

13a. Usually one enlarged sublabial scale in contact with infralabials; dark streaks present on anterior base of male dewlap; scales in vertebral double row weakly enlarged, about twice the size of adjacent scales……*Audantia australis*

13b. Usually two or three enlarged sublabial scales in contact with infralabials; no dark streaks on anterior base of male dewlap; scales in vertebral double row greatly enlarged, more than twice the size of adjacent scales……14

14a. 214–270 scales around midbody in males; all gorgetals widely spaced, more skin uncovered than covered by scales; hemipenis with an asulcate ridge……*Audantia aridius*

14b. 166–212 scales around midbody in males; upper portion of male dewlap mostly covered by gorgetals with little free skin; hemipenis with an asulcate finger-like processus…..……*Audantia higuey*

DISCUSSION

This study shows more diversity among the anoles of the genus *Audantia* of Hispaniola than reflected in the current literature. In this study, we recognize 14 species—four of which we describe as new species—and it is likely that more, undescribed, species are present. Table IV summarizes the taxonomic changes as a result of this study. Our phylogenetic tree (Fig. 1) shows that there is considerable genetic divergence among geographically isolated populations, indicating a lack of or reduced gene flow. Some of the species we recognize (e.g., *A. aridius*, *A. armouri*, *A. australis*, *A. higuey*, and *A. ravifaux*) exhibit considerable genetic structure, to a point that most of these subclades qualify as candidate species sensu Vieites *et al*. (2009). To test whether these 19 candidate species could be differentiated in external morphology, we scored the available specimens for a set of 39 characters of scalation and morphometrics. However, no prominent differentiation in morphology could be uncovered within the larger clades that we recognize as species level units, and therefore we tentatively consider the respective genetic subclades to be conspecific. More field and lab studies are needed in order to test the hypothesis that these diverging allopatric populations indeed are conspecific. Species delimitation methods using molecular data often generate a large number of putative (undescribed) species. However, many of the putative species so delimited are simply isolated populations that do not represent biological species (Sukumaran & Knowles, 2017). For this reason, and because our study includes a more comprehensive (systematic) delimitation of species, considering molecular, morphological, and geographic information, we did not use molecular (only) delimitation methods.

At first glance, many of the species of the genus *Audantia* are not easy to differentiate and depict a high degree of visual resemblance, mostly being morphologically conservative to a point that they can be called cryptic species. Glor *et al*. (2003:2393) had called this phenomenon in this group of lizards “Morphological evolutionary stasis”. Nonetheless, a detailed morphological analysis allows uncovering distinct although subtle morphological differences among the species of *Audantia*, the differentiating characters varying between species pairs.

The clade with specimens from the extreme western portion of the Tiburón Peninsula, Haiti, is assigned to *Audantia cybotes* sensu stricto, since the type locality of *A. cybotes* is “Western Hayti; from near Jeremie”. The specimens from the sister-clade could not only be differentiated by the genetic divergence shown in the phylogenetic tree, but also by morphology: For instance, specimens of *A. cybotes* from the western portion of the Tiburón Peninsula have keeled ventral scales, a double row of greatly enlarged mucronate vertebral scales and a male dewlap with no suffusions whereas the specimens from the central and eastern Tiburón Peninsula have smooth ventrals, only weakly enlarged non-mucronate vertebrals and a male dewlap with yellowish or orange suffusions. Therefore, the latter populations is recognized

as a distinct species, *A. australis*. The two species are sympatric at two locations, Morne Grand Bois and Morne Bois Pangnol, where they may be hybridizing (see below). In the case of *A. higuey* and *A. hispaniolae*, the DFAs (Figs. 4-5) show no overlapping polygons, indicating a high degree of differentiation in the morphological characters that were compared. *Audantia hispaniolae* and *A. higuey* are widely sympatric across the eastern portion of the Dominican Republic. Some of the recognized species are more readily differentiated in morphology, such as *A. ravifaux* (e.g., having smooth enlarged scales on anterior surface of thigh).

We examined all extant primary types of all nominal taxa previously recognized as synonyms of *Anolis cybotes* Cope, 1863. As mentioned in the introduction, the type material of *Audantia heatianus* is in poor condition. Nevertheless, these three specimens mostly resemble *A. cybotes* and given its type locality "Tiburon, Hayti" (Garman, 1887), *A. heatianus* is assigned to the synonymy of *A. cybotes*. Our genetic and morphological data support the recognition of *ravifaux* and *doris* as distinct species and therefore these two former subspecies of *A. cybotes* were elevated to species level. Barbour (1914) recognized *A. citrinellus* as a valid "beautiful little species, confined to Haiti," citing MCZ 1326 as a representative of this species. The online database of MCZ indicates that this specimen (from "Port au Prince, Hayti") was reidentified as "*Anolis cristatellus cristatellus*". In his list of the anoles "known to occur on the Neotropical islands" Barbour (1930b) states that the "type in Brit. Mus. ... is a young *A. cybotes*". The nominal species *A. citrinellus* has remained in the synonymy of *A. cybotes* ever since (e.g., Cochran, 1934; Schwartz, 1989). However, the examination of the holotype of *A. citrinellus* clearly revealed that in external morphology it has the characteristics of *Ctenonotus distichus* rather than of any species of the genus *Audantia*.

Most of the species treated in this work are distributed across the lowlands and but some reach the mid elevations of the Hispaniolan mountains. In contrast, *A. armouri* and *A. shrevei* occur primary in the highlands above 1650 masl. They both "occupy high-altitude pine forests in the Sierra de Bahoruco and Cordillera Central, respectively" (Schwartz & Henderson, 1991). Specimens assigned to *A. shrevei* are easily identified by having a patch of enlarged nuchal scales (Cochran, 1939), a morphological characteristic not found in the other species. Also supported by our genetic data, both nominal taxa are therefore confirmed as distinct species. Furthermore, our genetic data support the recognition of the nominal taxa *A. breslini*, *A. longitibialis*, *A. marcanoi*, *A. strahmi*, and *A. saxatilis* as distinct species.

Some aspects of the evolutionary history of the genus *Audantia* are revealed by the relationships (Fig. 1), distribution (Fig. 18), and habitat preferences of the species. Six of the 14 species are endemic to the North Island: *A. breslini*, *A. higuey*, *A. marcanoi*, *A. ravifaux*, *A. saxatilis,* and *A. shrevei*. We would add a seventh species, *A. hispaniolae*, to that list because of its broad distribution across the North Island, even though it encroaches the South Island in a portion of the Massif de la Selle. It also occurs on Gonave, an island that is intermediate between the North and South islands of Hispaniola and has received faunal elements from both areas (Schwartz, 1978). Six species are endemic to the South Island: *A. aridius*, *A. armouri*, *A. australis*, *A. cybotes*, *A. longitibialis*, and *A. strahmi*. *Audantia doris* is endemic to Gonave. The North Island is older (late Eocene), in terms of the earliest exposed land (Iturralde-Vinent & MacPhee, 1999), than the South Island (late Miocene, ~10 mya), and the most basal branching species (*A. marcano*i) occurs on the North Island. During the evolution of the genus, there were three invasions of the South Island: (1) The *longitibialis* species group (*A. longitibialis* and *A. strahmi*), the cybotes species group (*A. aridius*, *A. australis*, and *A. cybotes*), and *A. armouri*. Although we did not construct a timetree, it can be inferred that the crown ages (basal node times) of the two endemic South Island clades of multiple species (*cybotes* and *longitibialis* species groups) are younger than 10 mya. This infers a Miocene/

Pliocene evolution of the genus, in contrast to a previous estimate (Nicholson *et al*., 2012) of an early Eocene (54 mya) crown age, and also younger than estimates in Poe *et al*., (2017). In terms of habitat preferences, there is a trend in that the earliest-diverging species (*A. aridius*, *A. breslini*, *A. longitibialis*, *A. marcanoi, A. saxatilis, A. strahmi*) are xerophilic and the later-diverging species are mesophilic. This trend could be explained by global climate change during the evolution of *Audantia*, starting with late Miocene cooling (and drying) followed by Pliocene warming.

Although hybridization among anoles is rather rare (Losos, 2009), it is a possibility in areas where closely related species are sympatric (and possibly syntopic). For the species of *Audantia*, this phenomenon of hybridization is most likely for the species pairs *A. australis* / *A. cybotes*, *A. doris* / *A. hispaniolae*, *A. higuey* / *A. hispaniolae*, and *A. higuey* / *A. ravifaux*. Through alterations of distribution of the respective species and/or anthropogenic habitat changes (e.g., habitat fragmentation, land use change, and displacement of species), (Allendorf *et al*., 2001) but also abiotic (e.g., climatic) effects, secondary contact zones and areas of sympatry may occur. In those areas of contact, hybridization can occur (Harrison, 1993). In the case of *A. australis* / *A. cybotes* overlapping polygons in the DFAs indicate specimens with intermediate characters in this group (Figs. 6–7). Also, the genetically assigned *A. cybotes* occurring sympatrically with *A. australis* have smooth ventrals (like *A. australis*), whereas the allopatric *A. cybotes* have strongly keeled ventral scales. These observations possibly indicate genetic introgression, which could be studied in the future with methods that sample nuclear genes. The hypothesis of hybridization between the other named species could not be supported by the evaluated data. Further research is needed to confirm hybridization in some of these species pairs. The large amount of deforestation in Hispaniola, and especially in Haiti (Hedges *et al*., 2018), has greatly disrupted habitats and might provide an explanation for hybridization, if it exists.

Finally, since we have taken the liberty to suggest common names for the seven species of Audantia treated in detail in this work, we would also like to point out common names for the remaining species of this genus, already coined (Hedges *et al*., 2019): *Audantia armouri* (Black-throated Stout Anole), *A. breslini* (Northwestern Stout Anole; modified), *A. longitibialis* (Barahona Stout Anole), *A. marcanoi* (Red-fanned Stout Anole), *A. saxatilis* (Banded Stout Anole), *A. shrevei* (Cordillera Central Stout Anole), and *A. strahmi* (Bahoruco Stout Anole).

ZooBank registration. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the International Commission on Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information can be viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org. The LSID for this publication is as follows: urn:lsid:zoobank.org:pub:63E5E7E8-754C-45C7-B34A-36A262C2C7C2.

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Appendix 1. Specimens examined

***Audantia aridius*: Dominican Republic:** Barahona: 2.9 miles NW La Ciénaga, 355 m: SMF 104162–63; Barahona: SMF 26145–48; Barahona, on ground of Hotel Riviera, 12 m: SMF 104910; 11.3 km S Barahona (measured from Hotel Caribe), 21 m: USNM 329093; 20.8 km S Cabral, 975 m: USNM 329090–92; Paraíso, ca. 6–7 km NW, 180 m: USNM 329089; Barahona, Hotel Costa Larimar, 10 m: SMF 97895; Los Lirios, 1110 m: SMF 97892–94; near Cortico, Laguna, 1340 m: SMF 97896; near Polo, 855 m: MNHNSD (GK–4838); Pedernales: 6.1 km S Los Tres Charcos, 5 m: SMF 104160–61.

***Audantia armouri*: Dominican Republic:** Independencia: 16.7 km SE Puerto Escondido, 1690 m: USNM 575279; 23.1 km SE Puerto Escondido, 1690 m: SMF 104167; 23.9 km SE Puerto Escondido, 1690 m: SMF 104164–66, 104747–48, 104774, USNM 575275–78; Pedernales: Sierra de Bahoruco, El Gruce del Chucho, 2030 m: SMF 104751–56; Parque Nacional Sierra de Bahoruco, Canote – El Alcajé road, 1925 m: MNHNSD 23.3617, SMF 97820–23; 8.6 km NW Aceitillar (44.6 km N of Cabo Rojo), 1480 m: SMF 104731, 104749; Casetta Dos, ca. 22 km N Aceitillar by road, on ridge of Sierra de Bahoruco, 1750 m: SMF 104750, 104775, USNM 575280–81; 15 km SW El Aguacate, 2195 m: USNM 329119; 9.4 km S Aceitillar (26.6 km N Cabo Rojo), 710 m: SMF 104171. **Haiti:** Ouest: Morne Cardineau, 2060 m: SMF 104168–70, USNM 575282–83; Pic La Selle, 1927 m: SMF 104172–75, USNM 575284; Sud-Est: Gros Cheval, ca. 15 km W via logging roads (NE slope of Pic La Salle), 2020 m: USNM 286896; Gros Cheval, ca. 15 km W via logging roads (NE slope of Pic La Salle), 2020 m: USNM 329127–34.

***Audantia australis*: Dominican Republic:** Pedernales: 18.2 km N. Pedernales at stream (Los Arroyos border road), 200 m: SMF 104274–75, USNM 575287; 9.4 km S Aceitillar (26.6 km N of Cabo Rojo), 710 m: SMF 104272–73, USNM 575285–86; Altagracia, 670 m: SMF 104276; Los Arroyos, 1265 m: SMF 97897; Mencía–Altagracia road, 1 km S Altagracia, 700 m: SMF 104277; road to Pelempito, 755 m: SMF 99003–08. Haiti: Grand'Anse: 8.0 km SSW Baradères, 420 m: SMF 104270, 104913; Bourdon, 9.2 km E Anse-d'Hainault, 277 m: SMF 104914; Ouest: Berry, 1630 m: SMF 104278; Poye, 1285 m: SMF 104294, USNM 575291; Nippes: Morne Bois Pangnol, 1170 m: SMF 104291–92, USNM 575288; NW slope Morne Tête Boeuf, 1176 m: SMF 104287–88, USNM 575289–90; Sud: 11.6 km NW Les Anglais,

on Morne Grand Bois, 1208 m: SMF 104285; Caye Michel, previously called Caye Paul (10.7 km WNW Les Platons Citadel), 1120 m: SMF 104269, USNM 575297; 2.4 km N Ducis, 50 m: SMF 104265–66, 104909, USNM 575292–94; 5.8 km S Ducis, 50 m: SMF 104267–68, USNM 575295–96; Île-à-Vache, 15 m: SMF 104284, USNM 575301–04; Île-à-Vache, Port Morgan Hotel, 16 m: SMF 104289–90, USNM 575305–07; Mme Verette, 1369 m: SMF 104293; near Cabalice, St. Jean, 107 m: SMF 104283; near Côteaux, 30 m: SMF 104281; ca. 12 km NE Port Salut, 189 m: SMF 104279–80, USNM 575298–300); Port Salut, Darbouze, 93 m: SMF 104282; Sud-Est: Jacmel (grounds of Hotel Jacmelian), 0 m: SMF 104271; Morne D'Enfer, 1433 m: SMF 104286, USNM 575308–09.

***Audantia breslini*: Haiti:** Grand'Anse: 8.0 km SSW Baradères, 420 m: SMF 104194–95; Nord'Ouest: Bombardopolis, 490 m: SMF 104178–79, USNM 575310–13; Mole Saint-Nicolas at Rivière Côtes de Fer, 9.10 mi NE, 30 m: SMF 104177; 10.5 mi NE Mole Saint-Nicolas, 70 m: SMF 104176.

***Audantia cybotes*: Haiti:** no further data: NHMD R3793, R3796; Grand'Anse: Jérémie: MCZ 14346–47; 1.8 km E Anse-d'Hainault, 130 m: SMF 104190–92, USNM 575314; 0.8 km E Dame-Marie, 40 m: SMF 104188–89, 104208; 4.8 km N Les Irois, 100 m: SMF 104193; 8.0 km SSW Baradères, 420 m: SMF 104194–95; 5.8 km S Pestel, 375 m: SMF 104187; 3.95 km WSW Annete, on Morne Desbarrières, 1623 m: SMF 104198; 1.5 km N Carcasse, 35 m: SMF 104197; Grande Cayemite (helipad-camp), 74 m: SMF 104201–03; Nippes: Morne Bois Pangnol, 1170 m: SMF 104204–05; Sud: 11.6 km NW Les Anglais, on Morne Grand Bois, 1208 m: SMF 104200; east slope Morne Grand Bois, 1100 m: SMF 104206–07, USNM 575320–21; near Côteaux: 7 m, SMF 104196; 5 km NW Duplantin, on Morne Lézard, Grande Colline, 1777 m: SMF 104199.

***Audantia doris*: Haiti:** Artibonite: Gonave, Gran Source, 10 m: USNM 575322–23; Gonave, Nan Café spring area, 443 m: SMF 104210; Gonave: MCZ 13734–40; Gonave, near Richard on coast road, 7 m: SMF 104209.

***Audantia higuey*: Dominican Republic:** Hato Mayor: 22 km WNW El Valle (16 km to Trepada Alta, ca. 6 km by trail to Montebonito), 76 m: USNM 329101–06; Sabana de La Mar, ca 10 km W (airline) in Los Haitises, 5 m: USNM 329107–10; La Altagracia: Hotel Catalonia Bávaro, 10 m: MNHNSD (GK–4670), SMF 97869; Loma El Peñon (García), ca. 5 km airline N Bejucal, 100–290 m: SMF 104257; Manatí Park Bávaro, 20 m: MNHNSD (GK-4694–95), SMF 97870–72, 97874; San Cristóbal: vicinity of La Altagracia, W Santo Domingo, 40 m: SMF 99025.

***Audantia hispaniolae*: Dominican Republic:** Azua: Playa Chiquita, 14.1 km NW Cruce de Ocoa on Baní–Azua road, then 4.8 km S, 9 m: SMF 104951, USNM 575324; Bahoruco: Apolinar Perdomo, 900 m: SMF 104226–27, USNM 575328–29; Loma Monte Bonito, 1800 m: SMF 104228–29, 104917–26, USNM 575325–27; Barahona: Barahona; Loma del Curro, at crest of Sierra Martín García, 1061 m: SMF 104230–31, 104970–73, USNM 575330–32; Duarte: San Francisco de Macorís: SMF 22938; southern slopes of Loma Quita Espuela, 700–850 m: SMF 104221, 104959 60, USNM 575333–34; Batey Monati on east side of Río Payabo, 30 m: SMF 104915 16; El Seibo: El Seibo, 110 m: SMF 97867–68; Loma Herradura (3 km NE of Pedro Sánchez, airline), 520–560 m: SMF 104220; 5.3 km SW Miches, 100 m: SMF104218; 1.7 km W Sabana de La Mar, 11 m: USNM 329094–95; Elías Piña: 0.5 km N. Calimete, 1560 m: SMF 104237; Elías Piña: 0.6 km NE Rosa de la Piedra, 1340 m: SMF 104236, USNM 575335; 1.1 mi. NE Rosa de la Piedra, 1220 m: SMF 104238, USNM 575336; Río Limpio (CREAR), 700 m: USNM 329100; 13 km N Cacique Enriquillo (27 km N Los Pinos),

1870 m: USNM 329096–98; 17 km N Cacique Enriquillo (31 km N of Los Pinos), 1450 m: USNM 329099; Espaillat: 23.2 km N Tenares, thence 4.5 km W (= 0.2 km E Jaiba), 350 m: SMF 104222; Moca: SMF 25925–26, 25928, 26341; Hato Mayor: Las Pajas: SMF 25826; Sabana de la Mar: SMF 26024, 26073; ca. 4 km S Sabana de la Mar, 36 m: SMF 104239, 104240, 104927–31, USNM 575337–39); Hermanas Mirabal: Tenares, 23.2 km N of, thence 4.5 km W (= 0.2 km E Jaiba): 350: SMF 104961; Independencia: ca. 7 km W Los Pinos by road, 365 m: SMF 104242; Cacique Enriquillo, 5.1 km N of, 1576 m: SMF 104232; west of Puerto Escondido, 490 m: SMF 104241; La Altagracia: Loma El Peñon (García), ca. 5 km airline N Bejucal: 100–290 m: SMF 104219; La Vega: below Paso Bajito: SMF 25662, 25981–87; between Moca and SMF 25903; Constanza: SMF 22935–36; Jarabacoa: SMF 25625, 25645–54, 25660–61, 25973–74; 10.5 km W Jayaco, 1000 m: USNM 329111; 11 km W Jayaco on road to Constanza, 657 m: USNM 329118; 7 km W Jayaco on road to Constanza, 760 m: USNM 329113–17; Paso Bajito: SMF 34439; Reserva Científica Ébano Verde, Arroyazo, 1105 m: SMF 97898; Monte Cristi: Cayo Pablillo: SMF 25827–30; Monte Cristi: SMF 25841–42; Puerto Plata: 11 km from Puerto Plata: SMF 25929; 9 km from SMF 25927; 8.5 km NNE of Villa Elisa, 190 m: SMF 104964; above La Isabela, Río Isabela: SMF 25741; Balneario Colón, SMF 25871–80; Río Muñoz, 7 km from SMF 25898; 27 Cascadas, ca. 13 km airline WSW Puerto Plata, 165 m: MNHNSD 23.3630, 23.3632–33; Hotel Riu Bachata, ca. 6 km airline WNW Puerto Plata, 10 m: MNHNSD 23.3625; Loma Teleférico, ca. 1 km S Puerto Plata, 280–295 m: SMF 104758–60; near Yásica Arriba, 130 m: SMF 104761–64; 1.2–1.6 km SW Maimón, just west of mouth of the Río Maimón, 5 m: SMF 104223, USNM 575340; Punta Burén, 6.4 km NW Estero Hondo, 6 m: SMF 104224–25, 104962–63; Samaná: Bahía Príncipe El Portillo, Península Samaná, 10 m: MNHNSD (GK–4705), (GK–5087), SMF 97875–77; El Limón, Península Samaná, 30 m: MNHNSD (GK–4709), (GK–4713), SMF 97878–85; Samaná: SMF 26048 54; Sánchez Ramírez: 8.6 km N of, thence, 8.6 km E of Cotuí (beyond Aguacate), 109 m: SMF 104978; 8.6 km NE of, thence 8.1 km E Cotuí (= El Aguacate), 35 m: SMF 104955 57; San José de Ocoa: Cruce de Ocoa, 14.8 N of, thence 7.8 km SE on dirt road; at Martínez, near La Palma, 675 m: SMF 104952–54; San Juan: 3.2 km NNE El Azul, 1000 m: SMF 104234–35, USNM 575341; San Pedro de Macorís: Consuelo: SMF 25716–24; Gran Bahia Principe La Romana, 10 km E San Pedro de Macorís, 10 m: MNHNSD (GK–4636), SMF 97863–66; San Pedro de Macorís: SMF 25697, 25709–10; Santiago: Pass between Santiago and Puerto Plata: SMF 25868–69; Paso de Bao, 1300 m: USNM 575342; Guácara, 1169 m: SMF 104965–69; Monción: SMF 25759–65, 25785–94, 25798–801; Santo Domingo: Engombe at Río Haina: SMF 26125–27; Fortaleza at lower Río Haina: SMF 25525–27; Hotel Be Live Hamaca, Boca Chica, 10 m: SMF 97903; Hotel Don Juan, Boca Chica, 10 m: MNHNSD (GK–4739–40), (GK–4750), SMF 97886–91; Hotel Oasis Hamaca, Boca Chica, SMF 90421; km 17 Autopista Duarte, north of Santo Domingo, 55 m: SMF 97899–902; Mündung des Río Haina: SMF 25530–33; Río Haina: SMF 22937; Santa Ana, SMF 25547; Santo Domingo: SMF 22939–44; Santo Domingo Deutsch-Dominikanisches Tropenforschungsinstitut: SMF 25511–12, 25518, 25610–11, 30009; Tres Ojos, SMF 25557. Haiti: Artibonite: 13.0 km N Ca Soleil (on road to Terre Neuve), 460 m: USNM 575344; 19.5 km N Ca Soleil, 620 m: SMF 104216–17, USNM 575343; Anse-a-Galets, Sunshine Hotel, 10 m: SMF 104248–50, USNM 575348–50; Gonave, Ravine Picme, near Platon Balais, 205 m: SMF 104245–47, 104977, USNM 575345–46; Morne Basile, 1424 m: SMF 104253–55, USNM 575352–54; Morne Boeuf, 1760 m: SMF 104256, USNM 575351; Saint-Marc: SMF 26239–40; Centre: 16 km N Croix-des-Bouquets, 510 m: SMF 104215; Bonga, 1263 m: SMF 104244; ca. 4 km NW Ca Pierre by road, 1200 m: SMF 104251, 104975, USNM 575363; Chinchiron,

1154 m: SMF 104252, 104976; Kenskoff: SMF 26245–47; Nord: Cap-Haïtien: SMF 10867–913, 26249–50; Nord'Ouest: 1.1 miles S Douceur (8 mi E Port-de-Paix), 20 m: SMF 104233, USNM 575359; Ouest: Furcy (at The Lodge), 1575 m: SMF 104243, 104932–45, 104974, USNM 575360–62; Port-au-Prince: SMF 10919–30; Bernard (east of Robin and Furcy), 1300 m: SMF 104213–14, 104772, 104947, USNM 575357–58; 12.0 km ENE Petionville, 165 m: SMF 104950; 4.2 km E Carisse, by road, 210–260 m: SMF 104211, 104949, USNM 575356; 18.1 km E Thomazeau, 800 m: SMF 104212, 104948, USNM 575355.

***Audantia longitibialis*: Dominican Republic:** Pedernales: Bucan Detwi, 10 m: USNM 575370; 25.2 SE Pedernales, 180 m: SMF 104979; Isla Beata, ca. 2 km SE Punta Beata, 10 m: SMF 104263–64, USNM 575366–69; ca. 5 km SW Los Tres Charcos (ca. 0.5 km NW Fondo de Paraíso), 85 m: SMF 104258–59, USNM 575371.

***Audantia ravifaux*: Dominican Republic:** La Altagracia: Hotel Catalonia Bávaro, 10 m: SMF 97869; Manatí Park Bávaro, 20 m: SMF 97873; La Romana: Isla Saona: MCZ R-37468–69, 187412–17; Isla Saona, environs of Mano Juan: MCZ R-156221.

***Audantia saxatilis*: Dominican Republic:** Azua: Manantiales, 485 m: SMF 104303; Barahona: south of Fondo Negro, region of lower Río Yaque: SMF 25032; Independencia: N of La Descubierta, 134 m: SMF 104300. Haiti: Nord'Ouest: Mole Saint-Nicolas at Rivière Côtes de Fer, 9.10 mi NE, 30 m: USNM 575374; 1.5 mi WSW Mole Saint-Nicolas (along coast), 35 m: SMF 104302, USNM 575373; 6.3 mi W Port-de-Paix, 32 m: SMF 104301, USNM 575372.

***Audantia shrevei*: Dominican Republic:** La Vega: 13 km NW La Horma, 1770 m: USNM 329112; Santiago: Valle de Bao, 1800 m: SMF 104295–97, USNM 575375–76.

***Audantia strahmi*: Dominican Republic:** Independencia: west of Puerto Escondido, 490 m: SMF 104299, USNM 575377–78; Pedernales: Hoyo de Pelempito (H. de Aceitillar on topo map) east edge, 355 m: SMF 104298, 104773; road to Pelempito, 315 m: SMF 97997–99, MNHNSD 23.3615–16.

Appendix 2 . GenBank accession numbers for all sequences included in the study. The specimen ID is shown in the tree (Fig. 1) and is the laboratory sample number (SBH), previously published Genbank number (AY), or museum number: KU, Museum of Natural History, Kansas University; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; USNM, U. S. National Museum, Smithsonian; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt. Corresponding Museum IDs are given. N/A = not applicable (no sequence).

Sample Name	Specimen ID	Museum ID	Abbreviated locality	Cyt b	ND2
Audantia aridius	SBH192670	SMF104160	DO Los Tres Charcos	MK444022	MK443765
Audantia aridius	SBH192671	SMF104161	DO Los Tres Charcos	MK444023	MK443766
Audantia aridius	SBH266256	SMF104162	DO La Ciénaga	MK444077	MK443813
Audantia aridius	SBH266257	SMF104163	DO La Ciénaga	MK444078	MK443814
Audantia aridius	SBH101296	N/A	DO Barahona	MK443961	MK443710
Audantia aridius	SBH275004	SMF97892	DO Los Lirios	MK444198	MK443927
Audantia aridius	SBH275005	SMF97893	DO Los Lirios	N/A	MK443928
Audantia aridius	SBH275006	SMF97894	DO Los Lirios	N/A	MK443929

Sample Name	Specimen ID	Museum ID	Abbreviated locality	Cyt b	ND2
Audantia aridius	SBH275007	SMF97895	DO Barahona Hotel	MK444199	N/A
Audantia aridius	SBH275008	SMF97896	DO Cortico Laguna	MK444200	MK443930
Audantia aridius	SBH275009	N/A	DO Polo	MK444201	MK443931
Audantia aridius	KU316497	KU316497	DO S of Cabral	N/A	AY263144
Audantia aridius	KU316585	KU316585	DO Barahona	N/A	AY263138
Audantia aridius	KU316641	KU316641	DO Loma Remigio	N/A	AY263139
Audantia aridius	KU316889	KU316889	DO Laguna de Oviedo	N/A	AY263140
Audantia aridius	USNM 329090	USNM 329090	DO Cabral	MK444206	MK443939
Audantia aridius	USNM 329091	USNM 329091	DO Cabral	MK444207	MK443940
Audantia aridius	USNM 329092	USNM 329092	DO Cabral	MK444208	MK443941
Audantia aridius	USNM 329121	USNM 329121	DO Oviedo	MK444222	MK443955
Audantia aridius	USNM 329122	USNM 329122	DO Oviedo	MK444223	MK443956
Audantia aridius	USNM 329123	USNM 329123	DO Oviedo	MK444224	MK443957
Audantia armouri	SBH192580	SMF104171	DO Aceitillar	MK444020	MK443764
Audantia armouri	SBH269789	SMF104174	HT Pic La Selle	N/A	MK443887
Audantia armouri	SBH269881	SMF104172	HT Pic La Selle	MK444155	MK443888
Audantia armouri	SBH269882	SMF104175	HT Pic La Selle	MK444156	MK443889
Audantia armouri	SBH269939	SMF104173	HT Pic La Selle	N/A	MK443892
Audantia armouri	SBH269940	USNM 575284	HT Pic La Selle	N/A	MK443690
Audantia armouri	AY263011	N/A	DO Sierra de Bahoruco	N/A	AY263011
Audantia armouri	AY263012	N/A	DO Sierra de Bahoruco	N/A	AY263012
Audantia armouri	AY263013	N/A	DO Sierra de Bahoruco	N/A	AY263013
Audantia armouri	AY263014	N/A	DO Sierra de Bahoruco	N/A	AY263014
Audantia armouri	AY263015	N/A	DO Sierra de Bahoruco	N/A	AY263015
Audantia armouri	USNM 329127	USNM 329127	HT Gros Cheval	MK443965	MK443714
Audantia armouri	USNM 329128	USNM 329128	HT Gros Cheval	MK443966	MK443715
Audantia armouri	USNM 329129	USNM 329129	HT Gros Cheval	MK443967	MK443716
Audantia armouri	USNM 329130	USNM 329130	HT Gros Cheval	N/A	MK443717
Audantia australis	SBH191727	SMF104265	HT Ducis	MK443979	AY263120
Audantia australis	SBH191728	SMF104266	HT Ducis	MK443980	MK443728
Audantia australis	SBH191735	SMF104267	HT Ducis	MK443984	MK443732
Audantia australis	SBH191736	SMF104268	HT Ducis	MK443985	MK443733
Audantia australis	SBH192257	N/A	HT Caye Michel	MK443999	MK443745
Audantia australis	SBH192258	SMF104269	HT Caye Michel	N/A	MK443746
Audantia australis	SBH192278	N/A	HT 8KM SSW Baradères	MK444001	MK443748
Audantia australis	SBH192281	SMF104270	HT 8KM SSW Baradères	MK444004	MK443751
Audantia australis	SBH192330	N/A	HT Morne Rouge Peninsula	MK444005	MK443752
Audantia australis	SBH192359	SMF104271	HT Jacmel	MK444006	MK443706

Sample Name	Specimen ID	Museum ID	Abbreviated locality	Cyt b	ND2
Audantia australis	SBH192576	N/A	DO Aceitillar	MK444016	MK443760
Audantia australis	SBH192577	SMF104273	DO Aceitillar	MK444017	MK443761
Audantia australis	SBH266722	N/A	DO Los Arroyos	MK444090	MK443826
Audantia australis	SBH266723	N/A	DO Los Arroyos	MK444091	MK443827
Audantia australis	SBH267519	SMF104274	DO Pedernales	MK444098	MK443833
Audantia australis	SBH267533	SMF104275	DO Pedernales	MK444100	MK443835
Audantia australis	SBH267536	SMF104277	DO Altagracia	MK444101	MK443836
Audantia australis	SBH267543	SMF104276	DO Altagracia	MK444102	MK443837
Audantia australis	SBH268594	SMF104278	HT Berry	N/A	MK443680
Audantia australis	SBH268980	SMF104279	HT Port Salut	MK444115	MK443850
Audantia australis	SBH268981	SMF104280	HT Port Salut	MK444116	MK443851
Audantia australis	SBH269007	N/A	HT Côteaux	MK444120	MK443855
Audantia australis	SBH269008	N/A	HT Côteaux	MK444121	MK443856
Audantia australis	SBH269012	SMF104281	HT Côteaux	MK444122	MK443857
Audantia australis	SBH269015	SMF104282	HT Port Salut	MK444123	MK443681
Audantia australis	SBH269018	SMF104283	HT Cabalice Saint Jean	MK444124	MK443858
Audantia australis	SBH269468	SMF104284	HT Île-à-Vache	MK444147	MK443879
Audantia australis	SBH269763	SMF104285	HT Morne Grand Bois	MK444153	MK443689
Audantia australis	SBH269942	SMF104286	HT Morne D'Enfer	N/A	MK443691
Audantia australis	SBH274230	SMF104287	HT Morne Tête Boeuf	MK444167	MK443694
Audantia australis	SBH274250	SMF104291	HT Morne Bois Pangnol	MK444169	MK443901
Audantia australis	SBH274261	SMF104289	HT Île-à-Vache	MK444171	MK443697
Audantia australis	SBH274262	SMF104290	HT Île-à-Vache	MK444172	MK443698
Audantia australis	SBH274325	SMF104292	HT Morne Bois Pangnol	N/A	MK443701
Audantia australis	SBH274330	SMF104288	HT Morne Tête Boeuf	MK444178	MK443704
Audantia australis	SBH274879	SMF104293	HT Verettes	MK444183	MK443909
Audantia australis	SBH274893	SMF104294	HT Poye	MK444184	MK443910
Audantia australis	SBH191729	USNM 575292	HT Ducis	MK443981	MK443729
Audantia australis	SBH191730	USNM 575293	HT Ducis	MK443982	MK443730
Audantia australis	SBH191731	USNM 575294	HT Ducis	MK443983	MK443731
Audantia australis	SBH191737	USNM 575295	HT Ducis	MK443986	MK443734
Audantia australis	SBH191738	USNM 575296	HT Ducis	MK443987	MK443735
Audantia australis	SBH192259	USNM 575297	HT Caye Michel	MK444000	MK443747
Audantia australis	SBH192578	USNM 575285	DO Aceitillar	MK444018	MK443762
Audantia australis	SBH192579	USNM 575286	DO Aceitillar	MK444019	MK443763
Audantia australis	SBH267529	USNM 575287	DO Pedernales	MK444099	MK443834
Audantia australis	SBH268982	USNM 575298	HT Port Salut	MK444117	MK443852
Audantia australis	SBH268983	USNM 575299	HT Port Salut	MK444118	MK443853
Audantia australis	SBH268984	USNM 575300	HT Port Salut	MK444119	MK443854

Sample Name	Specimen ID	Museum ID	Abbreviated locality	Cyt b	ND2
Audantia australis	SBH269745	USNM 575301	HT Île-à-Vache	MK444149	MK443882
Audantia australis	SBH269747	USNM 575302	HT Île-à-Vache	MK444151	MK443688
Audantia australis	SBH269749	USNM 575303	HT Île-à-Vache	N/A	MK443884
Audantia australis	SBH269750	USNM 575304	HT Île-à-Vache	MK444152	MK443885
Audantia australis	SBH269943	USNM 575308	HT Morne D'Enfer	N/A	MK443692
Audantia australis	SBH269944	USNM 575309	HT Morne D'Enfer	N/A	MK443893
Audantia australis	SBH274263	USNM 575305	HT Île-à-Vache	MK444173	MK443699
Audantia australis	SBH274264	USNM 575306	HT Île-à-Vache	MK444174	MK443700
Audantia australis	SBH274265	USNM 575307	HT Île-à-Vache	N/A	MK443902
Audantia australis	SBH274326	USNM 575288	HT Morne Bois Pangnol	MK444175	MK443702
Audantia australis	SBH274328	USNM 575289	HT Morne Tête Boeuf	MK444176	MK443703
Audantia australis	SBH274329	USNM 575290	HT Morne Tête Boeuf	MK444177	MK443904
Audantia australis	SBH274894	USNM 575291	HT Poye	MK444185	MK443911
Audantia australis	SBH275000	SMF99004	DO Road to Pelempito	MK444196	MK443923
Audantia australis	SBH275001	SMF99005	DO Road to Pelempito	N/A	MK443924
Audantia australis	SBH275002	SMF99007	DO Road to Pelempito	N/A	MK443925
Audantia australis	SBH275003	SMF99008	DO Road to Pelempito	MK444197	MK443926
Audantia australis	SBH275010	SMF97897	DO Los Arroyos	MK444202	MK443932
Audantia australis	AY263121	N/A	DO N of Pedernales	N/A	AY263121
Audantia australis	AY263122	N/A	DO Alcoa Rd Pedernales	N/A	AY263122
Audantia breslini	SBH194550	N/A	HT Mole Saint-Nicolas	N/A	AY263018
Audantia breslini	SBH194564	SMF104176	HT Mole Saint-Nicolas	N/A	MK443809
Audantia breslini	SBH194591	SMF104178	HT Bombardopolis	MK444071	MK443809
Audantia breslini	SBH194592	SMF104179	HT Bombardopolis	MK444072	MK443810
Audantia breslini	SBH194602	N/A	HT Bombardopolis	N/A	AY263019
Audantia breslini	SBH194593	USNM 575310	HT Bombardopolis	MK444073	MK443811
Audantia breslini	SBH194594	USNM 575311	HT Bombardopolis	MK444074	MK443812
Audantia breslini	SBH194595	USNM 575312	HT Bombardopolis	MK444075	N/A
Audantia breslini	SBH194625	USNM 575313	HT Bombardopolis	MK444076	AY263020
Audantia breslini	AY263016	N/A	HT Port-de-Paix	N/A	AY263016
Audantia caudalis	SBH269255	SMF104912	HT Gonave	MK444133	MK443683
Audantia cybotes	SBH191752	SMF104187	HT Pestel	MK443988	AY263119
Audantia cybotes	SBH191956	SMF104188	HT Dame Marie	MK443989	AY263042
Audantia cybotes	SBH192018	SMF104190	HT Anse d'Hainault	MK443990	MK443736
Audantia cybotes	SBH192019	SMF104191	HT Anse d'Hainault	MK443991	MK443737
Audantia cybotes	SBH192020	N/A	HT Anse d'Hainault	MK443992	MK443738
Audantia cybotes	SBH192021	N/A	HT Anse d'Hainault	MK443993	MK443739
Audantia cybotes	SBH192022	SMF104192	HT Anse d'Hainault	MK443994	MK443740
Audantia cybotes	SBH192035	SMF104189	HT Dame Marie	MK443995	MK443741

Sample Name	Specimen ID	Museum ID	Abbreviated locality	Cyt b	ND2
Audantia cybotes	SBH192042	N/A	HT Les Irios	MK443996	MK443742
Audantia cybotes	SBH192043	SMF104193	HT Les Irois	MK443997	MK443743
Audantia cybotes	SBH192044	N/A	HT Les Irois	MK443998	MK443744
Audantia cybotes	SBH192279	SMF104194	HT 8KM SSW Baradères	MK444002	MK443749
Audantia cybotes	SBH192280	SMF104195	HT 8KM SSW Baradères	MK444003	MK443750
Audantia cybotes	SBH269030	SMF104196	HT Côteaux	MK444125	MK443859
Audantia cybotes	SBH269046	N/A	HT Bourdon	MK444126	MK443860
Audantia cybotes	SBH269056	N/A	HT Pratt	N/A	MK443861
Audantia cybotes	SBH269061	SMF104197	HT Carcasse	MK444127	MK443682
Audantia cybotes	SBH269455	SMF104200	HT Morne Grand Bois	MK444146	MK443687
Audantia cybotes	SBH269529	SMF104198	HT Morne Desbarrières	MK444148	MK443880
Audantia cybotes	SBH269739	N/A	HT Morne Desbarrières	N/A	MK443881
Audantia cybotes	SBH269767	SMF104199	HT Morne Lézard	MK444154	MK443886
Audantia cybotes	SBH274228	SMF104201	HT Grande Cayemite	MK444166	MK443693
Audantia cybotes	SBH274233	SMF104202	HT Grande Cayemite	MK444168	MK443695
Audantia cybotes	SBH274251	SMF104205	HT Morne Bois Pangnol	MK444170	MK443696
Audantia cybotes	SBH274327	SMF104204	HT Morne Bois Pangnol	N/A	MK443903
Audantia cybotes	SBH274331	SMF104203	HT Grande Cayemite	N/A	MK443705
Audantia cybotes	SBH274497	SMF104206	HT Morne Grand Bois	MK444180	MK443906
Audantia cybotes	SBH274498	SMF104207	HT Morne Grand Bois	MK444181	MK443907
Audantia cybotes	SBH269746	USNM 575319	HT Morne Grand Bois	MK444150	MK443883
Audantia cybotes	SBH274487	USNM 575320	HT Morne Grand Bois	MK444179	MK443905
Audantia cybotes	SBH274499	USNM 575321	HT Morne Grand Bois	MK444182	MK443908
Audantia cybotes	SBH103724	USNM 329124	HT Castillon	MK443963	MK443712
Audantia cybotes	SBH103725	N/A	HT Castillon	MK443964	MK443713
Audantia doris	SBH269270	SMF104210	HT Gonave	N/A	MK443867
Audantia doris	SBH269272	SMF104209	HT Gonave	MK444134	MK443684
Audantia doris	SBH269292	USNM 575322	HT Gonave	MK444140	MK443685
Audantia doris	SBH269293	USNM 575323	HT Gonave	MK444141	MK443686
Audantia higuey	SBH192433	SMF104257	DO Loma El Peñon	MK444011	MK443756
Audantia higuey	SBH267761	N/A	DO Los Limones	MK444105	MK443840
Audantia higuey	SBH274994	SMF97872	DO Bavaro	MK444191	MK443918
Audantia higuey	SBH275016	SMF99025	DO W Santo Domingo	MK444205	MK443938
Audantia higuey	AY263132	N/A	DO Madrigal	N/A	AY263132
Audantia higuey	AY263143	N/A	Not reported	N/A	AY263143
Audantia higuey	KU316731	KU316731	DO Santo Domingo	N/A	AY263133
Audantia higuey	KU316732	KU316732	DO Santo Domingo	N/A	AY263134
Audantia higuey	KU316733	KU316733	DO Santo Domingo	N/A	AY263135

Sample Name	Specimen ID	Museum ID	Abbreviated locality	Cyt b	ND2
Audantia higuey	KU316734	KU316734	DO Santo Domingo	N/A	AY263136
Audantia higuey	KU316735	KU316735	DO Santo Domingo	N/A	AY263137
Audantia higuey	USNM 329101	USNM 329101	DO El Valle	MK444213	MK443946
Audantia higuey	USNM 329102	USNM 329102	DO El Valle	MK444214	MK443947
Audantia higuey	USNM 329103	USNM 329103	DO El Valle	MK444215	MK443948
Audantia higuey	USNM 329104	USNM 329104	DO El Valle	MK444216	MK443949
Audantia higuey	USNM 329105	USNM 329105	DO El Valle	MK444217	MK443950
Audantia higuey	USNM 329107	USNM 329107	DO Sabana de la Mar	MK444218	MK443951
Audantia higuey	USNM 329108	USNM 329108	DO Sabana de la Mar	MK444219	MK443952
Audantia higuey	USNM 329109	USNM 329109	DO Sabana de la Mar	MK444220	MK443953
Audantia higuey	USNM 329110	USNM 329110	DO Sabana de la Mar	MK444221	MK443954
Audantia hispaniolae	SBH191637	SMF104211	HT Carisse	MK443972	MK443721
Audantia hispaniolae	SBH191696	SMF104772	HT Bernard	N/A	MK443723
Audantia hispaniolae	SBH191697	SMF104213	HT Bernard	MK443974	MK443724
Audantia hispaniolae	SBH191698	SMF104214	HT Bernard	MK443975	MK443725
Audantia hispaniolae	SBH191709	SMF104215	HT Croix-des-Bouquets	MK443978	AY263117
Audantia hispaniolae	SBH192416	SMF104216	HT Ca Soleil	MK444007	AY263118
Audantia hispaniolae	SBH192418	SMF104217	HT Ca Soleil	MK444009	MK443754
Audantia hispaniolae	SBH192434	SMF104219	DO Loma El Peñon	MK444012	MK443757
Audantia hispaniolae	SBH192439	SMF104218	DO Miches	MK444013	MK443758
Audantia hispaniolae	SBH192464	N/A	DO Las Lagunas	MK444014	N/A
Audantia hispaniolae	SBH192465	SMF104220	DO Loma Herradura	MK444015	MK443759
Audantia hispaniolae	SBH192997	SMF104951	DO Playa Chiquita	MK444025	MK443768
Audantia hispaniolae	SBH193030	SMF104952	DO Martínez	MK444026	MK443769
Audantia hispaniolae	SBH193031	SMF104953	DO Martínez	MK444027	MK443770
Audantia hispaniolae	SBH193032	N/A	DO Martínez	MK444028	MK443771
Audantia hispaniolae	SBH193036	SMF104954	DO Martínez	MK444029	MK443772
Audantia hispaniolae	SBH193071	SMF104955	DO Cotuí	MK444030	MK443773
Audantia hispaniolae	SBH193072	SMF104956	DO Cotuí	MK444031	MK443774
Audantia hispaniolae	SBH193073	SMF104957	DO Cotuí	MK444032	MK443775
Audantia hispaniolae	SBH193074	SMF104958	DO Cotuí	MK444033	MK443776
Audantia hispaniolae	SBH193160	SMF104221	DO Loma Quita Espuela	MK444034	MK443777
Audantia hispaniolae	SBH193163	SMF104959	DO Loma Quita Espuela	MK444037	MK443780
Audantia hispaniolae	SBH193164	SMF104960	DO Loma Quita Espuela	MK444038	MK443781
Audantia hispaniolae	SBH193227	SMF104222	DO Tenares	MK444040	MK443782
Audantia hispaniolae	SBH193244	SMF104223	DO Maimón	MK444041	MK443783
Audantia hispaniolae	SBH193249	SMF104224	DO Punta Burén	MK444042	MK443784
Audantia hispaniolae	SBH193250	SMF104962	DO Punta Burén	MK444043	MK443785
Audantia hispaniolae	SBH193251	SMF104963	DO Punta Burén	MK444044	MK443786

Sample Name	Specimen ID	Museum ID	Abbreviated locality	Cyt b	ND2
Audantia hispaniolae	SBH193252	N/A	DO Punta Burén	MK444045	MK443787
Audantia hispaniolae	SBH193260	SMF104225	DO Villa Elisa	MK444046	MK443788
Audantia hispaniolae	SBH193261	SMF104964	DO Villa Elisa	MK444047	MK443789
Audantia hispaniolae	SBH193319	SMF104969	DO Guácara	MK444050	MK443791
Audantia hispaniolae	SBH193326	N/A	DO Loma Gajo del Rodeo	MK444052	MK443793
Audantia hispaniolae	SBH194368	SMF104228	DO Loma Monte Bonito	MK444053	N/A
Audantia hispaniolae	SBH194369	SMF104229	DO Loma Monte Bonito	MK444054	MK443794
Audantia hispaniolae	SBH194381	SMF104226	DO Apolinar Perdomo	MK444058	MK443798
Audantia hispaniolae	SBH194382	SMF104227	DO Apolinar Perdomo	MK444059	MK443799
Audantia hispaniolae	SBH194455	SMF104230	DO Loma del Curro	MK444063	MK443802
Audantia hispaniolae	SBH194456	SMF104231	DO Loma del Curro	MK444064	MK443803
Audantia hispaniolae	SBH194491	SMF104232	DO Cacique Enriquillo	MK444068	N/A
Audantia hispaniolae	SBH194532	N/A	HT Mole Saint-Nicolas	N/A	MK443807
Audantia hispaniolae	SBH194562	SMF104233	HT Douceur	MK444069	MK443808
Audantia hispaniolae	SBH266271	SMF104234	DO El Azul	MK444079	MK443815
Audantia hispaniolae	SBH266272	SMF104235	DO El Azul	MK444080	MK443816
Audantia hispaniolae	SBH266342	SMF104236	DO Rosa de la Piedra	MK444082	MK443818
Audantia hispaniolae	SBH266344	SMF104238	DO Rosa de la Piedra	MK444084	MK443820
Audantia hispaniolae	SBH266346	SMF104237	DO Calimetes	MK444086	MK443822
Audantia hispaniolae	SBH266351	N/A	DO Rosa de la Piedra	MK444087	MK443823
Audantia hispaniolae	SBH266352	N/A	DO Rosa de la Piedra	MK444088	MK443824
Audantia hispaniolae	SBH266747	N/A	DO Carmona	MK444092	N/A
Audantia hispaniolae	SBH266936	SMF104239	DO Sabana de la Mar	MK444093	MK443828
Audantia hispaniolae	SBH266937	SMF104240	DO Sabana de la Mar	MK444094	MK443829
Audantia hispaniolae	SBH267609	SMF104241	DO Puerto Escondido	MK444103	MK443838
Audantia hispaniolae	SBH267616	SMF104242	DO Los Pinos	MK444104	MK443839
Audantia hispaniolae	SBH267805	N/A	DO El Valle	MK444106	MK443841
Audantia hispaniolae	SBH267806	N/A	DO El Valle	MK444107	MK443842
Audantia hispaniolae	SBH267807	N/A	DO El Valle	MK444108	MK443843
Audantia hispaniolae	SBH268655	SMF104974	HT Furcy	MK444109	MK443844
Audantia hispaniolae	SBH268657	SMF104243	HT Furcy	MK444110	MK443845
Audantia hispaniolae	SBH268682	SMF104244	HT Bonga	MK444114	MK443849
Audantia hispaniolae	SBH269245	SMF104247	HT Gonave	MK444128	MK443862
Audantia hispaniolae	SBH269247	SMF104245	HT Gonave	MK444130	MK443864
Audantia hispaniolae	SBH269249	SMF104246	HT Gonave	MK444132	MK443866
Audantia hispaniolae	SBH269279	SMF104248	HT Anse-à-Galets	MK444136	MK443869
Audantia hispaniolae	SBH269280	SMF104249	HT Anse-à-Galets	MK444137	MK443870
Audantia hispaniolae	SBH269281	SMF104250	HT Anse-à-Galets	MK444138	MK443871
Audantia hispaniolae	SBH269298	SMF104252	HT Chinchiron	MK444142	MK443873

Sample Name	Specimen ID	Museum ID	Abbreviated locality	Cyt b	ND2
Audantia hispaniolae	SBH269299	SMF104976	HT Chinchiron	MK444143	MK443874
Audantia hispaniolae	SBH269301	SMF104251	HT Ouest	N/A	MK443875
Audantia hispaniolae	SBH269307	SMF104975	HT Ouest	MK444144	MK443877
Audantia hispaniolae	SBH269934	N/A	HT Morne Boeuf	MK444158	MK443891
Audantia hispaniolae	SBH269945	SMF104253	HT Morne Basile	MK444159	MK443894
Audantia hispaniolae	SBH269946	SMF104254	HT Morne Basile	MK444160	MK443895
Audantia hispaniolae	SBH269952	SMF104255	HT Morne Basile	MK444164	MK443899
Audantia hispaniolae	SBH269953	SMF104256	HT Morne Boeuf	MK444165	MK443900
Audantia hispaniolae	SBH191607	USNM 575355	HT Thomazeau	MK443971	MK443720
Audantia hispaniolae	SBH191638	USNM 575356	HT Carisse	MK443973	MK443722
Audantia hispaniolae	SBH191707	USNM 575357	HT Bernard	MK443976	MK443726
Audantia hispaniolae	SBH191708	USNM 575358	HT Bernard	MK443977	MK443727
Audantia hispaniolae	SBH192417	USNM 575343	HT Ca Soleil	MK444008	MK443753
Audantia hispaniolae	SBH192421	USNM 575344	HT Ca Soleil	MK444010	MK443755
Audantia hispaniolae	SBH192996	USNM 575324	DO Playa Chiquita	MK444024	MK443767
Audantia hispaniolae	SBH193161	USNM 575333	DO Loma Quita Espuela	MK444035	MK443778
Audantia hispaniolae	SBH193162	USNM 575334	DO Loma Quita Espuela	MK444036	MK443779
Audantia hispaniolae	SBH193263	USNM 575340	DO Maimón	MK444048	MK443790
Audantia hispaniolae	SBH193324	USNM 575342	DO Paso de Bao	MK444051	MK443792
Audantia hispaniolae	SBH194370	USNM 575325	DO Loma Monte Bonito	MK444055	MK443795
Audantia hispaniolae	SBH194371	USNM 575326	DO Loma Monte Bonito	MK444056	MK443796
Audantia hispaniolae	SBH194372	USNM 575327	DO Loma Monte Bonito	MK444057	MK443797
Audantia hispaniolae	SBH194383	USNM 575328	DO Apolinar Perdomo	MK444060	MK443800
Audantia hispaniolae	SBH194384	USNM 575329	DO Apolinar Perdomo	MK444061	N/A
Audantia hispaniolae	SBH194457	USNM 575330	DO Loma del Curro	MK444065	MK443804
Audantia hispaniolae	SBH194458	USNM 575331	DO Loma del Curro	MK444066	MK443805
Audantia hispaniolae	SBH194459	USNM 575332	DO Loma del Curro	MK444067	MK443806
Audantia hispaniolae	SBH194563	USNM 575359	HT Douceur	MK444070	N/A
Audantia hispaniolae	SBH266273	USNM 575341	DO El Azul	MK444081	MK443817
Audantia hispaniolae	SBH266343	USNM 575335	DO Rosa de la Piedra	MK444083	MK443819
Audantia hispaniolae	SBH266345	USNM 575336	DO Rosa de la Piedra	MK444085	MK443821
Audantia hispaniolae	SBH266938	USNM 575337	DO Sabana de la Mar	MK444095	MK443830
Audantia hispaniolae	SBH266939	USNM 575338	DO Sabana de la Mar	MK444096	MK443831
Audantia hispaniolae	SBH266941	USNM 575339	DO Sabana de la Mar	MK444097	MK443832
Audantia hispaniolae	SBH268659	USNM 575360	HT Furcy	MK444111	MK443846
Audantia hispaniolae	SBH268660	USNM 575361	HT Furcy	MK444112	MK443847
Audantia hispaniolae	SBH268661	USNM 575362	HT Furcy	MK444113	MK443848
Audantia hispaniolae	SBH269246	USNM 575345	HT Gonave	MK444129	MK443863
Audantia hispaniolae	SBH269248	USNM 575346	HT Gonave	MK444131	MK443865

Sample Name	Specimen ID	Museum ID	Abbreviated locality	Cyt b	ND2
Audantia hispaniolae	SBH269278	USNM 575348	HT Anse-à-Galets	MK444135	MK443868
Audantia hispaniolae	SBH269282	USNM 575349	HT Anse-à-Galets	MK444139	MK443872
Audantia hispaniolae	SBH269306	USNM 575363	HT Ouest	N/A	MK443876
Audantia hispaniolae	SBH269357	USNM 575350	HT Anse-à-Galets	MK444145	MK443878
Audantia hispaniolae	SBH269933	USNM 575351	HT Morne Boeuf	MK444157	MK443890
Audantia hispaniolae	SBH269947	USNM 575352	HT Morne Basile	MK444161	MK443896
Audantia hispaniolae	SBH269948	USNM 575353	HT Morne Basile	MK444162	MK443897
Audantia hispaniolae	SBH269951	USNM 575354	HT Morne Basile	MK444163	MK443898
Audantia hispaniolae	SBH102931	N/A	DO Los Pinos	MK443962	MK443711
Audantia hispaniolae	SBH161505	USNM 329096	DO Cacique Enriquillo	MK444210	AY263093
Audantia hispaniolae	SBH161620	USNM 329100	DO Río Limpio CREAR	MK443968	MK443718
Audantia hispaniolae	SBH191605	SMF104212	HT Thomazeau	MK443969	AY263116
Audantia hispaniolae	SBH191606	SMF104948	HT Thomazeau	MK443970	MK443719
Audantia hispaniolae	SBH274988	SMF97863	DO La Romana	MK444186	MK443912
Audantia hispaniolae	SBH274989	N/A	DO La Romana	MK444187	MK443913
Audantia hispaniolae	SBH274990	SMF97867	DO El Seibo	MK444188	MK443914
Audantia hispaniolae	SBH274991	SMF97868	DO El Seibo	MK444189	MK443915
Audantia hispaniolae	SBH274993	SMF97870	DO Bávaro	N/A	MK443917
Audantia hispaniolae	SBH274996	SMF97876	DO El Portillo	MK444193	MK443707
Audantia hispaniolae	SBH274997	SMF97881	DO El Limón	MK444194	MK443920
Audantia hispaniolae	SBH274998	SMF97884	DO El Limón	MK444195	MK443921
Audantia hispaniolae	SBH274999	N/A	DO Boca Chica	N/A	MK443922
Audantia hispaniolae	SBH275011	SMF97898	DO Ébano Verde	MK444203	MK443933
Audantia hispaniolae	SBH275012	N/A	DO Puerto Plata	N/A	MK443934
Audantia hispaniolae	SBH275013	SMF99018	DO Loma Teleférico	MK444204	MK443935
Audantia hispaniolae	SBH275014	SMF99021	DO Yásica Arriba	N/A	MK443936
Audantia hispaniolae	SBH275015	SMF99024	DO Yásica Arriba	N/A	MK443937
Audantia hispaniolae	AY263027	N/A	DO Pepillo Salcedo	N/A	AY263027
Audantia hispaniolae	AY263028	N/A	DO Monte Cristi	N/A	AY263028
Audantia hispaniolae	AY263029	N/A	DO Cayo Monte Grande	N/A	AY263029
Audantia hispaniolae	AY263030	N/A	DO Cayo Monte Grande	N/A	AY263030
Audantia hispaniolae	AY263031	N/A	DO Isla Cabras	N/A	AY263031
Audantia hispaniolae	AY263032	N/A	DO Isla Cabras	N/A	AY263032
Audantia hispaniolae	AY263033	N/A	DO Isla Cabras	N/A	AY263033
Audantia hispaniolae	AY263034	N/A	DO Isla Cabras	N/A	AY263034
Audantia hispaniolae	AY263035	N/A	DO Isla Cabras	N/A	AY263035
Audantia hispaniolae	AY263043	N/A	DO Sosua	N/A	AY263043
Audantia hispaniolae	AY263044	N/A	DO Sosua	N/A	AY263044
Audantia hispaniolae	AY263045	N/A	DO Sosua	N/A	AY263045

Sample Name	Specimen ID	Museum ID	Abbreviated locality	Cyt b	ND2
Audantia hispaniolae	AY263046	N/A	DO Sosua	N/A	AY263046
Audantia hispaniolae	AY263047	N/A	DO Sosua	N/A	AY263047
Audantia hispaniolae	AY263053	N/A	DO San Francisco de Macorís	N/A	AY263053
Audantia hispaniolae	AY263054	N/A	DO San Francisco de Macorís	N/A	AY263054
Audantia hispaniolae	AY263055	N/A	DO San Francisco de Macorís	N/A	AY263055
Audantia hispaniolae	AY263056	N/A	DO San Francisco de Macorís	N/A	AY263056
Audantia hispaniolae	AY263057	N/A	DO San Francisco de Macorís	N/A	AY263057
Audantia hispaniolae	AY263063	N/A	DO Hato Mayor	N/A	AY263063
Audantia hispaniolae	AY263064	N/A	DO Hato Mayor	N/A	AY263064
Audantia hispaniolae	AY263065	N/A	DO Hato Mayor	N/A	AY263065
Audantia hispaniolae	AY263066	N/A	DO Hato Mayor	N/A	AY263066
Audantia hispaniolae	AY263067	N/A	DO Hato Mayor	N/A	AY263067
Audantia hispaniolae	AY263073	N/A	DO Bonao	N/A	AY263073
Audantia hispaniolae	AY263074	N/A	DO Nagua	N/A	AY263074
Audantia hispaniolae	AY263075	N/A	DO Los Haitises	N/A	AY263075
Audantia hispaniolae	AY263076	N/A	DO Los Haitises	N/A	AY263076
Audantia hispaniolae	AY263077	N/A	DO Los Haitises	N/A	AY263077
Audantia hispaniolae	AY263078	N/A	DO Los Haitises	N/A	AY263078
Audantia hispaniolae	AY263079	N/A	DO Los Haitises	N/A	AY263079
Audantia hispaniolae	AY263080	N/A	DO Los Haitises	N/A	AY263080
Audantia hispaniolae	AY263081	N/A	DO Miches	N/A	AY263081
Audantia hispaniolae	AY263082	N/A	DO Miches	N/A	AY263082
Audantia hispaniolae	AY263083	N/A	DO Miches	N/A	AY263083
Audantia hispaniolae	AY263084	N/A	DO Miches	N/A	AY263084
Audantia hispaniolae	AY263085	N/A	DO Miches	N/A	AY263085
Audantia hispaniolae	AY263086	N/A	DO Sánchez	N/A	AY263086
Audantia hispaniolae	AY263087	N/A	DO Las Terrenas	N/A	AY263087
Audantia hispaniolae	AY263088	N/A	DO Las Terrenas	N/A	AY263088
Audantia hispaniolae	AY263089	N/A	DO Las Terrenas	N/A	AY263089
Audantia hispaniolae	AY263090	N/A	DO Las Terrenas	N/A	AY263090
Audantia hispaniolae	AY263091	N/A	DO Las Terrenas	N/A	AY263091
Audantia hispaniolae	AY263097	N/A	DO Copey	N/A	AY263097
Audantia hispaniolae	AY263098	N/A	DO Dajabón	N/A	AY263098
Audantia hispaniolae	AY263099	N/A	DO Los Hidalgos	N/A	AY263099
Audantia hispaniolae	AY263100	N/A	DO Los Hidalgos	N/A	AY263100
Audantia hispaniolae	AY263101	N/A	DO Los Hidalgos	N/A	AY263101
Audantia hispaniolae	AY263102	N/A	DO Los Hidalgos	N/A	AY263102

Sample Name	Specimen ID	Museum ID	Abbreviated locality	Cyt b	ND2
Audantia hispaniolae	AY263103	N/A	DO Los Hidalgos	N/A	AY263103
Audantia hispaniolae	AY263104	N/A	DO Maizal	N/A	AY263104
Audantia hispaniolae	AY263105	N/A	DO San Juan	N/A	AY263105
Audantia hispaniolae	AY263106	N/A	DO San Juan	N/A	AY263106
Audantia hispaniolae	AY263107	N/A	DO San Juan	N/A	AY263107
Audantia hispaniolae	AY263108	N/A	DO San Juan	N/A	AY263108
Audantia hispaniolae	AY263109	N/A	DO San Juan	N/A	AY263109
Audantia hispaniolae	AY263110	N/A	DO Comendador	N/A	AY263110
Audantia hispaniolae	AY263111	N/A	DO Comendador	N/A	AY263111
Audantia hispaniolae	AY263112	N/A	DO Comendador	N/A	AY263112
Audantia hispaniolae	AY263113	N/A	DO Comendador	N/A	AY263113
Audantia hispaniolae	AY263114	N/A	DO Comendador	N/A	AY263114
Audantia hispaniolae	AY263115	N/A	DO Aguacate	N/A	AY263115
Audantia hispaniolae	KU290359	KU290359	DO El Azul	MK443958	MK443708
Audantia hispaniolae	KU290360	KU290360	DO El Azul	MK443959	MK443709
Audantia hispaniolae	KU316466	KU316466	DO Los Yayas	N/A	AY263094
Audantia hispaniolae	KU316467	KU316467	DO Los Yayas	N/A	AY263095
Audantia hispaniolae	KU316468	KU316468	DO Los Yayas	N/A	AY263096
Audantia hispaniolae	KU316477	KU316477	DO Neyba	N/A	AY263092
Audantia hispaniolae	KU316726	KU316726	DO Boca Chica	N/A	AY263058
Audantia hispaniolae	KU316727	KU316727	DO Boca Chica	N/A	AY263059
Audantia hispaniolae	KU316728	KU316728	DO Boca Chica	N/A	AY263060
Audantia hispaniolae	KU316729	KU316729	DO Boca Chica	N/A	AY263061
Audantia hispaniolae	KU316794	KU316794	DO Bayahibe	N/A	AY263068
Audantia hispaniolae	KU316851	KU316851	DO La Vega	N/A	AY263048
Audantia hispaniolae	KU316852	KU316852	DO La Vega	N/A	AY263049
Audantia hispaniolae	KU316853	KU316853	DO La Vega	N/A	AY263050
Audantia hispaniolae	KU316855	KU316855	DO La Vega	N/A	AY263051
Audantia hispaniolae	KU316860	KU316860	DO La Vega	N/A	AY263052
Audantia hispaniolae	KU316863	KU316863	DO Bonao	N/A	AY263069
Audantia hispaniolae	KU316864	KU316864	DO Bonao	N/A	AY263070
Audantia hispaniolae	KU316866	KU316866	DO Bonao	N/A	AY263071
Audantia hispaniolae	KU316867	KU316867	DO Bonao	N/A	AY263072
Audantia hispaniolae	KU316898	KU316898	DO La Romana	N/A	AY263062
Audantia hispaniolae	USNM 329094	USNM 329094	DO Sabana de la Mar	N/A	MK443942
Audantia hispaniolae	USNM 329095	USNM 329095	DO Sabana de la Mar	MK444209	MK443943
Audantia hispaniolae	USNM 329097	USNM 329097	DO Cacique Enriquillo	MK444211	MK443944
Audantia hispaniolae	USNM 329098	USNM 329098	DO Cacique Enriquillo	MK444212	MK443945
Audantia longitibialis	KU317191	KU317191	DO Los Tres Charcos	N/A	AY263010

Sample Name	Specimen ID	Museum ID	Abbreviated locality	Cyt b	ND2
Audantia longitibialis	USNM 549616	USNM 549616	DO Pedernales	N/A	AY263009
Audantia marcanoi	AY263005	N/A	DO Recodo	N/A	AY263005
Audantia marcanoi	AY263006	N/A	DO Recodo	N/A	AY263006
Audantia ravifaux	SBH274992	SMF97869	DO Bávaro	MK444190	MK443916
Audantia ravifaux	SBH274995	SMF97873	DO Bávaro	MK444192	MK443919
Audantia ravifaux	AY263123	N/A	DO La Romana	N/A	AY263123
Audantia ravifaux	AY263124	N/A	DO La Romana	N/A	AY263124
Audantia ravifaux	AY263125	N/A	DO La Romana	N/A	AY263125
Audantia ravifaux	AY263126	N/A	DO La Romana	N/A	AY263126
Audantia ravifaux	AY263127	N/A	DO Punta Cana Docks	N/A	AY263127
Audantia ravifaux	AY263128	N/A	DO Punta Cana Docks	N/A	AY263128
Audantia ravifaux	AY263129	N/A	DO Punta Cana Docks	N/A	AY263129
Audantia ravifaux	AY263130	N/A	DO Punta Cana Docks	N/A	AY263130
Audantia ravifaux	AY263131	N/A	DO Punta Cana Docks	N/A	AY263131
Audantia ravifaux	KU316797	KU316797	DO Isla Saona	N/A	AY263141
Audantia ravifaux	KU316829	KU316829	DO Isla Catalina	N/A	AY263142
Audantia saxatilis	SBH194433	SMF104303	DO Manantiales	MK444062	MK443801
Audantia saxatilis	SBH266697	N/A	DO La Zurza	MK444089	MK443825
Audantia saxatilis	AY263021	N/A	DO Canoa	N/A	AY263021
Audantia saxatilis	AY263022	N/A	DO Monte Río	N/A	AY263022
Audantia saxatilis	AY263023	N/A	DO Puerto Escondido	N/A	AY263023
Audantia saxatilis	AY263024	N/A	DO Baní	N/A	AY263024
Audantia saxatilis	AY263025	N/A	DO Baní	N/A	AY263025
Audantia saxatilis	KU317446	KU317446	DO Neyba	N/A	AY263026
Audantia shrevei	SBH193297	USNM 575376	DO Valle de Bao	MK444049	AY263036
Audantia shrevei	AY263037	N/A	DO San José de Ocoa	N/A	AY263037
Audantia shrevei	AY263038	N/A	DO San José de Ocoa	N/A	AY263038
Audantia shrevei	AY263039	N/A	DO San José de Ocoa	N/A	AY263039
Audantia shrevei	AY263040	N/A	DO San José de Ocoa	N/A	AY263040
Audantia shrevei	AY263041	N/A	DO San José de Ocoa	N/A	AY263041
Audantia strahmi	SBH192664	SMF104773	DO Hoyo de Pelempito	MK444021	N/A
Audantia strahmi	AY263007	N/A	DO Rd to Los Mercedes	N/A	AY263007
Audantia strahmi	AY263008	N/A	DO Aguacate	N/A	AY263008
Ctenonotus cristatellus	MVZ235204	MVZ235204	US Bosque Estatal	MK443960	MK443679
Ctenonotus distichus	SBH193223	SMF104946	DO Tenares	MK444039	AY263004