Norops tropidonotus is a ground anole found in the pine-oak and broad-leaf forests of Nuclear Central America, characterized by its stout body, medium size, large keeled dorsal scales, and deep tube-like axillary mite pockets. In the following contribution, the authors provide evidence for the recognition of four species in what formerly was considered as a single species, *N. tropidonotus*. Pictured here is an adult male of one of the new species, from near Pico Bonito Lodge, Departamento de Atlántida, Honduras, displaying its large dewlap.

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A taxonomic revision of the *Norops tropidonotus* complex (Squamata, Dactyloidae), with the resurrection of *N. spilorhipis* (Álvarez del Toro and Smith, 1956) and the description of two new species

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Abstract: We describe two new species of anoles from Honduras, which previously have been referred to as *Norops tropidonotus* by different authors: *Norops mccraniei* sp. nov. from the Chortís Highlands of Honduras, El Salvador, northern Nicaragua, and eastern Guatemala; and *Norops wilsoni* sp. nov. from the Atlantic slopes of the Cordillera Nombre de Dios (departments of Atlántida and Colón). Furthermore, we resurrect *Anolis tropidonotus spilorhipis* Álvarez del Toro and Smith, 1956 from synonymy with *Norops tropidonotus*. These four species are similar in external morphology, but differ by molecular distances, phylogenetic relationships, and in hemipenial morphology, as well as in subtle differences in several scalation and morphometric characters. Each of the six species in the *N. tropidonotus* complex exhibits a parapatric to allopatric distribution pattern.

Key Words: Cryptic species, DNA barcoding, hemipenial morphology, Nuclear Central America, 16S

Resumen: Se describen dos especies nuevas de anolis de Honduras, que anteriormente se han referido como *Norops tropidonotus* por diferentes autores: *Norops mccraniei* sp. nov. de las Chortís Highlands de Honduras, El Salvador, el norte de Nicaragua y el este de Guatemala; y *Norops wilsoni* sp. nov. de la vertiente Atlantica de la Cordillera Nombre de Dios (departamentos de Atlantida y Colón). Ademas, revalidamos *Anolis tropidonotus spilorhipis* Álvarez del Toro y Smith, 1956 de la sinonimía con *Norops tropidonotus*. Estas cuatro especies son similares en su morfología externa, pero difieren entre si por distancias moleculares, relaciones filogenéticas, en la morfología de los hemipenes, y además en diferencias sutiles en varios caracteres de escamación y morfometría. Cada una de las seis especies en el complejo de *N. tropidonotus* exhibe un patrón parapátrico a alopátrico de distribución.

Palabras Claves: ADN, códigos de barras, especies crípticas, morfología del hemipene, Centroamérica Norte, 16S

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INTRODUCTION

Nuclear Central America supports a diverse anole fauna that is reasonably well known (Köhler and Acevedo, 2004; McCranie and Köhler, 2015). One of the prominent components of the anole fauna at lowland and mid-elevations in this region is a robust ground anole, characterized by the presence of distinctly enlarged and strongly keeled dorsal scale rows, a tube-like axillary pocket, and a large orange male dewlap with a dark central streak, usually referred to as *Norops* (or *Anolis*) *tropidonotus*. Peters (1863: 135) described *Norops tropidonotus* (as *Anolis tropidonotus*) based on six syntypes from "Huanusco in Mexico" collected by Dr. Hille (lectotype ZMB 382, examined by GK). Smith and Taylor (1950: 60) suggested that the type locality was "probably, Huatusco, Veracruz," Mexico. Stuart (1955: 27) designated ZMB 382 as the lectotype for this taxon. Bocourt (1873a: 1) introduced the new species *Anolis metallicus* based on two syntypes from "Mexique" (MNHN 2890 and 1994.987, formerly MNHN 2890 and 2890A; examined by GK). In 1906, Barbour and Cole described *Anolis yucatanicus* based on three specimens (two adults and one juvenile; MCZ R-7036, R-119960–61, all three formerly under number MCZ 7036; examined by GK) from "Chichen-Itza, Yucatan," Mexico. Finally, Álvarez del Toro and Smith (1956: 9) described *Anolis tropidonotus spilorhipis* (holotype UIMNH 37972; examined by GK) from "Cerro Ombligo, 1280 m," Chiapas, Mexico, specified by Álvarez del Toro and Smith (1956: 3) as being "4 km. SSW of Villa Allende" and the latter village also known as San Fernando, "some 18 km. N Tuxtla Gutierrez." For most of the 20th century, these nominal taxa have been assigned to a single species, *Norops* (or *Anolis*) *tropidonotus* (e.g., Barbour, 1934; Peters and Donoso-Barros, 1970; Lee, 1996; Campbell, 1998). More recently, McCranie and Köhler (2001) described *N. wampuensis*, a species similar to *N. tropidonotus* in external appearance, but differing in size and a few subtle scalation characters (see Köhler, 2008; McCranie and Köhler, 2015). *Norops compressicauda* (Smith and Kerster, 1955) is another species similar to *N. tropidonotus* in scalation and body proportions, but which differs strikingly by the presence of a pink male dewlap and blue iris color in life. From this point on, we refer to the following species as the *Norops tropidonotus* complex: *N. compressicauda*, *N. tropidonotus*, *N. wampuensis*, and the three species-level lineages defined below.

In this study, we evaluate the molecular systematics (16S barcoding), as well as geographic variation of color in life, hemipenial morphology, scalation, and morphometrics of these anoles in order to clarify the taxonomic situation of the *N. tropidonotus* complex in Nuclear Central America.

MATERIALS AND METHODS

The specimens examined for this study were personally collected or borrowed from museums (See Appendix 1 for specimens examined). We followed the unified species concept (de Queiroz, 2007) in evaluating whether multiple species exist within a certain species complex. As lines of evidence for species delimitation, we applied a criterion for reproductive isolation (using molecular data) and a phenotypic criterion (external morphology: coloration, morphometrics, and scalation, as well as hemipenial morphology). For the former, we employed the genetic distinctness of the 16S rRNA gene that has been used widely in DNA barcoding studies of tropical herpetofauna (e.g., Vieites et al., 2009). We cut tissue samples from thigh muscle or the tip of the tail of selected individuals before they came into contact with formalin, and stored tissues in 98% non-denatured ethanol or SED buffer (20% DMSO, 0.25 M EDTA, pH 7.5, NaCl saturated). The tissue samples collected by GK were deposited in the collection of the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany. We extracted DNA following the protocol of Ivanova et al. (2006). To eliminate potential PCR-inhibiting contaminants, we incubated the tissue samples for 14 hrs at 4°C in 200 µL low PBS buffer (20 µL PBS in 180µL of water) before overnight digestion with the vertebrate lysis buffer at 56°C. After extraction, the DNA was eluted in 50 µL TE buffer. A fragment of the mitochondrial 16S rRNA gene was amplified in an Eppendorf Mastercycler® using the following protocol: initial denaturation for 2 min at 94°C; followed by 40 cycles with denaturation for 35 s at 94°C, hybridization for 35 s at 48.5°C, and elongation for 60 s at 72°C; and final elongation for 10 min at 72°C. The reaction mix for each sample contained 1 µL DNA template, 14 µL water, 2.5 µL PCR-buffer, 1 µL 25 mM $MgCl_2$, 4 µL 2.5 mM dNTPs (Invitrogen), 0.5 µL (containing 2.5 units) Taq Polymerase (PeqLab), and 1 µL of each primer (forward: L2510, 5'–CGCCTGTTTATCAAAAACAT–3'; reverse: H3056, 5'–CCGGTCTGAACTCAGATCACGT–3'; Eurofins MWG Operon).

We obtained a total of 52 16S sequences from populations assigned to the *Norops tropidonotus* complex, and added eight sequences of other *Norops* (six *N. uniformis* [Cope, 1885], one *N. compressicauda*, and one *N. lemurinus* [Cope, 1861]) as outgroup taxa, based on their previously proposed affinity to *N. tropidonotus* (see Appendix 3 for GenBank accession numbers).

We aligned the sequences with MUSCLE (Edgar, 2004) using the default settings in Geneious (Drummond et al., 2010). The manually refined final alignment of 60 sequences contained 581 positions, of which 116 were variable (excluding the outgroup). Using MEGA 5 (Tamura et al., 2011), we computed uncorrected pairwise genetic distances, determined HKY+G as the best-fitting substitution model using the Bayesian Information Criterion, and conducted a Maximum Likelihood (ML) analysis with 10,000 bootstrap replicates and gaps as a fifth character (i.e., using all sites). Using MrBayes 3.1.2, we conducted a Bayesian inference of phylogeny (BI; Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) running over 2×10^6 generations in two parallel runs with four chains each, sampled trees every 1,000 generations, and discarded the first 5% (burnin = 100) after verifying the previous convergence of the parallel runs by visually checking the logfile in Geneious. In evaluating the uncorrected *p*-distances calculated for our sample, we followed other recently published barcoding studies on Mesoamerican anoles (Lotzkat et al., 2011, 2013; Köhler et al., 2012, 2014a, b), as well as in the relative positions that the clades in question assume in the inferred phylogenetic trees.

We performed the application of a phenotypic criterion by examining external morphology: coloration, morphometrics, and scalation, as well as the hemipenial morphology of specimens (see Appendix 1). We preserved specimens by injecting a solution of 5 mL absolute (i.e., 36%) formalin in 1 L of 96% ethanol into the body cavity and thighs, after sprinkling the everted hemipenes and extended dewlaps with this solution, and stored them in 70% ethanol. Whenever possible, we everted the hemipenes of male specimens by injecting 70% ethanol into the hemipenial pockets after manually pre-everting the hemipenes. The abbreviations for museum collections follow Sabaj Pérez (2014), and the JHT field series numbers are associated with specimens deposited in the UF Herpetology collection in May of 2009, but presumed lost. We recorded the geographic coordinates and elevation by using Garmin GPS receivers with built-in altimeters. All of the coordinates are in decimal degrees and WGS 84 datum, and all the elevations are in meters above sea level. The capitalized colors and color codes (the latter in parentheses) are those of Köhler (2012) in the color descriptions of preserved specimens. We followed Köhler (2012) for the terminology of markings used in the color descriptions in life, and used Köhler (2014) for nomenclature and the definitions of morphological characters. We measured head length from the tip of the snout to the anterior margin of the ear opening, and snout length from the tip of the snout to the anterior border of the orbit. We determined head width with the broad tips of the calipers aligned with the levels of the posterior margin of the eye and supralabial scales, respectively, with the calipers held in a vertical position relative to the head. We counted dorsal and ventral scales at midbody along the midline, measured tail height and width at the point reached by the heel of the extended hind leg, and counted subdigital lamellae on Phalanges II to IV of Toe IV of the hind limbs, and separately on the distal phalanx. We considered the scale directly anterior to the circumnasal to be a prenasal. When we found variation in the bilateral symmetry of scale characters, we present this as right side/left side.

We cleared and stained selected specimens (see Appendix 2) using the method proposed by Mayorga (1965) and stored them in Glycerin. We examined the cleared and stained specimens for variation in skeletal characters, focusing on the cranium.

RESULTS

We acquired 60 16S sequences from our samples, with a maximum length of 581 bp and with 125 variable and 78 parsimony-informative sites. The results of our analyses of this 16S sequence data indicate a high degree of genetic differentiation among several populations formerly referred to as *Norops tropidonotus* (Fig. 1; Table 1). Our Bayesian and ML phylogenetic analyses produced congruent topologies that recovered four reciprocally monophyletic clusters (Fig. 1), which have a bimodal distribution of intra-cluster (0.0–1.1%) and between-cluster (2.9–4.5%) genetic distances (Table 1). The three clades, made up of samples from the Atlantic versant of Mexico and northern Guatemala, from Chiapas, and from eastern Nuclear Central America, together form an unresolved polytomy, sister to a fourth clade made up of samples from the piedmont of the Cordillera Nombre de Dios in Honduras. We interpret the high degree of genetic distinctiveness among these four geographically discrete genetic clusters as evidence for a lack of gene flow, and conclude that these four lineages represent species-level units.

Thus, we recognize four species among the anoles formerly referred to as *N. tropidonotus*: Species A (northern edge of the Central Depression of Chiapas), Species B (Atlantic slopes of southern Mexico, including the Yucatan Peninsula and the El Petén region of Guatemala), Species C (Atlantic slopes of the Cordillera Nombre de Dios in northern Honduras), and Species D (Chortís Highlands of Honduras, El Salvador, Nicaragua, and Guatemala). This four species hypothesis is supported by the results of our analysis of hemipenial morphology (Fig. 2). Males of our Species B are unique among all the OTUs by the presence of a small, unilobed hemipenis (vs. large and bilobed) with the sulcus spermaticus opening into a single broad concave area at the base of the apex (vs. a closed sulcus spermaticus on the apical branches) and the absence of an asulcate processus (vs. asulcate processus present). Males of our Species A differ from males of our Species C and D by the presence of a single asulcate ridge-like processus on the distal part of the truncus (vs. two asulcate processi present, a finger-like one at the base of the apex and a conical one at the base of the truncus in Species D and a single finger-like one at the base of the apex in Species C, respectively). In morphometric characters and in scalation, these four species are more conservative and not easily differentiated (Table 2, Fig. 3). Subtle differences among most of these species are evident, however, further supporting the recognition of each of these as a distinct species. Our examination of the cleared and stained specimens did not yield any consistent osteological differences among the taxa studied (Fig. 4).

Our Species B includes specimens from the general area of the type locality of *Norops tropidonotus* (i.e., Veracruz, Mexico; our OTU 2); thus, this is the valid name for this species. The type locality of the nominal species *Anolis tropidonotus spilorhipis* Álvarez del Toro and Smith, 1956 is from the general area of our OTU 1 (northern edge of the Central Depression of Chiapas) and therefore, this is the valid name for this species and herewith we resurrect this nominal taxon from the synonymy with *Norops tropidonotus* (i.e., *Norops spilorhipis*). The type locality of the nominal species *Anolis metallicus* Bocourt, 1873a is too vague ("Mexique") to be of use in allocating this name to one of our species. Based on its external morphology, however, we assign it to our OTU 2 (*N. tropidonotus sensu stricto*); thus, *N. metallicus* remains in the synonymy of *N. tropidonotus*. The type locality of the nominal species *Anolis yucatanicus* Barbour and Cole, 1906 is from the general area of our OTU 2 (*N. tropidonotus sensu stricto*) and remains in the synonymy of *N. tropidonotus*. No names are available for our Species C and D, so we describe each as a new species below.

Norops mccraniei sp. nov.

Figs. 2d, 4a, 5–7, 14a

Holotype: SMF 100107, adult male, from Municipalidad de Gualaco: Montaña de Jacaleapa, headwaters of Río del Oro, E slope Cerro de Bañaderos, 15.083288°N, 86.208250°W, elev. 1,180 m asl, Departamento de Olancho, Honduras; collected by Josiah H. Townsend, Onán Reyes-Calderón, and Mark Bonta on 12 April 2011; original field number JHT-3393.

Paratypes: All from Municipalidad de Gualaco, Departamento de Olancho, Honduras: SMF 100108, same collecting data as holotype except collected on 11 April 2011; SMF 100104–06, seepage bog approximately 3.75 km N Saguay, 15.145257°N, 86.041291°W, elev. 580 m, collected by Josiah H. Townsend, David Medina, Melissa Medina-Flores, and Onán Reyes-Calderón on 10 April 2011; SMF 100109, pine forest lagoon below El Norte, 15.060539°N, 86.174181°W, elev. 980 m, collected by Josiah H. Townsend, Onán Reyes-Calderón, and Mark

Bonta on 11 April 2011; SMF 100110, Parque Nacional Montaña de Botaderos: Municipalidad de Gualaco, Cerro de las Cruces, 15.360621°N, 86.063470°W, elev. 1,160 m, collected by Josiah H. Townsend, David Medina, Melissa Medina-Flores, Onán Reyes-Calderón, Mark Bonta, Christopher Begley, Ricardo Steiner, and Robert Hyman on 15 April 2011; SMF 100111–12, Parque Nacional Montaña de Botaderos: Municipalidad de Gualaco, Quebrada Las Delicias, 15.370624°N, 86.047456°W, elev. 1,205 m, collected by Josiah H. Townsend, Melissa Medina-Flores, Onán Reyes-Calderón, David Medina, Mark Bonta, Christopher Begley, Ricardo Steiner, and Robert Hyman on 16 April 2011. SMF 100104–05, 100108, 100111 are adult males, the remaining paratypes are adult females, except for SMF 100109, which is a subadult female.

Referred specimens: see Appendix 1.

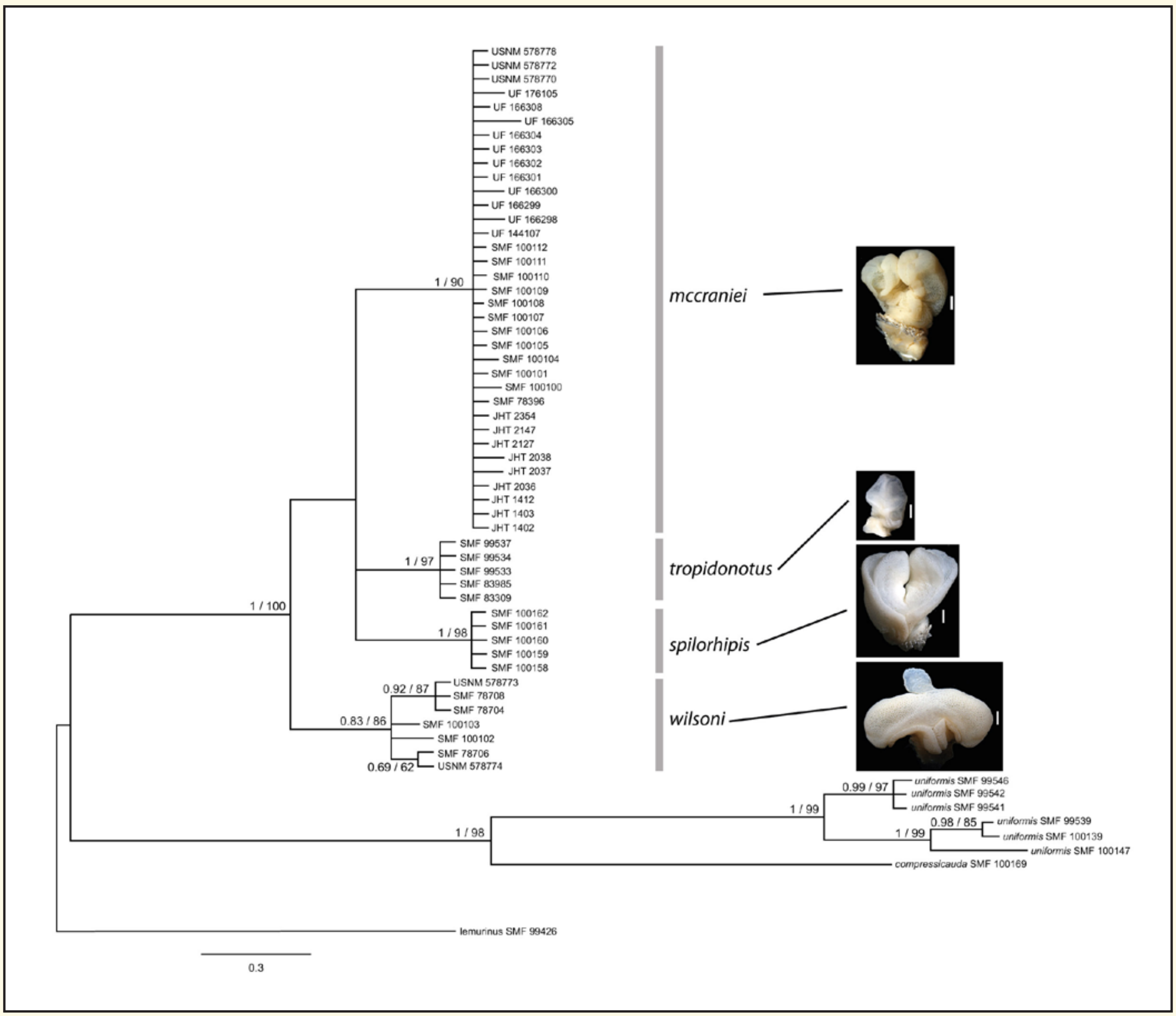

Fig. 1. Results of molecular genetic analyses. Consensus tree from Bayesian analysis of 16S sequences. At nodes, bootstrap values (recovered in the Maximum Likelihood inference of phylogeny) are preceded by Bayesian posterior probabilities. All hemipenis images are drawn to same scale. Scale bars equal 1.0 mm.

Table 1. Comparison of intraspecific and interspecific *p*-distances for 16S among members of the *Norops tropidonotus* complex; intraspecific differences are in bold.

	N. mccraniei	*N. spilorhipus*	*N. tropidonotus*	*N. wilsoni*
Norops mccraniei (*n* = 35)	**0.000–0.008**	0.032–0.044	0.032–0.044	0.032–0.045
Norops spilorhipus (*n* = 5)	0.032–0.044	**0.000**	0.029–0.034	0.034–0.042
Norops tropidonotus (*n* = 5)	0.032–0.044	0.029–0.034	**0.000**	0.036–0.037
Norops wilsoni (*n* = 6)	0.032–0.045	0.034–0.042	0.036–0.037	**0.000–0.011**

***Diagnosis*:** A medium-sized (maximum snout–vent length (SVL) 54.5 mm in males, 53.0 mm in females) species (our Species D of the *Norops tropidonotus* complex) of the genus *Norops* (*sensu* Nicholson et al., 2012) that is most similar in external morphology to *N. tropidonotus*, *N. compressicauda*, *N. spilorhipis*, *N. wampuensis*, and a species described below (our Species C of the *Norops tropidonotus* complex). These five species and *N. mccraniei* are differentiated from all other anoles by a combination of the following characters: (1) distinctly enlarged and strongly keeled dorsal scale rows, (2) a tube-like axillary pocket, (3) scales anterior to ear opening keeled and much larger than small and granular scales posterior to ear opening, and (4) a lack of enlarged postcloacal scales in males. *Norops mccraniei* differs from the other five species in the *Norops tropidonotus* complex by mean genetic distances of 3.2–4.5%. *Norops mccraniei* can be distinguished from *N. compressicauda* by the presence of a large orange male dewlap with a dark central streak (vs. a pink male dewlap in *N. compressicauda*) and a brownish-red iris color (vs. blue in *N. compressicauda*). *Norops mccraniei* differs from *N. tropidonotus* by the presence of a large, bilobed hemipenis with a large asulcate processus (vs. hemipenis small, unilobate without an asulcate processus in *N. tropidonotus*). *Norops mccraniei* differs from *N. wampuensis* by the presence of a distinct dark streak in the male dewlap and a slightly larger size reaching 54.5 mm in males, 53.0 mm SVL in females (vs. distinct dark central streak absent in male dewlap and males and females reaching 51 mm SVL in *N. wampuensis*). *Norops mccraniei* differs from *N. spilorhipis* by the presence of a hemipenis with two asulcate processi, a finger-like one at the base of the apex and a conical one at the base of the truncus (vs. a single asulcate ridge-like processus on the distal part of the truncus). For differences between *N. mccraniei* and the species described below, see the account of the new species. *Norops mccraniei* differs from the somewhat similar Central American species *N. humilis* (Peters, 1863), *N. marsupialis* (Taylor, 1956), *N. quaggulus* (Cope, 1885), and *N. uniformis* by the presence of keeled scales anterior to ear opening, much larger than small and granular scales posterior to ear opening, and a larger size, reaching 54.5 mm in males, 53.0 mm SVL in females (vs. scales anterior and posterior to ear opening subequal, small, and granular, SVL of adults < 51 mm in *N. humilis*, < 49 mm in *N. marsupialis*, < 42 mm in *N. quaggulus*, and < 42 mm in *N. uniformis,* respectively).

***Description of the holotype*:** Adult male, as indicated by everted hemipenes and a well-developed dewlap; snout–vent length 52.0 mm; tail length 79.0 mm, tail incomplete; tail slightly compressed in cross section, tail height 2.7 mm, tail width 1.7 mm; axilla to groin distance 19.6 mm; head length 13.3 mm, head length/snout–vent length ratio 0.26; snout length 5.4 mm; head width 8.7 mm; longest toe of adpressed hind limb reaching to a point between eye and nostril; shank length 16.0 mm, shank length/head length ratio 1.20; longest finger of adpressed forelimb reaching about 3.0 mm beyond anterior insertion of hind limb; dorsal head scales strongly keeled in internasal, prefrontal, frontal, and parietal areas, mostly unicarinate, some tricarinate, mostly oriented longitudinally; a moderate frontal depression present; parietal depression shallow; 7 postrostrals; anterior nasal single, contacting rostral and 1st supralabial; 8 internasals; canthal ridge sharply defined; scales comprising supraorbital semicircles keeled, largest scale in semicircles about same size as largest supraocular scale; supraorbital semicircles not well defined; one scale separating supraorbital semicircles at narrowest point; 2/2 scales separating supraorbital semicircles and interparietal at narrowest point; interparietal not well defined, only slightly enlarged relative to adjacent scales, surrounded by scales of moderate size, longer than wide, smaller than ear opening; three rows of about 6–7 moderately enlarged, keeled supraocular scales; several enlarged supraoculars in broad contact with supraorbital semicircles; 2 elongate superciliaries, one above the other; 3 enlarged canthals; 7 scales between second canthals; 8 scales between posterior canthals; loreal region slightly concave, 18/17 strongly keeled loreal scales in maximum of four horizontal rows; 5 supralabials and 5 infralabials to level below center of eye; suboculars weakly to strongly keeled, narrowly in contact with supralabials; ear opening vertically oval; scales anterior to ear opening enlarged, keeled, much larger than those posterior to ear opening; 6 postmentals, outer pair largest; keeled granular scales present on chin and throat; male dewlap moderately large, extending to level of axilla; no nuchal crest or dorsal ridge; about 10–12 middorsal scale rows greatly enlarged, strongly keeled, paramedian scales larger than vertebral scales, dorsal scales lateral to middorsal series abruptly larger than granular lateral scales; no enlarged scales scattered among keeled, imbricate laterals; 26 dorsal scales along vertebral midline between levels of axilla and groin; 14 dorsal scales along vertebral midline contained in one head length; ventral scales on midsection smaller than largest dorsal scales; ventral body scales strongly keeled, mucronate, imbricate; 33 ventral scales along midventral line between levels of axilla and groin; 20 ventral scales contained in one head length; 78 scales around midbody; tube-like, scaleless axillary pocket present; precloacal scales keeled; no enlarged postcloacal scales in males; all subcaudal scales keeled, mucronate; lateral caudal scales keeled, mucronate, homogeneous although indistinct division in segments discernable; dorsal medial caudal scales keeled, not enlarged, not forming crest; most scales on anterior surface of antebrachium strongly keeled, unicarinate; digital pads dilated, dilated pad about two times width of non-dilated scales on distal phalanx; distal phalanx narrower than and raised from dilated pad; 26/25 lamellae under phalanges II–IV of 4th toe; and 7 scales under distal phalanx of 4th toe.

The completely everted hemipenis is a large bilobate organ with well-developed, long lobes; sulcus spermaticus bordered by well-developed sulcal lips and bifurcating at base of apex with the branches continuing as closed furrows to the tip of the lobes where they open into small concave areas, one on each lobe; a finger-like asulcate processus at the base of the apex and a conical one at the base of the truncus; lobes strongly calyculate, truncus with folds.

After about five years in preservative, the coloration was recorded as follows: dorsal surface of head Ground Cinnamon (270) with a Dark Brownish Olive (127) interorbital bar and a suffusion of Dark Neutral Gray (299) in parietal region; dorsal surfaces of neck and limbs Dark Neutral Gray (299) with suffusions of Pratt's Payne's Gray (293); dorsal surfaces of body and tail Smoke Gray (266) with Olive-Brown (278) blotches and Sepia (279) chevrons; ventral surface of head Pale Pinkish Buff (3) with Sepia (279) suffusions; and ventral surfaces of body and limbs Smoke Gray (267).

Variation**:** The paratypes and referred specimens agree well with the holotype in general morphology and scalation (see Table 2). The coloration in life of several individuals of this species was reported in McCranie and Köhler (2015: 179) as follows: "KU 194307 (Finca Naranjito, Cortés, Honduras), adult male: dorsum brown with darker brown middorsal markings; dewlap reddish orange with burnt orange central streak and pale yellow scales, including marginals. KU 194305 (Finca Naranjito, Cortés, Honduras), adult female: dorsum pale bronze-brown with wide, dark brown-bordered tan middorsal stripe; belly cream; some scales of throat with reddish orange bases. KU 194306 (Finca Naranjito, Cortés, Honduras), adult female: middorsal pale area scalloped and outlined by brown; dark brown interocular bar present."

Natural history notes**:** *Norops mccraniei* inhabits a wide variety of habitats, particularly those associated with upland pine-oak forests and adjacent areas of both drier and wetter habitats (Fig. 8). This anole frequently is encountered in both natural and disturbance-related edge habitats, including fence rows and agricultural lands, and often is observed during the daytime while active on the ground or low vegetation. It typically sleeps on the ground under leaf litter or other cover, and females are more terrestrial than males (Jackson, 1973). This species is a common inhabitant of moderate and intermediate elevation coffee plantations throughout its range. The ecological distribution includes the Premontane Moist Forest formation and peripherally into the Lowland Arid Forest, Lowland Dry Forest, Lowland Moist Forest, Premontane Dry Forest, Lower Montane Wet Forest, and Lower Montane Moist Forest formations. Jackson (1973) reported on the ecology and demographics of a population of *N. mccraniei* (as *Anolis tropidonotus*) from an undisturbed old growth pine-oak forest outside of Siguatepeque, Departamento de Comayagua, Honduras, and estimated a home-range size of 115–190 m^2 for males and 20–35 m^2 for females. We have found *N. mccraniei* in sympatry with congeners *N. cupreus* (Hallowell, 1860), *N. lemurinus*, *N. rodriguezii* (Bocourt, 1873b), and *N. yoroensis* McCranie, Nicholson, and Köhler, 2001.

Geographic distribution**:** *Norops mccraniei* occurs at low, moderate, and intermediate elevations (200–1,740 m) throughout much of Honduras except for the Atlantic slopes of the Cordillera Nombre de Dios in northern Honduras, as well as in extreme northwestern El Salvador, northern Nicaragua, and eastern Guatemala (Fig. 9). This species appears to be absent from the Caribbean slopes of the Cordillera Nombre de Dios in northern Honduras and the eastern lowlands of La Mosquitia in Honduras and northeastern Nicaragua.

***Etymology*:** The specific name *mccraniei* honors our friend and colleague James Randall (Randy) McCranie, who is one of the leading authorities of the Honduran herpetofauna. Randy is known for his thorough and detailed herpetological work and has authored numerous articles on the amphibians and reptiles of Honduras, as well as several monographic treatments of its herpetofauna.

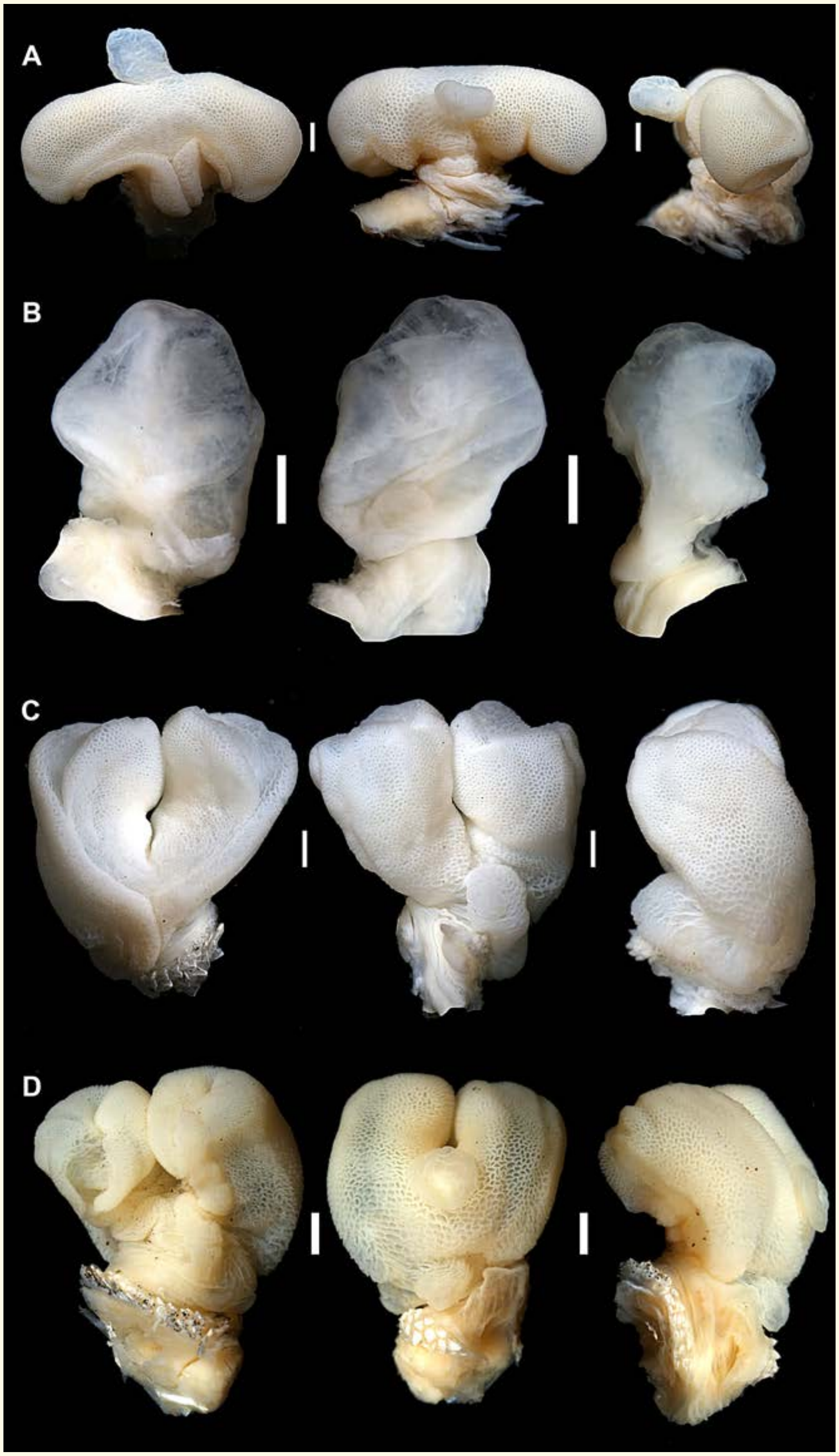

Fig. 2. Hemipenes of (a) *N. wilsoni* (SMF 78039); (b) *N. tropidonotus* (SMF 83989); (c) *Norops spilorhipis* (SMF 100163); (d) *N. mccraniei* (SMF 100108). Sulcate view left, asulcate view in center, lateral view right. Scale bars equal 1.0 mm.

Table 2. Selected measurements, proportions, and scale characters of *Norops tropidonotus* and related species. Range is followed by mean value and standard deviation in parentheses.

		Norops tropidonotus	***Norops spilorhipis***	***Norops mccraniei***	***Norops wilsoni***	***Norops compressicauda***
		♂15, ♀13	♂6, ♀6	♂16, ♀18	♂13, ♀14	♂7, ♀3
Maximum SVL	Males	56.5	61.0	54.5	59.0	55.0
	Females	58.0	56.0	53.0	53.0	43.5
Tail length / SVL	Males	1.62–2.00 (1.81 ± 0.13)	1.43–1.81 (1.65 ± 0.16)	1.71–1.85 (1.78 ± 0.05)	1.62–1.78 (1.70 ± 0.12)	1.48–1.56 (1.52 ± 0.04)
	Females	1.53–1.77 (1.64 ± 0.08)	1.46–1.47 (1.47 ± 0.01)	1.60–1.72 (1.66 ± 0.04)	1.44–1.53 (1.48 ± 0.04)	1.47–1.54 (1.51 ± 0.04)
Vertical diameter of tail / horizontal diameter of tail	Males	1.29–1.63 (1.45 ± 0.10)	1.44–1.63 (1.55 ± 0.07)	1.24–1.63 (1.48 ± 0.12)	1.38–1.55 (1.47 ± 0.07)	1.50–1.76 (1.67 ± 0.09)
	Females	1.29–1.71 (1.45 ± 0.12)	1.22–1.67 (1.47 ± 0.23)	1.16–1.44 (1.32 ± 0.09)	1.30–1.56 (1.45 ± 0.09)	1.35–1.38 (1.36 ± 0.02)
Axilla–groin distance / SVL	Males	0.36–0.43 (0.39 ± 0.02)	0.36–0.40 (0.38 ± 0.01)	0.34–0.42 (0.39 ± 0.02)	0.36–0.43 (0.39 ± 0.02)	0.32–0.41 (0.36 ± 0.03)
	Females	0.36–0.45 (0.39 ± 0.03)	0.38–0.43 (0.40 ± 0.02)	0.39–0.46 (0.42 ± 0.02)	0.37–0.44 (0.40 ± 0.03)	0.38–0.40 (0.39 ± 0.01)
Head length / SVL	Males	0.25–0.28 (0.26 ± 0.01)	0.23–0.25 (0.24 ± 0.01)	0.26–0.28 (0.27 ± 0.01)	0.25–0.28 (0.27 ± 0.01)	0.27–0.29 (0.28 ± 0.01)
	Females	0.24–0.27 (0.26 ± 0.01)	0.24–0.26 (0.25 ± 0.00)	0.25–0.28 (0.26 ± 0.01)	0.26–0.30 (0.27 ± 0.01)	0.27 (0.27 ± 0.00)
Head length / head width	Males	1.45–1.59 (1.53 ± 0.04)	1.52–1.58 (1.55 ± 0.02)	1.42–1.62 (1.53 ± 0.05)	1.49–1.64 (1.56 ± 0.05)	1.59–1.65 (1.61 ± 0.03)
	Females	1.52–1.57 (1.55 ± 0.02)	1.52–1.58 (1.55 ± 0.02)	1.44–1.57 (1.52 ± 0.04)	1.49–1.62 (1.56 ± 0.05)	1.53–1.60 (1.56 ± 0.04)
Head width / SVL	Males	0.16–0.18 (0.17 ± 0.01)	0.15–0.16 (0.16 ± 0.00)	0.16–0.18 (0.17 ± 0.01)	0.16–0.18 (0.17 ± 0.01)	0.17–0.18 (0.17 ± 0.00)
	Females	0.15–0.18 (0.17 ± 0.01)	0.15–0.17 (0.16 ± 0.01)	0.16–0.18 (0.17 ± 0.00)	0.17–0.19 (0.17 ± 0.01)	0.17–0.18 (0.17 ± 0.00)
Snout length / SVL	Males	0.10–0.11 (0.11 ± 0.00)	0.10–0.11 (0.10 ± 0.00)	0.10–0.12 (0.11 ± 0.00)	0.10–0.11 (0.11 ± 0.00)	0.11–0.13 (0.12 ± 0.01)
	Females	0.10–0.11 (0.11 ± 0.00)	0.10–0.11 (0.11 ± 0.00)	0.10–0.12 (0.11 ± 0.00)	0.11–0.12 (0.11 ± 0.01)	0.11–0.12 (0.11 ± 0.01)
Snout length / head length	Males	0.40–0.42 (0.41 ± 0.01)	0.41–0.43 (0.42 ± 0.01)	0.39–0.44 (0.41 ± 0.01)	0.39–0.42 (0.40 ± 0.01)	0.41–0.48 (0.43 ± 0.02)
	Females	0.40–0.42 (0.41 ± 0.01)	0.41–0.44 (0.43 ± 0.01)	0.39–0.45 (0.42 ± 0.01)	0.39–0.42 (0.40 ± 0.01)	0.39–0.44 (0.42 ± 0.02)
Shank length / SVL	Males	0.29–0.34 (0.31 ± 0.01)	0.28–0.30 (0.29 ± 0.01)	0.28–0.33 (0.30 ± 0.01)	0.28–0.32 (0.30 ± 0.01)	0.28–0.31 (0.30 ± 0.01)
	Females	0.27–0.33(0.30 ± 0.02)	0.28–0.30 (0.29 ± 0.01)	0.27–0.32 (0.29 ± 0.01)	0.27–0.32 (0.29 ± 0.01)	0.29–0.31 (0.29 ± 0.01)
Shank length / head length	Males	1.09–1.28 (1.18 ± 0.05)	1.16–1.24 (1.20 ± 0.03)	1.04–1.23 (1.13 ± 0.06)	1.06–1.15 (1.11 ± 0.03)	1.01–1.12 (1.06 ± 0.03)
	Females	1.01–1.20 (1.14 ± 0.06)	1.14–1.17 (1.16 ± 0.02)	1.02–1.19 (1.10 ± 0.05)	1.03–1.10 (1.07 ± 0.02)	1.05–1.13 (1.08 ± 0.04)
Number of medial dorsal scales in one head length	Males	12–20 (16.0 ± 2.0)	15–18 (17.0 ± 1.4)	12–18 (14.9 ± 2.0)	12–17 (14.3 ± 1.5)	14–18 (15.7 ± 1.4)
	Females	14–19 (16.3 ± 1.9)	14–18 (16.0 ± 1.4)	12–18 (15.0 ± 1.8)	12–16 (14.0 ± 1.3)	13–17 (15.3 ± 2.1)

Number of medial ventral scales in one head length	Males	18–24 (20.7 ± 1.6)	18–26 (22.0 ± 3.2)	16–25 (21.4 ± 2.6)	18–26 (21.7 ± 2.6)	24–32 (26.3 ± 2.7)
	Females	16–22 (18.9 ± 1.6)	16–22 (19.8 ± 2.5)	14–22 (18.0 ± 2.3)	15–26 (27.3 ± 3.4)	18–26 (22.7 ± 4.2)
Number of medial dorsal scales between levels of axilla and groin	Males	20–29 (26.0 ± 2.4)	28–32 (30.5 ± 1.4)	23–35 (27.1 ± 3.3)	23–28 (25.0 ± 1.7)	22–28 (24.9 ± 2.5)
	Females	25–31 (27.7 ± 1.9)	29–36 (32.3 ± 2.4)	25–32 (28.8 ± 2.0)	23–30 (26.6 ± 2.0)	24–29 (26.7 ± 2.5)
Number of medial ventral scales between levels of axilla and groin	Males	30–36 (32.7 ± 1.7)	32–41 (37.8 ± 3.3)	30–36 (33.4 ± 2.0)	28–39 (34.0 ± 2.7)	34–44 (39.0 ± 3.7)
	Females	29–35 (27.1 ± 1.9)	34–38 (35.8 ± 1.6)	27–35 (30.7 ± 2.3)	30–39 (33.6 ± 2.8)	35–41 (38.7 ± 3.2)
Number of scales around midbody	Males	64–78 (72.1 ± 4.2)	78–88 (81.3 ± 3.7)	70–94 (78.6 ± 7.7)	62–78 (70.0 ± 4.2)	66–74 (71.4 ± 3.0)
	Females	68–80 (73.2 ± 4.9)	74–86 (80.0 ± 5.1)	70–90 (75.4 ± 5.3)	62–74 (68.9 ± 3.8)	68–70 (69.3 ± 1.2)
Subdigital lamellae on Phalanges II–IV of Toe IV		25–31 (27.1 ± 1.2)	23–28 (25.5 ± 1.7)	24–29 (25.9 ± 1.5)	23–31 (26.9 ± 1.8)	22–25 (23.8 ± 1.1)
Subdigital lamellae on distal phalanx of Toe IV		6–9 (7.3 ± 0.7)	7–9 (7.9 ± 0.5)	7–9 (7.5 ± 0.6)	7–9 (7.7 ± 0.6)	6–7 (6.2 ± 0.4)
Number of scales between supraorbital semicircles		1–2 (1.8 ± 0.4)	1–2 (1.7 ± 0.5)	0–3 (1.3 ± 0.6)	1–2 (1.4 ± 0.5)	2–3 (2.5 ± 0.5)
Number of scales between interparietal plate and supraorbital semicircles		2–4 (2.8 ± 0.6)	2–3 (2.8 ± 0.3)	1–3 (2.6 ± 0.4)	1–3 (2.3 ± 0.4)	2–3 (2.8 ± 0.3)
Number of scales between subocular scales and supralabials		0–1 (0.9 ± 0.4)	0–1 (0.9 ± 0.3)	0–1 (0.6 ± 0.5)	0–1 (0.9 ± 0.3)	1 (1.0 ± 0.0)
Number of supralabials to level below center of eye		5–8 (5.9 ± 0.6)	5–7 (5.9 ± 0.7)	5–6 (5.4 ± 0.6)	5–7 (5.8 ± 0.5)	6–7 (6.3 ± 0.5)
Number of infralabials to level below center of eye		5–7 (5.8 ± 0.7)	5–7 (5.9 ± 0.7)	4–7 (5.5 ± 0.6)	5–6 (5.6 ± 0.5)	6–8 (6.8 ± 0.6)
Number of sublabials		0	0–1 (0.1 ± 0.3)	0–1 (0.0 ± 0.1)	0	0
Total number of loreals		19–35 (27.6 ± 3.7)	22–37 (30.7 ± 4.4)	17–35 (25.6 ± 4.8)	23–41 (29.3 ± 4.6)	36–43 (38.5 ± 2.3)
Number of horizontal loreal scale rows		4–6 (5.4 ± 0.6)	5–6 (5.8 ± 0.4)	4–6 (5.3 ± 0.6)	5–7 (5.5 ± 0.7)	6–7 (6.3 ± 0.5)
Number of postrostrals		7–8 (7.4 ± 0.5)	7–9 (7.4 ± 0.7)	6–8 (7.2 ± 0.6)	6–8 (7.2 ± 0.5)	7–8 (7.7 ± 0.5)
Number of postmentals		5–7 (5.9 ± 0.4)	4–7 (5.4 ± 0.8)	4–8 (5.9 ± 1.0)	4–6 (4.9 ± 0.8)	6–8 (6.6 ± 1.0)
Number of scales between nasals		8–10 (8.9 ± 0.7)	8–10 (9.3 ± 0.8)	7–10 (8.5 ± 0.7)	8–10 (8.4 ± 0.6)	8–11 (9.5 ± 0.8)
Number of greatly enlarged supraoculars		0–4 (0.8 ± 1.0)	0–3(1.3 ± 0.9)	0–3 (0.5 ± 0.8)	0–3 (0.3 ± 0.7)	0–5 (1.5 ± 1.5)
Number of moderately enlarged supraoculars		4–11 (7.5 ± 1.8)	4–10 (6.8 ± 1.9)	3–10 (6.8 ± 1.5)	4–10 (7.2 ± 1.5)	2–6 (4.3 ± 1.3)
Number of scales between 2nd canthals		7–9 (8.4 ± 0.7)	7–9 (8.1 ± 0.9)	6–9 (7.5 ± 0.8)	7–9 (8.0 ± 0.6)	7–9 (7.9 ± 0.6)
Number of scales between posterior canthals		9–14 (10.7 ± 1.2)	9–11 (9.9 ± 0.9)	8–12 (9.7 ± 1.4)	9–12 (10.7 ± 0.8)	9–11 (9.7 ± 0.7)
Number of rows of moderately to greatly enlarged dorsal scales		10–14 (11.8 ± 1.1)	11–14 (12.8 ± 1.0)	10–14 (12.2 ± 0.9)	10–13 (11.7 ± 0.8)	10–12 (11.2 ± 0.8)

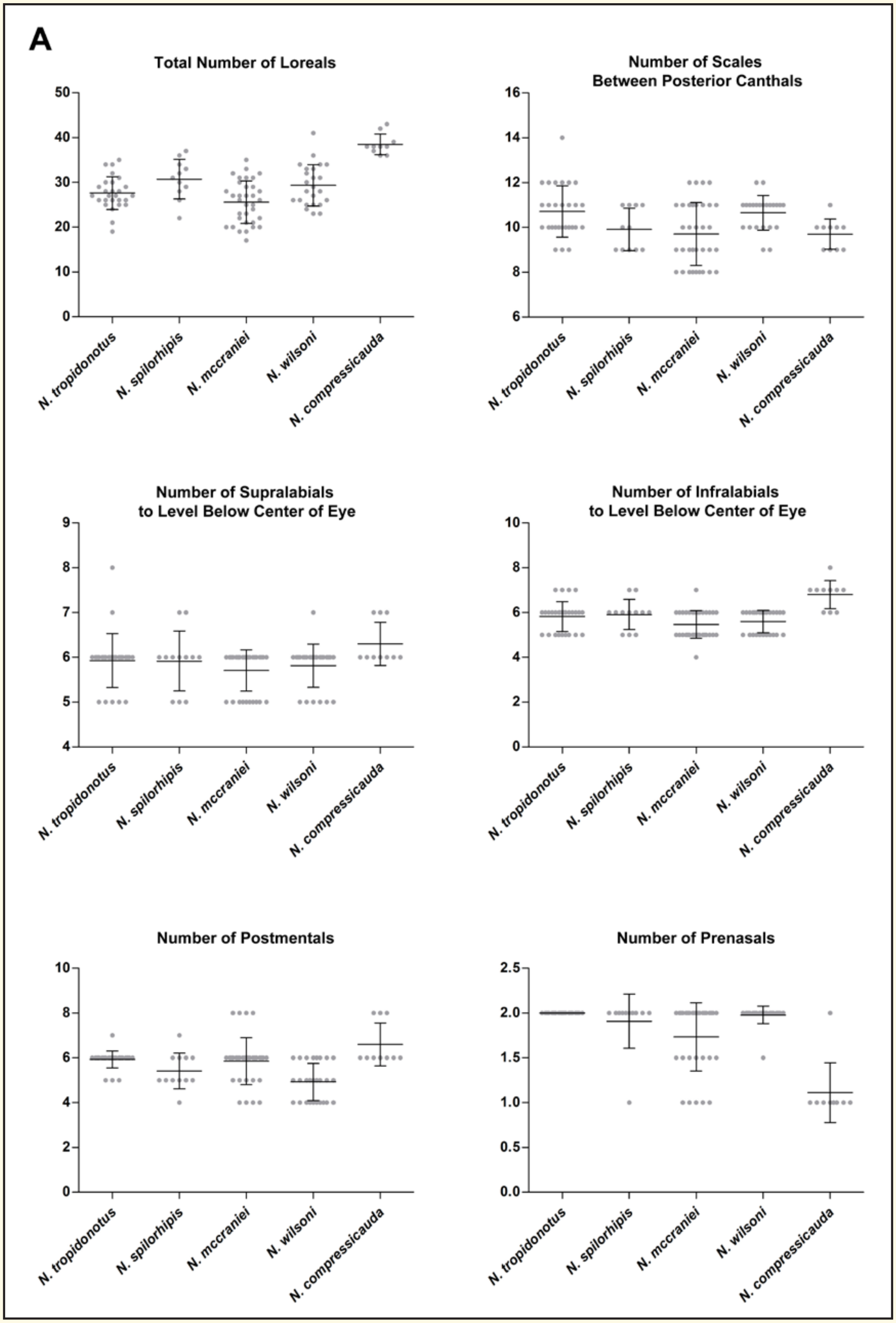

Fig. 3. (A) Scatter plots illustrating morphological variation in the species related to *Norops tropidonotus*.

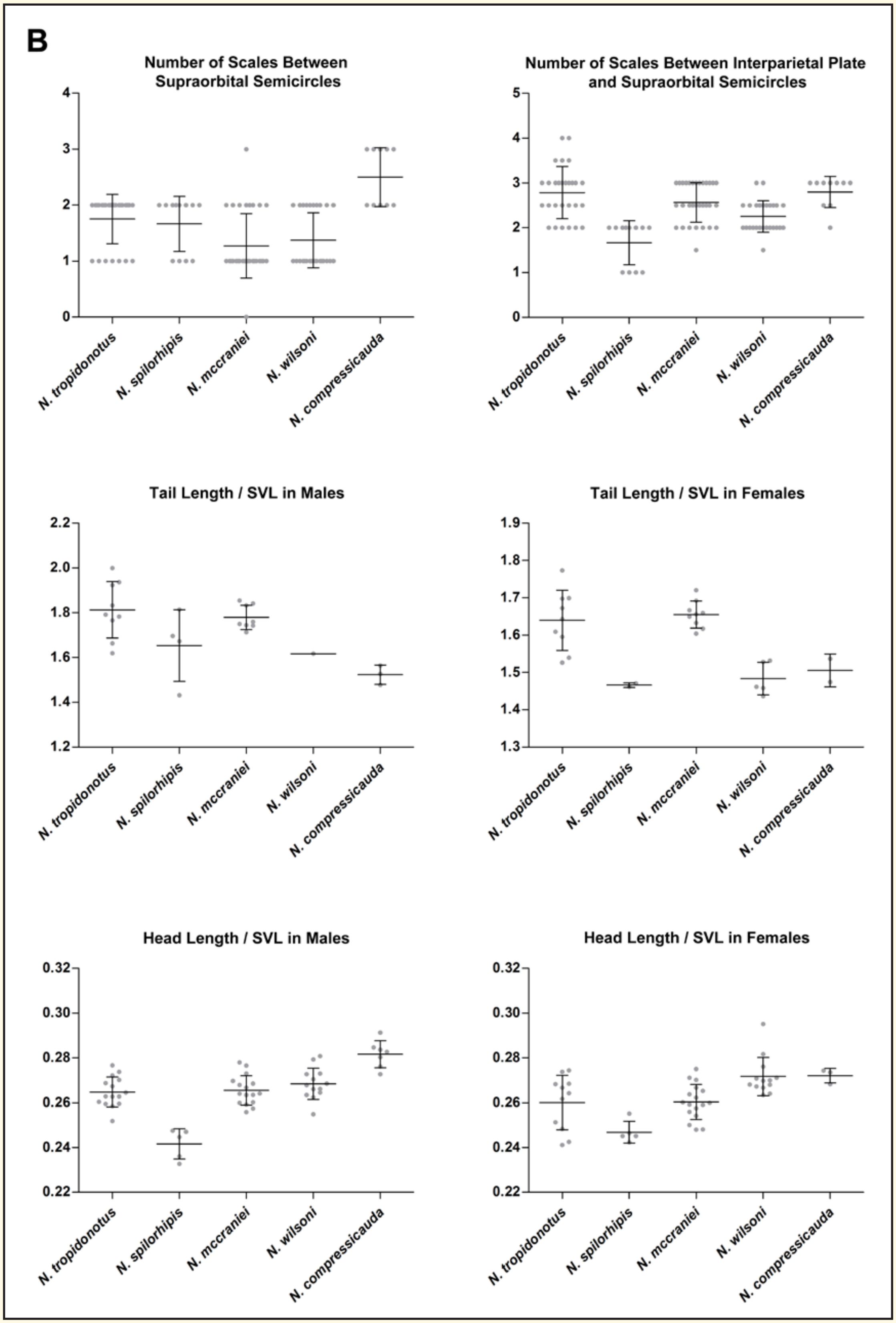

Fig. 3. (B) Scatter plots illustrating morphological variation in the species related to *Norops tropidonotus*.

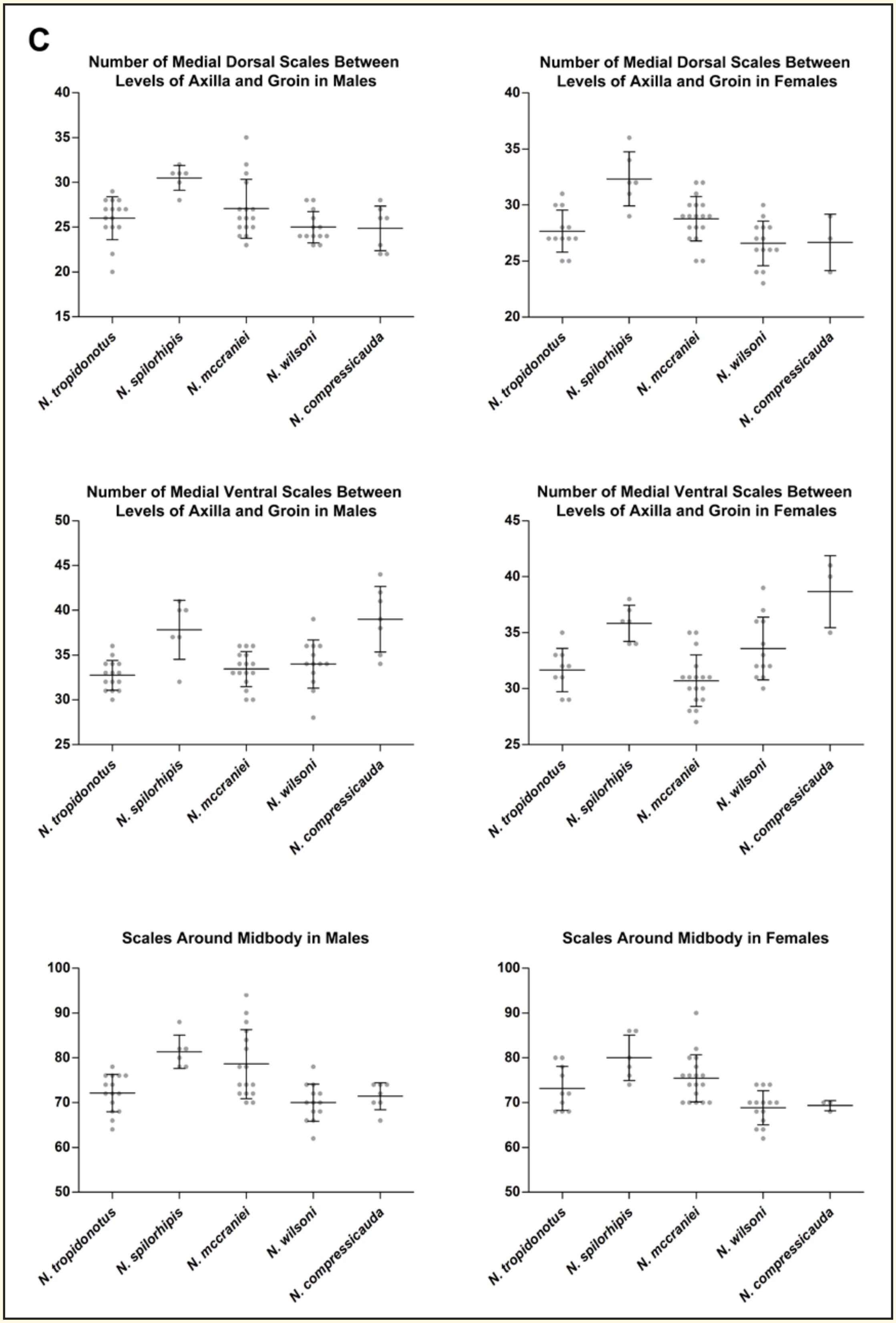

Fig. 3. (C) Scatter plots illustrating morphological variation in the species related to *Norops tropidonotus*.

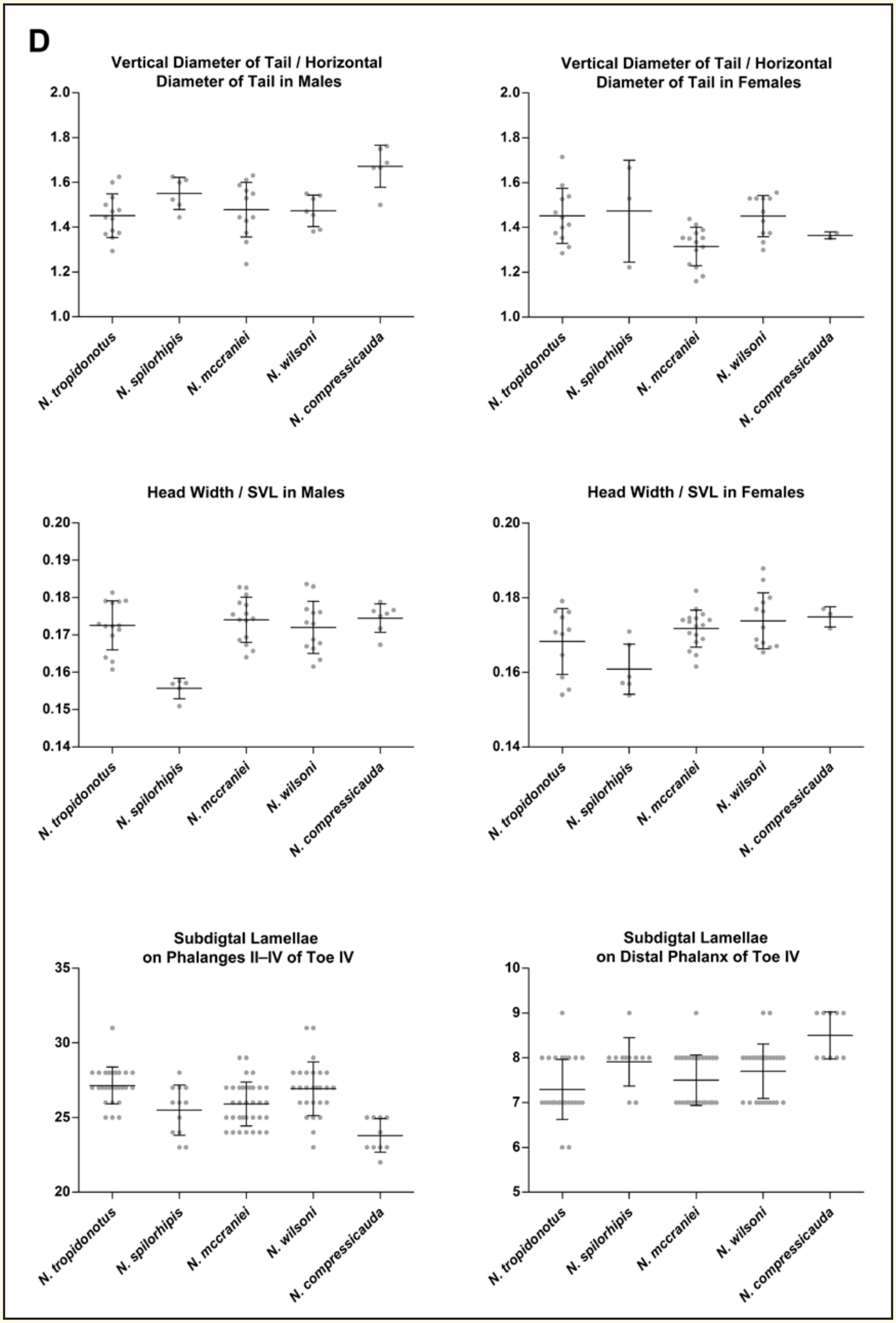

Fig. 3. (D) Scatter plots illustrating morphological variation in the species related to *Norops tropidonotus*.

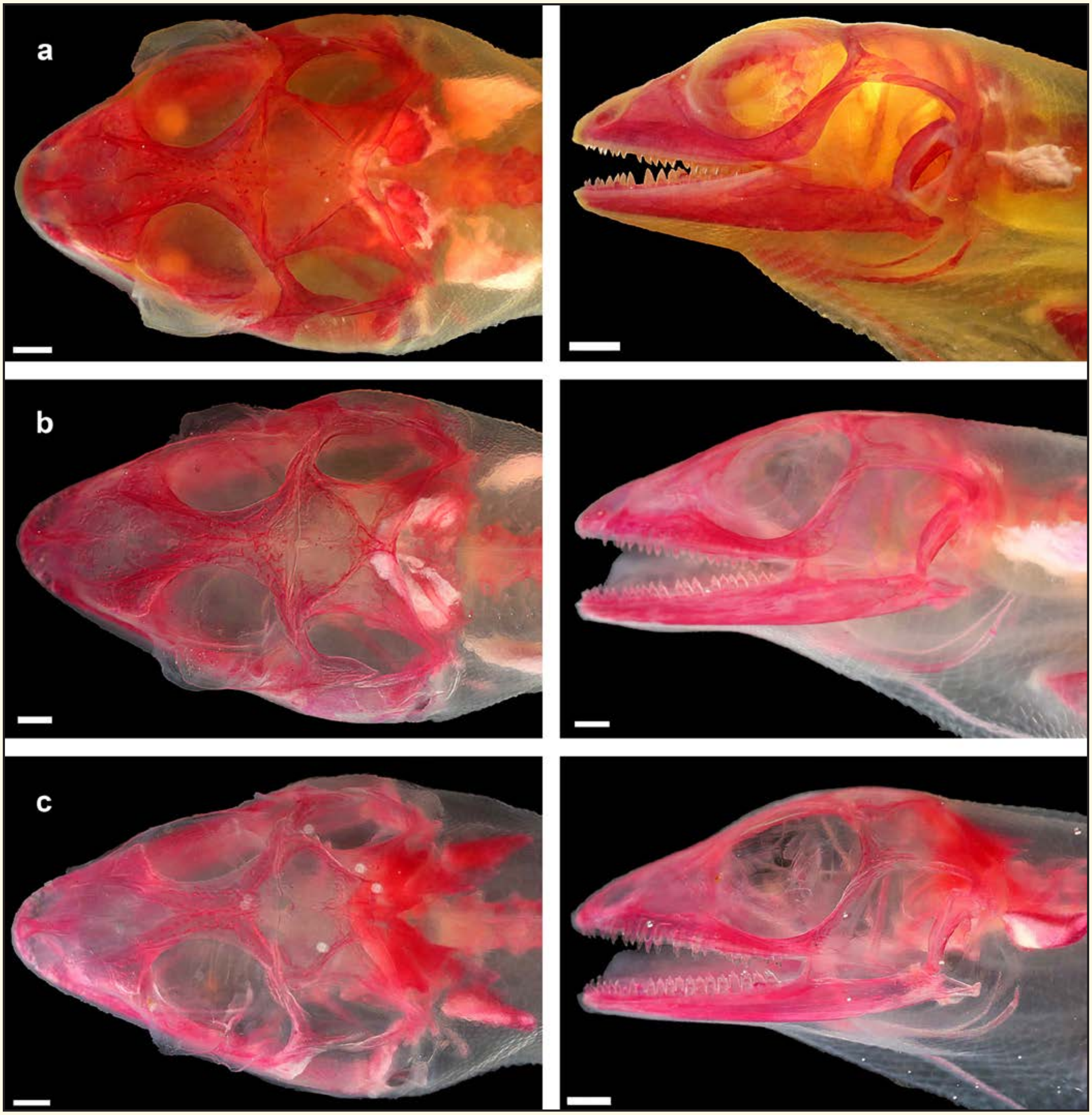

Fig. 4. Cleared and stained specimens: (a) *Norops mccraniei* (SMF 79059); (b) *N. wilsoni* (SMF 79057); and (c) *N. wampuensis* (SMF 79904). Dorsal view left, lateral view right. Scale bars equal 1.0 mm.

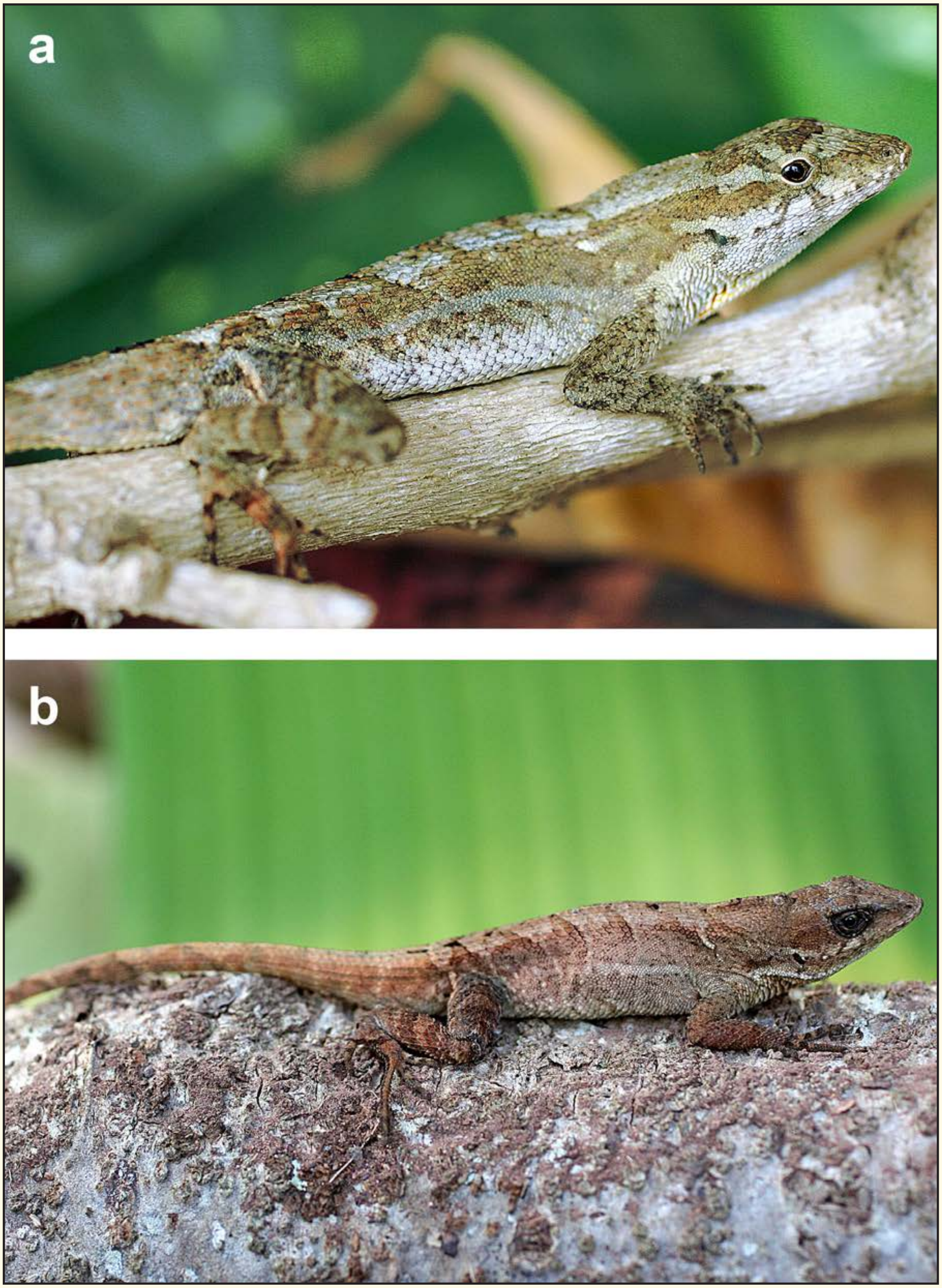

Fig. 5. *Norops mccraniei* in life: (a) adult male from the vicinity of the type locality in Jacaleapa, Departamento de Olancho, Honduras; and (b) adult male from Los Planes, Parque Nacional Montaña de Yoro, Departamento de Francisco Morazán, Honduras.

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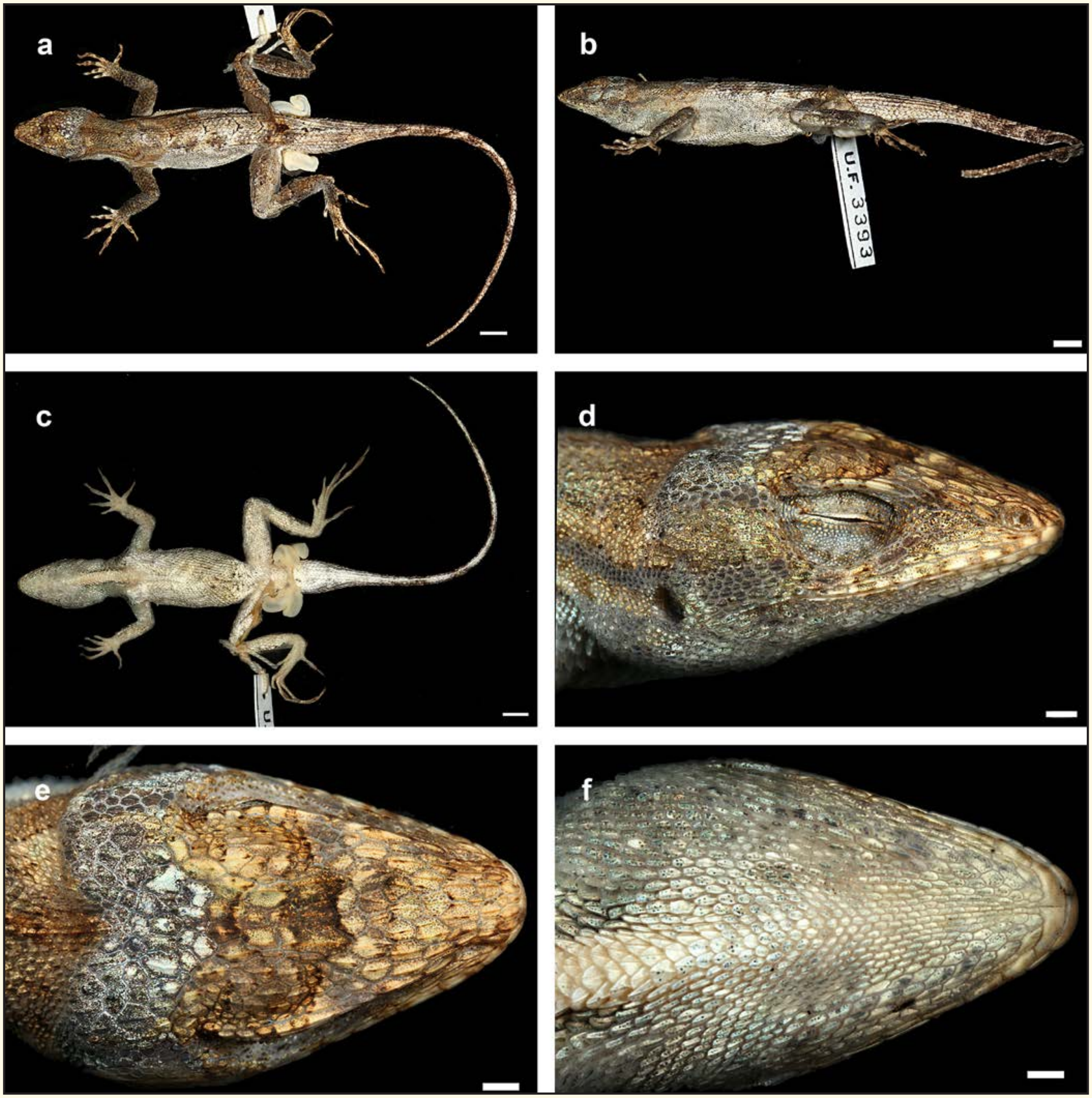

Fig. 6. Holotype of *Norops mccraniei* (SMF 100107): (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; and (f) ventral view of head. Scale bars equal 5.0 mm in (a–c) and 1.0 mm in (d–f), respectively. © Gunther Köhler

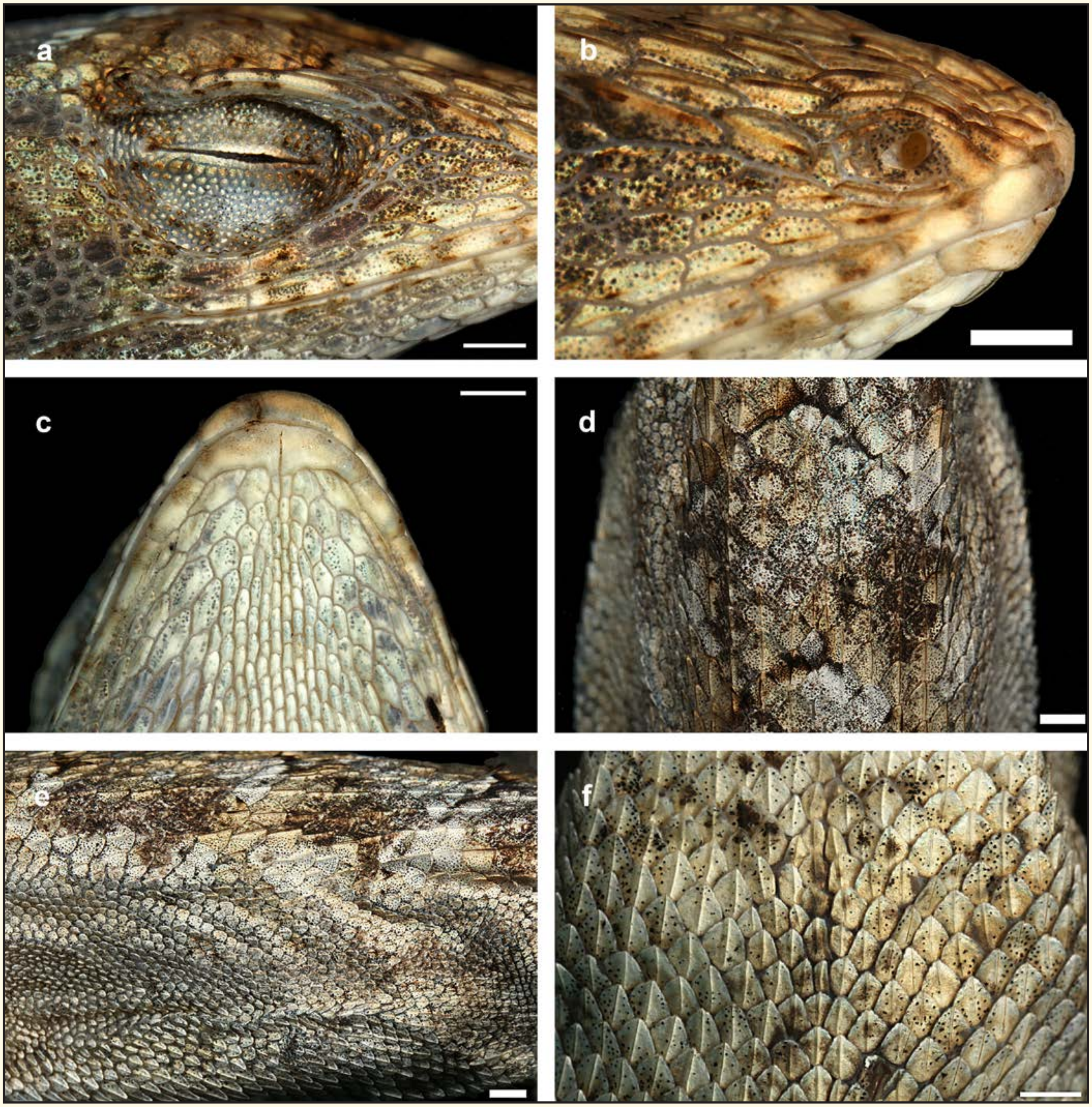

Fig. 7. Holotype of *Norops mccraniei* (SMF 100107): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region (e) flank region; and (f) midventer. Scale bars equal 1.0 mm.

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Fig. 8. Habitat of *Norops mccraniei*: (A) Parque Nacional Montaña de Yoro, Montaña de la Sierra, elev. 1,650 m, Departamento de Francisco Morazán, Honduras; (B) Parque Nacional Montana de Botaderos: Municipalidad de Gualaco, Cerro de las Cruces, elev. 1,160 m, Departamento de Olancho, Honduras; (C) Montaña de Jacaleapa, near type locality, elev. 1,180 m, Departamento de Olancho, Honduras.

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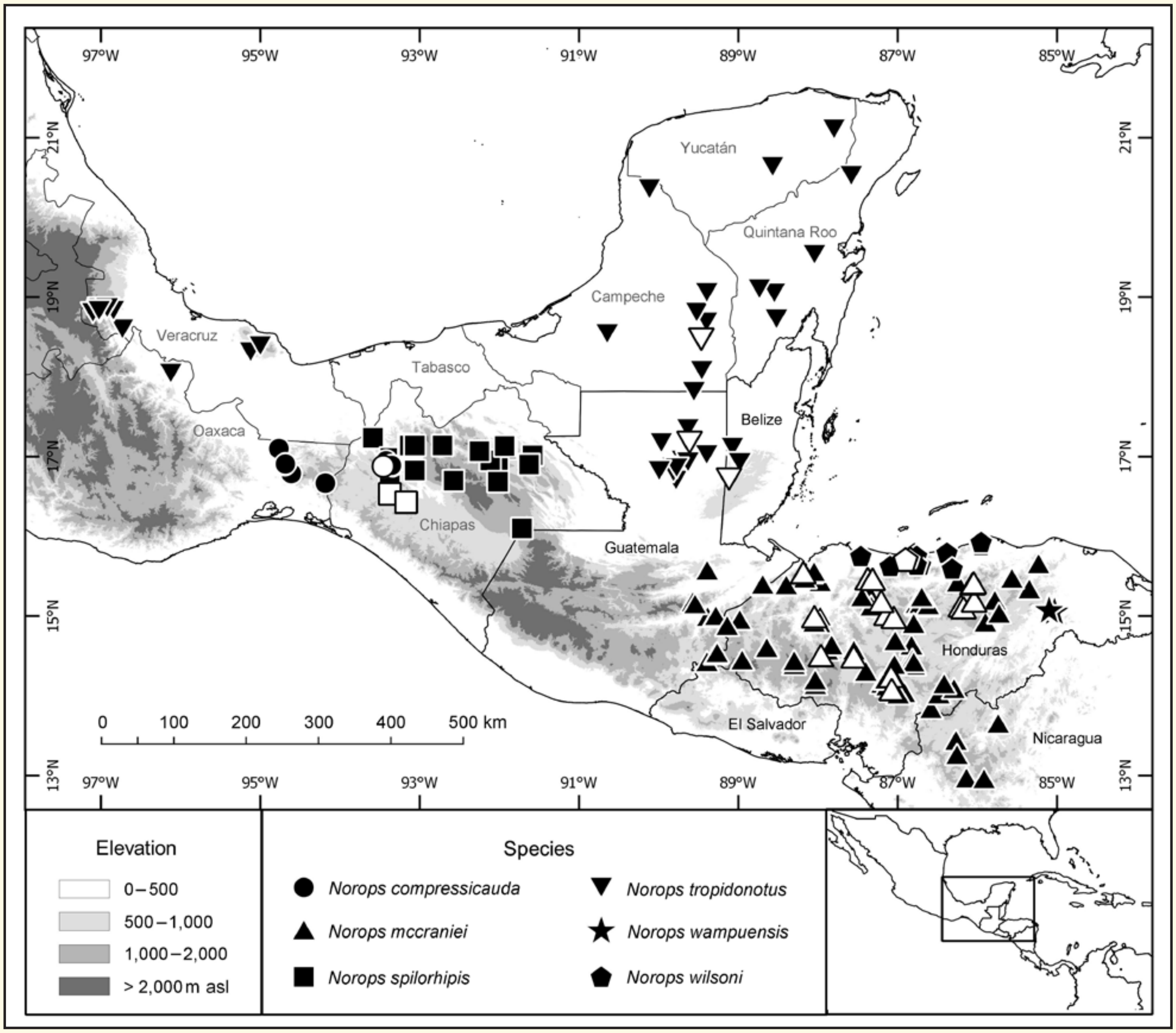

Fig. 9. Map indicating collecting localities of the species related to *Norops tropidonotus*. Each symbol can represent one or more adjacent localities. Hollow symbols indicate localities from where barcoded specimens were analyzed in this study.

Norops wilsoni sp. nov.

Figs. 2a, 4b, 10–12, 14b

***Holotype*:** SMF 78040, adult male, from Parque Nacional Pico Bonito, Estación Forestal CURLA, 15.70167°N, 86.84667°W, elev. 170 m asl, Departamento de Atlántida, Honduras; collected by Gunther Köhler on 23 July 1995; original field number GK-044.

***Paratypes*:** All from Parque Nacional Pico Bonito, Estación Forestal CURLA, 15.70167°N, 86.84667°W, 120–160 m, Departamento Atlántida, Honduras: SMF 78039, 79057–58, collected by Gunther Köhler on 22 July 1995; SMF 78704–07, 81055, collected by Gunther Köhler on 23 March 1996; SMF 78708–09, collected by Gunther Köhler on 27 March 1996; SMF 79943–46, 79948–50, collected by James R. McCranie and Larry David Wilson on 8 June 1996. SMF 78039, 78705–06, 79943–44, 79949 are adult males, the remaining paratypes are adult females. SMF 79057 and 81055 are cleared and stained specimens.

***Diagnosis*:** A medium-sized (maximum SVL 59.0 mm in males, 53 mm in females) species (our Species C of the *Norops tropidonotus* complex) of the genus *Norops* (*sensu* Nicholson et al., 2012) that is most similar in external morphology to *N. tropidonotus*, *N. compressicauda*, *N. spilorhipis*, *N. mccraniei*, and *N. wampuensis*. These five species and *N. wilsoni* are differentiated from all other anoles by a combination of the following characters: (1) distinctly enlarged and strongly keeled dorsal scale rows, (2) a tube-like axillary pocket, (3) scales anterior to ear opening keeled and much larger than small and granular scales posterior to ear opening, and (4) a lack of enlarged postcloacal scales in males. *Norops wilsoni* differs from the other five species in the *Norops tropidonotus* complex by mean genetic distances of 3.6–4.5%. *Norops wilsoni* can be distinguished from *N. compressicauda* by the presence of a large orange male dewlap with a dark central streak (vs. a pink male dewlap in *N. compressicauda*) and a brownish-red iris color (vs. blue in *N. compressicauda*). *Norops wilsoni* differs from *N. tropidonotus* by the presence of a large, bilobed hemipenis with a large asulcate processus (vs. hemipenis small, unilobate without an asulcate processus in *N. tropidonotus*). *Norops wilsoni* differs from *N. wampuensis* by the presence of a distinct dark streak present in the male dewlap and a slightly larger size reaching 59.0 mm in males, 53 mm in females (vs. distinct dark central streak absent in male dewlap and males and females reaching 51 mm SVL in *N. wampuensis*). *Norops wilsoni* differs from *N. spilorhipis* and from *N. mccraniei* in having a hemipenis with a single asulcate finger-like processus at the base of the apex (vs. a single asulcate ridge-like processus on the distal part of the truncus in *N. spilorhipis* and two asulcate processi present, a finger-like one at the base of the apex and a conical one at the base of the truncus in *N. mccraniei*, respectively). *Norops wilsoni* differs further from *N. mccraniei* by its shorter tail (ratio tail length/SVL 1.62–1.78, mean 1.70 in males and 1.44–1.53, mean 1.48, in females of *N. wilsoni* vs. 1.71–1.85, mean, 1.78 in males and 1.60–1.72, mean, 1.66, in females of *N. mccraniei*) and fewer scales around midbody (62–78, mean 69.4 in *N. wilsoni* vs. 70–94, mean 76.9, in *N. mccraniei*), as well as in the mean values of several additional morphometric and scalation characters (see Table 2, Fig. 3). Also, *Norops wilsoni* differs further from *N. mccraniei* in male dewlap coloration (orange with a large diffuse dark central area in *N. wilsoni* vs. orange with a central dark streak in *N. mccraniei*). *Norops wilsoni* differs from the somewhat similar Central American species *N. humilis*, *N. marsupialis*, *N. quaggulus*, and *N. uniformis* by the presence of keeled scales anterior to the ear opening, much larger than small and granular scales posterior to ear opening, and a larger size, reaching 59.0 mm in males, 53 mm in females (vs. scales anterior and posterior to ear opening subequal, small, and granular, SVL of adults < 51 mm in *N. humilis*, < 49 mm in *N. marsupialis*, < 42 mm in *N. quaggulus*, and < 42 mm in *N. uniformis,* respectively).

***Description of the holotype*:** Adult male, as indicated by everted hemipenes and a well-developed dewlap; snout–vent length 59.0 mm; tail length 40.0 mm, tail incomplete; tail slightly compressed in cross section, tail height 3.7 mm, tail width 2.4 mm; axilla to groin distance 21.2 mm; head length 15.7 mm, head length/snout–vent length ratio 0.27; snout length 6.1 mm; head width 9.9 mm; longest toe of adpressed hind limb reaching to anterior margin of eye; shank length 17.5 mm, shank length/head length ratio 1.11; longest finger of adpressed forelimb reaching about 1.0 mm beyond anterior insertion of hind limb; dorsal head scales strongly keeled in internasal, prefrontal, frontal, and parietal areas, unicarinate, keels mostly oriented longitudinally; frontal depression absent or weak; parietal depression absent; 7 postrostrals; anterior nasal divided, lower section contacting rostral and 1st supralabial; 9 internasals; canthal ridge sharply defined; scales comprising supraorbital semicircles keeled, largest scale in semicircles about same size as largest supraocular scale; supraorbital semicircles poorly defined; two scales separating supraorbital semicircles at narrowest point; 2/3 scales separating supraorbital semicircles and interparietal at narrowest point; interparietal not well defined, only slightly enlarged relative to adjacent scales, surrounded by scales of moderate size, longer than wide, smaller than ear opening; three rows of about 7 moderately enlarged, keeled supraocular scales; several enlarged supraoculars in broad contact with supraorbital semicircles; 2 elongate, overlapping superciliaries, posterior one shorter; 3 enlarged canthals; 8 scales between second canthals; 10 scales between posterior canthals; loreal region slightly concave, 28/29 strongly keeled loreal scales in maximum of six horizontal rows; 6 supralabials and 5 infralabials to level below center of eye; suboculars strongly keeled, separated from supralabials by one row of scales; ear opening vertically oval; scales anterior to ear opening enlarged, keeled, much larger than those posterior to ear opening; 5 postmentals, outer pair largest; keeled granular scales present on chin and throat; male dewlap moderately large, extending to level of chest; male dewlap with 8 oblique gorgetal-sternal scale rows, about 6–7 scales per row; no nuchal crest or dorsal ridge; 10–12 middorsal scale rows greatly enlarged, strongly keeled, paramedian scales larger than vertebral scales, dorsal scales lateral to middorsal series abruptly larger than granular lateral scales; no enlarged scales scattered among keeled, imbricate laterals; 23

dorsal scales along vertebral midline between levels of axilla and groin; 15 dorsal scales along vertebral midline contained in one head length; ventral scales on midsection smaller than largest dorsal scales; ventral body scales strongly keeled, mucronate, imbricate; 32 ventral scales along midventral line between levels of axilla and groin; 26 ventral scales contained in one head length; 68 scales around midbody; tube-like, scaleless axillary pocket present; precloacal scales not keeled; no enlarged postcloacal scales in males; all subcaudal scales keeled, mucronate; lateral caudal scales keeled, mucronate, homogeneous although indistinct division in segments discernable; dorsal medial caudal scales keeled, not enlarged, not forming crest; most scales on anterior surface of antebrachium strongly keeled, unicarinate; digital pads dilated, dilated pad about two times width of non-dilated scales on distal phalanx; distal phalanx narrower than and raised from dilated pad; 27/27 lamellae under phalanges II–IV of 4th toe; 7 scales under distal phalanx of 4th toe.

The completely everted hemipenis is a large bilobate organ with well-developed, long lobes; sulcus spermaticus bordered by well-developed sulcal lips and bifurcating at base of apex with the branches continuing as closed furrows to the tip of the lobes where they open into small concave areas, one on each lobe; a finger-like asulcate processus at the base of the apex; lobes strongly calyculate, truncus with folds.

After more than 20 years in preservative, the coloration was recorded as follows: dorsal surfaces of head, body, limbs, and tail Grayish Horn Color (268) with Sepia (279) diamonds on dorsum; flanks Glaucous (289); ventral surface of head Pale Pinkish Buff (3) with Glaucous (289) suffusions; dewlap Buff (5) with a Raw Umber (23) central suffusion; venter Pale Buff (1) with a suffusion of Light Neutral Gray (297); and ventral surfaces of limbs Pale Pinkish Buff (3) with Glaucous (289) suffusions.

***Variation*:** The paratypes and referred specimens agree well with the holotype in general morphology and scalation (see Table 2). Coloration in life of several individuals of this species was reported in McCranie and Köhler (2015: 179) as follows: "USNM 565477 (from the type locality), adult male: dorsal surface of body Brownish Olive (29 [= Color 29 in Smithe 1975–1981]) with darker brown posteriorly directed chevrons; dorsal surface of head Brownish Olive; dorsal surface of tail brown with pale brown crossbands; ventral and subcaudal surfaces dirty white, mottled with brown; dewlap Chrome Orange (16) with Geranium (12) streak, dewlap scales yellow; iris brown with pale brown rim. KU 220123 (from about 2 km S of Nueva Armenia, Dpto. Atlántida, Honduras), adult male: dorsum pale rust brown with tan stripe from axilla to groin; dorsal surfaces of limbs and tail rust brown with tan crossbars; venter white; dewlap reddish orange with burnt orange central streak and yellow scales, including marginals. USNM 570095 (from Quebrada de Oro, Dpto. Atlántida, Honduras), adult male: dorsal surface of head brown with obscure darker broad interorbital bar; lateral surface of head brown; middorsal area of enlarged scales gray-brown with middorsal series of about six spots (tan with dark brown posterior edging) from just posterior to level of axilla to above vent, increasing in size posteriorly by expansion of posterior edging, each connected to pair of obscure oblique lines creating vague chevrons; lateral surface of body brown with small scattered cream spots, obscure narrow gray-brown band between axilla and groin; dorsal surfaces of forelimbs brown with rust patina; dorsal surfaces of hind limbs brown with rust patina and rust-tan crossbars on shanks; tail pale brown with obscure narrow darker brown crossbands; chin and belly cream with vague brown smudging; dewlap reddish orange with burnt orange central streak and pale yellow scales, including marginals; iris copper red with gold ring around pupil."

***Natural history notes*:** *Norops wilsoni* inhabits the Lowland Moist Forest and Premontane Wet Forest formations, and most commonly is encountered around the edges and agricultural areas converted from broadleaf rainforest, as well as along streams through rainforest (Fig. 13). All specimens in the type series of *N. wilsoni* collected by GK were encountered during the daytime, while the lizards were active on the ground or on low vegetation. Other anole species recorded at the collecting sites of *N. wilsoni* are *N. cupreus*, *N. lemurinus*, and *N. zeus* Köhler and McCranie, 2001.

***Geographic distribution*:** As presently understood, *Norops wilsoni* is restricted to the Atlantic slopes of the Cordillera Nombre de Dios in the departments of Atlántida and Colón in northern Honduras, at elevations from near sea level to 980 m (Fig. 9).

***Etymology*:** The specific name *wilsoni* honors our friend and colleague Larry David Wilson, who is one of the leading authorities of the Honduran herpetofauna. Since the 1960s, Larry has been working on the taxonomy, zoogeography, and conservation of the amphibians and reptiles of Honduras and has written numerous scientific articles and monographic treatments of its herpetofauna.

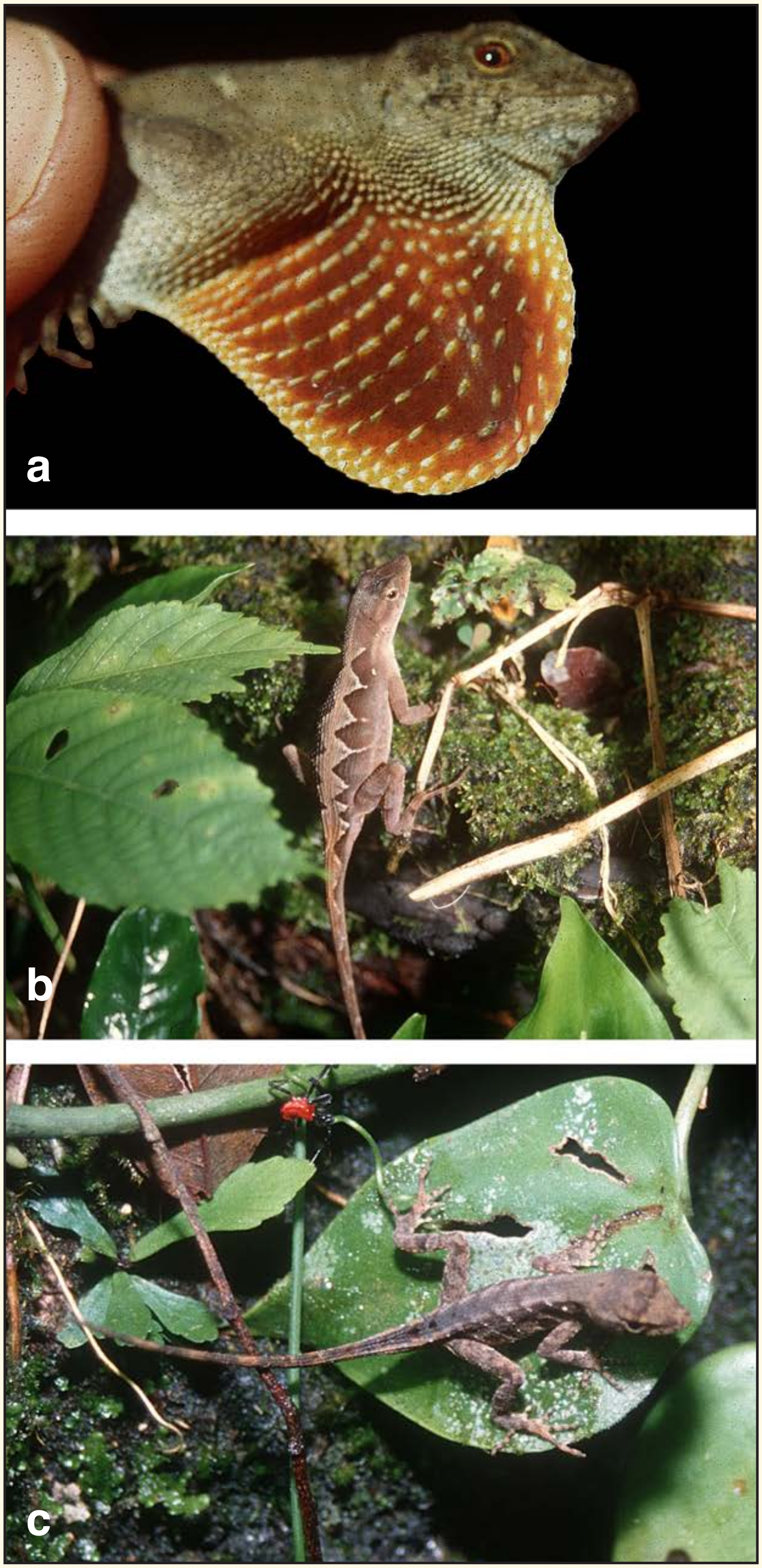

Fig. 10. *Norops wilsoni* in life. (a) SMF 78039 (male); (b) adult female (not collected); and (c) subadult male (not collected).

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Fig. 11. Holotype of *Norops wilsoni* (SMF 78040): (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; and (f) ventral view of head. Scale bars equal 5.0 mm in (a–c) and 1.0 mm in (d–f), respectively. © Gunther Köhler

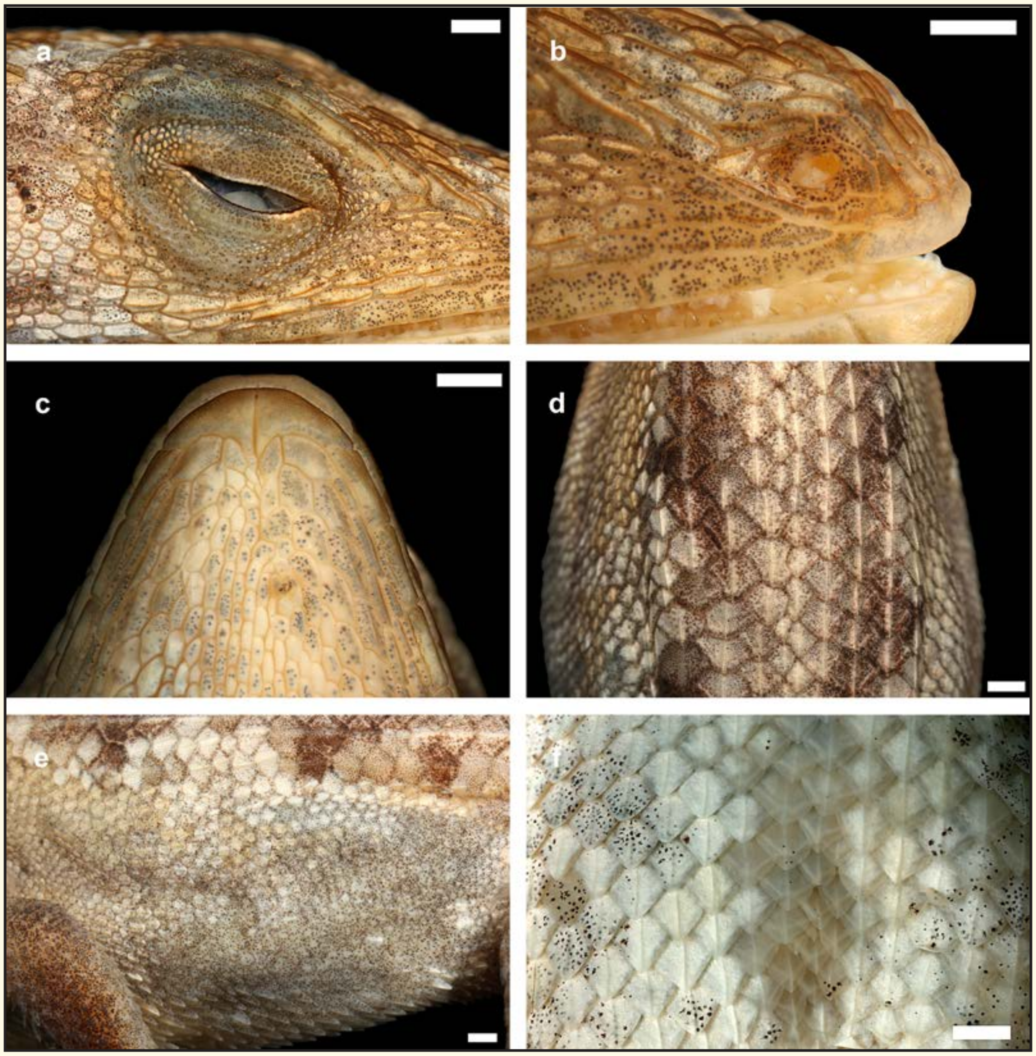

Fig. 12. Holotype of *Norops wilsoni* (SMF 78040): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region (e) flank region; and (f) midventer. Scale bars equal 1.0 mm.

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DISCUSSION

Males of most species in the *Norops tropidonotus* complex have similarly colored dewlaps, albeit subtle differences exist (see Fig. 14a–e). In contrast, *N. compressicauda* exhibits a strikingly different male dewlap coloration (Fig. 14f). As now defined, *N. tropidonotus* (*sensu stricto*) occurs along the Atlantic versant from central Veracruz, Mexico, to northeastern Guatemala, including the Yucatan Peninsula, with a distribution that is exclusive of the Nuclear Central American highlands (Fig. 9). Based on our data, however, there is a significant hiatus between the populations referred to as *N. tropidonotus* on the Yucatan Peninsula and those in Veracruz, Mexico. Additional fieldwork is needed to clarify whether these actually are allopatric, or the result of collection bias. Unfortunately, we do not have barcoding data for the Veracruz populations, and thus relied on hemipenial data for the assumption that these populations are conspecific with those on the Yucatan Peninsula.

Within Nuclear Central America (NCA), the species of the *N. tropidonotus* complex exhibit a pattern of diversification consistent with the recognition of distinct biogeographical provinces corresponding to the western portion of NCA (*N. compressicauda* and *N. spilorhipis*) and the Chortís Block portion of eastern NCA (*N. mccraniei* and *N. wilsoni*). It remains unclear whether the distributional gap separating the easternmost populations of *N. spilorhipis*

Fig. 13. Habitat of *Norops wilsoni* at the type locality. © Gunther Köhler

from the westernmost populations of *N. mccraniei*, encompassing the majority of the highlands of Guatemala, reflects the biogeographic history of these lineages or simply is an artifact of undersampling. These anoles, however, typically are abundant around agricultural areas and disturbed habitats where they occur, and, given the rather intensive study of the Guatemala herpetofauna over the past half century (Stuart, 1955; Campbell, 1998), it is unlikely that they simply escaped notice.

Our results reveal an endemic radiation of anoles in the *Norops tropidonotus* complex in the Chortís Block, a region recognized as a distinct biogeographic province in Central America (Townsend, 2014). In addition to the genetic and morphological differences, the three endemic species are both ecologically and physiographically isolated from one another. *Norops mccraniei* inhabits pine-oak forest and lowland and premontane dry forest habitats, and also is found in association with agricultural disturbance in both lowland and highland wet forests throughout the interior portions of the Chortís Highlands. *Norops wampuensis* is known only from three localities in undisturbed broadleaf rainforest near the confluence of the Río Wampu and Río Patuca in the Caribbean Lowlands of east-central Honduras (McCranie and Köhler, 2001, 2015). *Norops wilsoni* joins the ranks of the rich endemic herpetofauna of the windward slopes of the Cordillera Nombre de Dios along the northern coast of Honduras, which includes at least 33 other endemic species of amphibians and reptiles (Townsend et al., 2012).

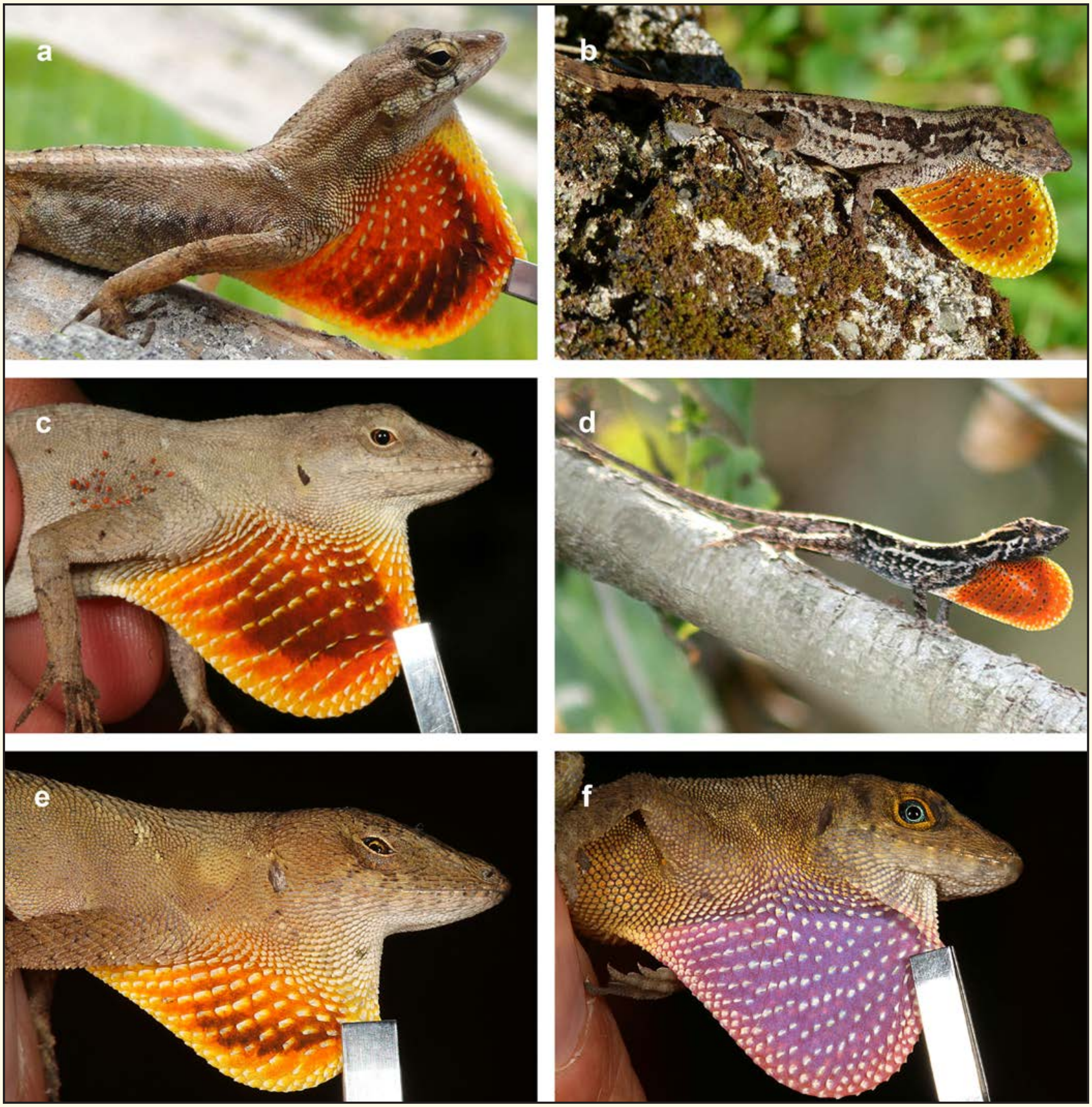

Fig. 14. Male dewlaps in life of (a) *Norops mccraniei* (near Agua Zarca, Departamento de Santa Barbara, Honduras, not collected); (b) *N. wilsoni* (Estación Forestal CURLA, Departamento de Atlántida, Honduras, not collected); (c) *N. spilorhipis* (SMF 100160); (d) *N. tropidonotus* (Estado de Veracruz, Mexico, not collected); (e) *N. tropidonotus* (SMF 99535); and (f) *N. compressicauda* (SMF 100165).

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Appendix 1. Comparative material examined.

Norops compressicauda.—**MEXICO:** CHIAPAS: 11 km airline NW Berriozábal, 915 m: SMF 100165–66; confluence of Ríos El Frances and El Cedro, Municipio de Berriozabal: SMF 81591; Laguna Belgica, 990 m: SMF 100167–70; region of Rancho El Cairo, Municipio de Berriozabal: SMF 81588–90; OAXACA: between Rodulfo Figueroa and Díaz Ordaz Mountain NW of El Baúl: UTA R51882–85; El Modelo, Río Chalchijapa: AMNH 65007–07; La Gloria: UIMNH 35625; Río los Milagros, Sta. María Chimalapa: AMNH 65004–05; Santa Maria Chimalapa, Río Los Milagros: AMNH 65004–06.

Norops mccraniei.—**GUATEMALA:** IZABAL: on road between El Estor and Finca Semuc: UTA R22079; Sierra de Caral trail from Finca La Firmeza to Cerro Pozo de Agua–Cerro Negro Norte, Municipio de Morales: UTA R40628–29; Sierra de Caral, between Cerro Negro Norte y Pozo de Agua, Municipio de Morales: UTA R40607–10; Sierra de Caral, Cerro Pozo de Agua, Municipio de Morales: UTA R40621; Sierra de Caral, Morales Aldea Negro Norte, NW of Cerro El Aguacate: UTA R33451; Sierra de Caral, Negro Norte, Municipio de Morales: UTA R33452–63, R37577–79, R40611–12, R40613–20, R40622–27; ZACAPA: 13.0 km W La Union: UTA R33464; La Unión: CM 57487–503, 57505–68; La Unión, Cerro del Mono, Finca El Chorro (S slope of mountain): UTA R37576; Río Hondo, Aldea Jones, Quebrada, 565 m: SMF 82989–95; Sierra Las Minas, Jones road to Finca Alejandria (Samayoa) ca. 6.0 km to W: UTA R33465–67. **HONDURAS:** COMAYAGUA: Parque Nacional Cerro Azul Meámbar, Río Bonito, 1,555 m: USNM 578772; Parque Nacional Montaña de Comayagua, Cerro El Volcán, 1,720 m: UF 166298; 10 km SW Siguatepeque: SMF 77740; Montaña de Comayagua, 1,250–1,530 m: SMF 79250, 79928–29; Siguatepeque: UF 72116–71, 72174; COPÁN: Río Amarillo, 750 m: SMF 91742; Ruinas de Copán: AMNH 63365, 70270, 124038, UIMNH 52517–18; CORTÉS: Buenos Aires, 1,100–1,300 m: JHT–1402–03, 1412, UF 144107; 6 km N Agua Azul: AMNH 149656–57; Buenos Aires, 1,200 m: SMF 77729–34; Lago de Yojoa: AMNH 70289, UF 72175; Naranjito, 1050 m: SMF 79248–49; road from Cofradía to Buenos Aires, 200 m: SMF 77735; Zapotal, Lago de Yojoa: SMF 78117; EL PARAISO: Cerro El Bromadero near Agua Fría, near Danlí: AMNH 70267–69; EL PARAÍSO: Las Manos Finca Las Manos Carretera El Paraíso–Las Manos: UTA R41443, R52143; Mapachín, 800 m: SMF 91745; Río Guayambre near Chichicaste: AMNH 70285; Valle de Jamastrán: AMNH 70286; FRANCISCO MORAZÁN: Between Los Planes and Cataguana, 1,700 m: JHT–2038; Los Planes, 1,420–1,500 m: JHT–2036–37; Parque Nacional La Tigra, El Rosarío, 1,500 m: UF 176105; PN La Tigra, Rancho Quemado, 1,420 m: USNM 578770; Reserva Biológica Cerro Uyuca, Cabot Biological Station, 1,620 m: JHT–2147; Río Maralito between Los Planes and Cataguana, 1,550 m: JHT–2127; Parque Nacional Montaña de Yoro, Montaña de la Sierra, 1,780 m: UF 166308; Cerro Uyuca, 1,350–1,400 m: AMNH 70389, 70395, CM 64602: SMF 78427–28, 79059; Cerro Uyuca, 1,730 m: SMF 79251; Distrito Central above San Juancito in Parque Nacional La Tigra: UTA R17216; Finca La Montanita on Hwy to Zambrano: CM 59123; immediate vicinity of Tegucigalpa, N of Tegucigalpa: AMNH 69088; La Montañita, between Tegucigalpa and El Zamorano: AMNH 70266; La Montañuela above Tabla Grande: AMNH 70265; Los Corralitos, 1,350 m: SMF 91301; Montaña de Guaimaca, above city of Guaimaca: AMNH 70271; near km 14 en CA 4 Pinares del Uyuca: UTA R52144; Rancho San Diego, ca. 12 mi S Guaimaca: AMNH 69087; Reserva Biologica El Chile: SMF 80890–93; Reserva Biologica El Chile, San Marcos de Guaimaca: SMF 79055; Río Yeguare, near EAP: AMNH 70272–79, 142458–61; road from San Juan de Flores to Talango: UF 90218; San Francisco: AMNH 70280–84; San Ignacio, 950 m: SMF 82727–34; Zambrano: CM 59122; INTIBUCÁ: 15.0 km NW La Esperanza, 1,470–1,540 m: SMF 79937–42; 18.1 km NW La Esperanza, 1,740 m: SMF 79935–36; Valle de Otoro, 740 m: SMF 78396; La Paz: 8 km S Marcala: UF 72172; Marcala: CM 64603; LEMPIRA: Parque Nacional Cerro Celaque, 1,440–1,470 m: SMF 79245, 79934; Parque Nacional Cerro Celaque, near Centro de Visitantes, 1,400–1,450 m: SMF 78710–12, 91302; OCOTEPEQUE: El Mojanal, 1,350 m: SMF 91303; Quebrada de Cotanmill, 1,200 m: SMF 88674; San Marcos: UF 72173; OLANCHO: El Norte: SMF 100101; Laguna El Juncal: SMF 100100; Municipalidad de Gualaco: Montaña de Jacaleapa, quebrada in headwaters of Río del Oro, E slope Cerro de Banaderos, 1,180 m: SMF 100107–08; Municipalidad de Gualaco: pine forest lagoon below El Norte, 980 m: SMF 100109; Municipalidad de Gualaco: seepage bog aprox. 3.75 km N Saguay, 580 m: SMF 100104–06; Parque Nacional Montana de Botaderos: Municipalidad de Gualaco, Cerro de las Cruces, 1,160: SMF 100110–12; 11.5 km NNE La Colonia, Quebrada de Las Marías, 600–660 m: SMF 78804–08, 78831–33; 6.6 km S San Esteban, 470 m: SMF 79252; El Carbón: SMF 91348; El Dictamo and Parque Nacional La Muralla Centro de Visitantes, between: USNM 342291–306; El Vallecito: USNM 342307; Montana de las Parras: USNM 342318–27; Montana de Liquidambar: USNM 342315–17; Montana del Ecuador: USNM 342313–14; near Los Planes: USNM 342308–12; Parque Nacional La Muralla, Centro de Visitantes, Sendero El Pizote: USNM 342345; Parque Nacional La Muralla, El Díctamo, 1,000 m: SMF 79104, 79947; Parque Nacional La Muralla, Montaña Las Parras, 1,100 m: SMF 79095; Parque Nacional La Muralla, Quebrada El Pinol, 1,180 m: SMF 79096–97, 79103; Piedras Blancas, 1100 m: SMF 91744; Piedras Negras, near: USNM 342360; Quebrada de las Mesetas: USNM 342328–34; Quebrada El Pinol: USNM 342335–37; Quebrada La Calentura: USNM 342338–44; Río Cuaca, 900 m: SMF 91344–47; Río de Enmedio: USNM 342351–59; Terrero Blanco:

USNM 342346–50; trail to Las Canoas: SMF 91349; Vallecito, 765 m: SMF 91743; SANTA BÁRBARA: Compañia Agrícola Paradise (former Plowden Finca), 700 m: JHT–2354, USNM 578778; Lago de Yojoa, Hacienda El Sauce: SMF 43898; Quimistan: USNM 128088–89; YORO: Along road between La Fortuna and Texíguat campsite, 1,100–1,300 m: UF 166299–301; Refugio de la Vida Silveste Texíguat, logging area along road below camp, 1,500–1,515 m: UF 166302–05; W of San Pedro, Hacienda Santa Ana, 200': FMNH 5230; 10 km W Yoro: ANSP 30689–90, 30693; 2.5 km NNE La Fortuna, 1,550 m: SMF 79253–55; 32.0 km (by road) W Yoro, on road to Morazán: USNM 217595–98; 6.6 km (by road) W Yoro, Sierra de Yoro: USNM 217599; Jaral, N end of Lake Yojoa, 2000': FMNH 5231–35; mountains west of San Pedro, on trail at 2,000–2,500': FMNH 5227–28; Portillo Grande, 4,100': FMNH 21871; Subirana Valley: UMMZ 77855 (1–40); Subirana Valley, 2,800': FMNH 21849; W of San Pedro, Hacienda Santa Ana, 200': FMNH 5229–30. **NICARAGUA:** ESTELÍ: 6 km E San Isidro: UMMZ 116398; Finca Daraili, 5 km N and 14 km E Condega: KU 85721; Reserva Natural Miraflores, Finca Caldera, 1,200 m: SMF 79675–77; JINOTEGA: Kilambe, El Diamante, Finca La Concepción: SMF 84734–36; MATAGALPA: Matagalpa: UMMZ 58541 (1–3), 58546 (1–6). **EL SALVADOR**, SANTA ANA: Montecristo, Majada Vieja: MUHNES 731.

Norops spilorhipis.—**MEXICO:** CHIAPAS: 0.5 km E Coapilla: MZ–UNICACH 183–84; 1.1 km S, 4.9 km E San Cristobal de las Casas: ENCB 12941; 10 km N, 1.5 km E Raudales [= Raudales de Malpaso]: ENCB 1932–35; 10 km NW San Fernando: SMF 56669, 62115; 2 km E El Real: KU 41651; 2.2 km N, 1 km W Naja: ENCB 11082; 26 km N Ocozocuautla: ENCB 10225; 5 km S, 9.2 km E Ocosingo: ENCB 11083; 7 km (by road) N Ocosingo, on road to Palenque: USNM 266280; Cañon de Sumidero, 4 km N, 5.3 km W Tuxtla Gutiérrez: ENCB 11085, 11095–96; Cerro Brujo, 1,220 m: SMF 100160–64; El Chango, near Ocozocoautla: UIMNH 37353; Esquipola, 2 km S, 2.5 km E Coapilla: MZ–UNICACH 347; Jetja (Lacandones): AMNH 66426–30, 142450, 142452–56; Lagunas de Montebello: SMF 77286; Llano Grande, 2.8 km S, 5.4 km E Coapilla: MZ–UNICACH 348–50; Monte Bello, near Comitán: UMMZ 95259; Monte Libanon, 100 km E San Cristobal de las Casas: UMMZ 95228; Ocosingo: KU 41649–50, 30; Ocozocoautla: FMNH 106883, 122017; Ocozocoautla, km 5 carretera Aeropuerto–Llano San Juan: MZ–UNICACH 708; Rancho Alegre, 955 m: SMF 100155–59; Rancho Dolores, 1.5 km S, 6 km E Coapilla: MZ–UNICACH 342–46; Rancho El Molino, 2.5 km N, 3 km E Coapilla: ENCB 16702–03; Rancho San Antonio, El Potrero, 1 km N, 3.5 km E Coapilla: MZ–UNICACH 337–41, 617–20; Río Tzaconeja, 4 mi S Altamirano: KU 41652; Simojovel: UMMZ 99854; Vicente Guerrero, 1 km N, 10 km E Coapilla: ENCB 16713–16.

Norops tropidonotus.—**BELIZE:** CAYO: ca. 0.6 km N Augustine, Vaca Plateau, at entrance trail to Río Frío Cave: USNM 333091; Caracol, Vaca Plateau, 510 m: SMF 83309; El Cayo: USNM 75118; Mountain Pine Bridge, Augustine: CM 105946–47. **GUATEMALA:** PETÉN: El Remate: UTA R40606; Flores Yaxha Aguada de la Posa Maya: UTA R37573–74; km 449 on CA 13, 5 km N Santa Ana, 175 m: SMF 83993; km 465 on CA 13, near Granja Sta. Ana: 250 m: SMF 83992; Macanché, Hotel El Retiro, 250 m: SMF 83975–83, 83987–91; Pacomon: USNM 71391; ruins of Tikal, Parque National Tikal, 255 m: SMF 83985; San Antonio ca. 15.0 km SW San Benito: UTA R40605; Santa Rita: USNM 71387; Tikal: UTA R23623–24, R34998, R37575, R40601; Uaxactún: AMNH 70931, UTA R40600, R40602–04; Uaxactún, just N of old airstrip: UTA R50330; Yaxhá, N of western lake: UTA R50329. **MEXICO:** CAMPECHE: Becán, 285 m: SMF 99533–37; Encarnacion: FMNH 122020; 1 km SE Cristóbal Colón: MZ–CIQRO 788; 2 km S Cristóbal Colón: MZ–CIQRO 1517; 4 km SW El Refugio: MZ–CIQRO 1259; 4.5 km S Cristóbal Colón: MZ–CIQRO 1529; Brecha a flores Magón, El Papagayo: MZ–CIQRO 567; Ejido Laguna Alvarado Selva Mediana: MZ–CIQRO 1097; Matamoros: FMNH 36542–43; Zona Arqueológica de Calakmul: MZ–CIQRO 1152; OAXACA: Tuxtepec: USNM 46908; QUINTANA ROO: near Reforma: SMF 99538; 8 km SW La Pantera, municipio de Othón P. Blanco: MZ–CIQRO 915; boundery of Campeche and Quintana Roo, Dist of Xkanha: AMNH 7862; Canán, municipio de Othón P. Blanco: MZ–CIQRO 909; Coba: FMNH 27338; municipio de Felipe Carillo Puerto, Zona 5, Transecto 2, inicio: MZ–CIQRO 1875; VERACRUZ: Perez: FMNH 5972, 31522–23; San Jose de Gracia: FMNH 122019; 5 mi S Catemaco, near Agua Mineral: UIMNH 86943, 86945; Barranca Metlac, 2 mi W Fortin: UMMZ 115055 (1–6), 118196, 119636 (1–2); below Córdoba, near San Lorenzo: FMNH 105723, 106884–86, 106888, 105723; Cordoba: CM 41253, 41674–79, 43554, FMNH 38629–33, UIMNH 511848, USNM 19019; Coyame, 7 mi E Catemaco: UIMNH 36879; Cuautlapán: AMNH 149654, FMNH 106892, 106895–96, 105722, UIMNH 20074, 20078–80, 26640, 60869–70, 64257–58, 64260, UMMZ 105009, 115056; Metlac: UMMZ 85423; mountain immediately SE Cuautlapán [Cerro Chicahuaxtla]: FMNH 70778, UIMNH 60868; Mtzorongo: USNM 46650; Ojo de Agua near Potrero Viejo: UMMZ 102024–25; Orizaba: USNM 30196–205; Potrero Viejo: FMNH 106881–82, 106887, 106889–91, 106893, 122015–16, 122018, 122021, 125088: SMF 43812, UIMNH 20062–63, 20065, 20069, 20163, 48847–48, UMMZ 85426; Río Atoyac, 4 mi NW Potrero: UMMZ 97977 (1–3); vicinity of Cuautlapan: USNM 224813; YUCATÁN: Chichen Itzá: FMNH 36541, 106894; Coluba 28 km E Sucopo: FMNH 36469

Norops wampuensis.—**HONDURAS:** OLANCHO: alongside Río Wampú between Ríos Sausa and Aner: SMF 79907–15; confluence of Quebrada Siksatara and Río Wampú: SMF 79246–47, 79906, USNM 539197; confluence of Ríos Aner and Wampú: SMF 79902–05, USNM 539193–95; confluence of Ríos Sausa and Wampú: USNM 539196.

Norops wilsoni.—**HONDURAS:** ATLÁNTIDA: above Pico Bonito Lodge, 120: SMF 91350–51; Cordillera Nombre de Dios, Camino La Colorada–Los Planes: UTA R52139–40; E shore of Río Santiago, 2 km S Naranjal: UF 90219–21; La Ceiba: CM 29009; Lancetilla: AMNH 70432, 70435–37, FMNH 22905–09: SMF 79098–102; Parque Nacional Pico Bonito, Estación Forestal CURLA, 120–170 m: SMF 78039–40, 78057–58, 78704–09, 79943–46, 79948–50; Parque Nacional Pico Bonito, Liberia: SMF 79056; Parque Nacional Pico Bonito, S Yaruka, 7.4 km SE La Ceiba, 130 m: SMF 79931–33; Parque Nacional Pico Bonito, small tributary of Quebrada de Oro (tributary of Río Viejo) near Meraz's homestead, 580 m: USNM 539838–39; Quebrada de Oro, 820–980 m: SMF 79244, 79930; Río Cangrejal, Los Lobos (village), near La Ceiba: SMF 79152–54; Nombre de Dios, Roma: SMF 100102; Parque Nacional Pico Bonito, Estación Forestal CURLA, 150 m: USNM 578773–74; Pico Bonito Lodge, 120 m: SMF 100103; COLÓN: Balfate: AMNH 58612–15, 58627; Barranco: ANSP 28126, 33150–54; Los Planes: CM 29367; mountains just S of Trujillo: CM 64620–21; Trujillo: CM 64613–16, 64618, 64623, LSUMZ 22430.

Appendix 2. Cleared and stained specimens.

Norops mccraniei.—SMF 79059, 79254, 79939–40.

Norops wilsoni.—SMF 79904, 79908.

Norops wampuensis.—SMF 79056–57, 79098.

Appendix 3. GenBank accession numbers for the 16S sequences used in this study.

Species	Specimen Voucher	GenBank Accession #
Norops compressicauda	SMF 100169	KU671014
Norops lemurinus	SMF 99426	KU671013
Norops mccraniei	JHT 1402	KU671011
Norops mccraniei	JHT 1403	KU671010
Norops mccraniei	JHT 1412	KU671009
Norops mccraniei	JHT 2036	KU671008
Norops mccraniei	JHT 2037	KU671007
Norops mccraniei	JHT 2038	KU671006
Norops mccraniei	JHT 2127	KU671005
Norops mccraniei	JHT 2147	KU671004
Norops mccraniei	JHT 2354	KU671003
Norops mccraniei	SMF 100100	KU670996
Norops mccraniei	SMF 100101	KU670995
Norops mccraniei	SMF 100104	KU670992
Norops mccraniei	SMF 100105	KU670991
Norops mccraniei	SMF 100106	KU670990
Norops mccraniei	SMF 100107	KU670989
Norops mccraniei	SMF 100108	KU670988
Norops mccraniei	SMF 100109	KU670987
Norops mccraniei	SMF 100110	KU670986

Norops mccraniei	SMF 100111	KU670985
Norops mccraniei	SMF 100112	KU670984
Norops mccraniei	SMF 78396	KU671002
Norops mccraniei	UF 144107	KU670975
Norops mccraniei	UF 166298	KU670974
Norops mccraniei	UF 166299	KU670973
Norops mccraniei	UF 166300	KU670972
Norops mccraniei	UF 166301	KU670971
Norops mccraniei	UF 166302	KU670970
Norops mccraniei	UF 166303	KU670969
Norops mccraniei	UF 166304	KU670968
Norops mccraniei	UF 166305	KU670967
Norops mccraniei	UF 166308	KU670966
Norops mccraniei	UF 176105	KU670965
Norops mccraniei	USNM 578770	KU670964
Norops mccraniei	USNM 578772	KU670963
Norops mccraniei	USNM 578778	KU670961
Norops spilorhipis	SMF 100158	KU670983
Norops spilorhipis	SMF 100159	KU670982
Norops spilorhipis	SMF 100160	KU670981
Norops spilorhipis	SMF 100161	KU670980
Norops spilorhipis	SMF 100162	KU670979
Norops tropidonotus	SMF 83309	KU670998
Norops tropidonotus	SMF 83985	KU670997
Norops tropidonotus	SMF 99533	KU670978
Norops tropidonotus	SMF 99534	KU670977
Norops tropidonotus	SMF 99537	KU670976
Norops uniformis	SMF 100139	KU670960
Norops uniformis	SMF 100147	KU670959
Norops uniformis	SMF 99539	KU670958
Norops uniformis	SMF 99541	KU670957
Norops uniformis	SMF 99542	KU670956
Norops uniformis	SMF 99546	KU670955
Norops wilsoni	SMF 100102	KU670994
Norops wilsoni	SMF 100103	KU670993
Norops wilsoni	SMF 78704	KU671001
Norops wilsoni	SMF 78706	KU671000
Norops wilsoni	SMF 78708	KU670999
Norops wilsoni	USNM 578773	KU670962
Norops wilsoni	USNM 578774	KU671012

Gunther Köhler received a degree in Veterinary Medicine (Staatsexamen) at the University Gießen, Germany in 1993, and a doctoral degree at Goethe University Frankfurt am Main, Germany in 1995; since that time he has been the Curator of Herpetology at the Senckenberg Research Institute, Frankfurt am Main, Germany. His research focuses on the Neotropical herpetofauna, primarily that of Central America and Mexico. To date, Gunther has authored 27 books and 201 research papers on amphibians and reptiles.

Josiah Townsend received a Bachelors in Wildlife Ecology and Conservation, Masters in Latin American Studies, and Doctoral degree in Interdisciplinary Ecology from the University of Florida. Currently he is a faculty member in the Department of Biology at Indiana University of Pennsylvania. His research focuses on the systematics, evolution, and conservation of the northern Central American herpetofauna, and he has co-authored two books, co-edited *Conservation of Mesoamerican Amphibians and Reptiles*, and authored or co-authored 102 scientific papers and notes to date.

Claus Bo P. Petersen received a Bachelor of Science in Biology from the Faculty of Science, University of Copenhagen, Denmark, where he currently is enrolled in the Master's Program in Biology. His research is centered on herpetological systematics, with a current emphasis on the taxonomy of Mesoamerican dactyloid lizards. Claus Bo has co-authored several scientific papers, including a recently published monograph on the anoles of the Pacific versant of Mexico, in the states Oaxaca, Guerrero, and Puebla.