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A CRYPTIC NEW SPECIES OF ANOLE (SQUAMATA: DACTYLOIDAE) FROM THE LENCA HIGHLANDS OF HONDURAS, PREVIOUSLY REFERRED TO AS *NOROPS CRASSULUS* (COPE, 1864)

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ABSTRACT

We describe a cryptic **new species** of *Norops* Wagler, 1830, ***Norops caceresae***, from mixed transitional and broadleaf cloud forest formations in the Lenca Highlands of southwestern Honduras. This population was previously considered conspecific with *Norops crassulus* (Cope, 1864) of Guatemala, El Salvador, and Mexico, despite it being entirely disjunct (> 100 km) from any of those populations. Recent molecular work revealed consistent, deep mitochondrial and nuclear distinctiveness between this population and all other anoles of the *N. crassulus* species group, prompting a thorough morphological investigation of this population. This new species is most similar in external morphology to *N. crassulus* sensu stricto, but is readily distinguished by molecular distinctiveness, distribution, and morphology.

Key Words: Chortís Block; lizard; Mesoamerica; morphology; Nuclear Central America; Reptilia; taxonomy

RESUMEN

Describimos una **nueva especie** críptica de *Norops* Wagler, 1830, ***Norops caceresae***, de las formaciones mixtas de bosque nuboso transiciónal y de hoja ancha en las tierras altas de Lenca, en el suroeste de Honduras. Anteriormente, esta población se consideraba conespecífica con *Norops crassulus* (Cope, 1864) de Guatemala, El Salvador y México, a pesar de ser completamente disyunto (> 100 km) de cualquiera de esas poblaciones. El trabajo molecular reciente reveló una especificidad mitocondrial y nuclear consistente y profunda entre esta población y todos los demás *Norops* del grupo de especies de *N. crassulus*, lo que provocó una investigación morfológica exhaustiva de esta población. Esta nueva especie es muy similar en morfología externa a *N. crassulus* sensu stricto, pero se distingue fácilmente por su distintividad molecular, distribución y morfología.

Palabras Clave: Bloque Chortís, largatija, Mesoamerica, morfología, Centroamerica Nuclear, Reptilia, taxonomía

INTRODUCTION

The anoles (Squamata: Dactyloidae) of Central America's highlands are a ubiquitous component of the region's diverse herpetofauna. Systematic studies based upon molecular and morphological evidence continue to reveal underestimated, and often cryptic, diversity, helping to resolve long-standing taxonomic problems and leading to the descriptions of numerous new species (e.g., Köhler et al. 2014a, 2016; Nicholson and Köhler 2014; Poe et al. 2015; Gray et al. 2016, Poe and Ryan 2017).

Norops crassulus (Cope, 1864) has long been a taxonomically confusing highland anole (Stuart 1942, 1955; Meyer and Wilson 1971). Currently, this taxon is assigned to populations from a number of disjunct highland areas across Nuclear Central America, with isolated populations found at intermediate-to-high elevations (1300–3000 m above sea level) in Chiapas, Mexico, throughout central Guatemala, in the Salvadoran Cordillera, and in the Lenca Highlands (departments of Intibucá, La Paz, and Lempira) of Honduras (Köhler 2008; McCranie and Köhler 2015). A fifth population, previously referred to as *Norops sminthus* (Dunn and Emlen, 1932) (Nicholson et al. 2012), *N. crassulus* (McCranie and Köhler 2015), or *Anolis* aff. *A. morazani* Townsend and Wilson, 2009 (Hofmann and Townsend 2017), is found in the Sierra de Agalta in Departamento de Olancho in eastern Honduras. Despite work by Stuart (1942, 1955) and Meyer and Wilson (1971), *N. crassulus* and the other members of its subgroup (sensu McCranie and Köhler 2015) remain a complicated and unresolved group of anoles.

Hofmann and Townsend (2017) recently presented a multilocus phylogenetic investigation into the evolution and biogeography of the *Norops crassulus* subgroup, revealing

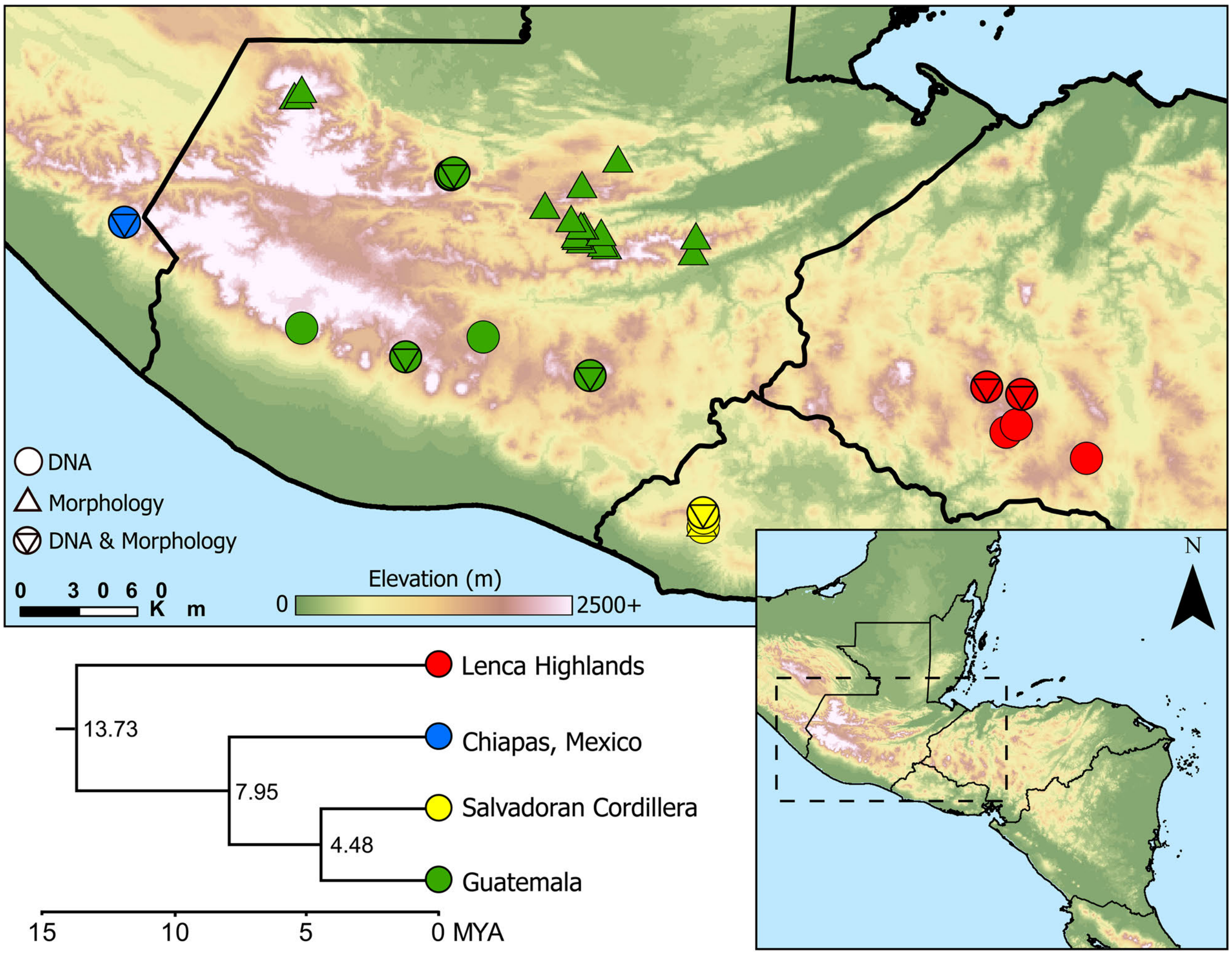

Fig. 1.—Distribution of *Norops crassulus* sensu lato used in this study, with inset phylogeny (summarized from Hofmann and Townsend 2017) showing the divergence times and relationships of the four major lineages.

cryptic diversity within the taxon *N. crassulus* that corresponded to disjunct populations following well-known biogeographic breaks in Nuclear Central America. Most distinct was the population of *N. crassulus* sensu lato from the Lenca Highlands region of Honduras, which was estimated to have diverged from populations in Guatemala, El Salvador, and Mexico more than 13 million years before present (YBP) (Fig. 1; Hofmann and Townsend 2017). Uncorrected p-distances for mitochondrial DNA between the Lenca population and the other lineages of *N. crassulus* sensu lato (Table 1) were found to be comparable to or greater than distances between other recently described anoles and closely related taxa, and the distinctiveness of this lineage was well-supported by mitochondrial and nuclear gene trees, as well as a coalescent species tree (Hofmann and Townsend 2017). This study also revealed that populations attributed to *N. crassulus* in previous studies represented an unnamed sister lineage to *Norops anisolepis* (Smith et al., 1968), and was otherwise not closely related to any of the populations assigned to *N. crassulus.* The only other genetic sample assigned to *N. crassulus* that has appeared in published phylogenetic studies, SMF 78830 from the Sierra de Agalta in Olancho, Honduras (McCranie and Köhler 2015), was shown to represent a lineage closely related to *N. morazani* (Hofmann and Townsend 2017).

In light of the evolutionary distinctiveness of the lineages, we further investigated the taxonomic status of populations assigned to *Norops crassulus* sensu lato using analyses of morphological data. Based on the deep evolutionary history and historical biogeography of this lineage, and the analyses of morphological variation presented herein, we provide a formal description of the Lenca Highland populations of these anoles as a new species.

TABLE 1

Genetic distances (uncorrected pairwise distances) for the four lineages of *Norops crassulus* sensu lato, summarized from Hofmann and Townsend (2017). Intralineage distances for each gene are in the shaded box. Interlineage distances are in the lower-left triangle. A dash (-) indicates sequence data is only available for a single individual for that gene; therefore, no intraspecific genetic distances could be calculated.

	Gene	**Lenca Highlands**	**Salvadoran Cordillera**	**Guatemala**	**Mexico**
Lenca Highlands	*16S*	0.005			
	ND2	0.008			
	COI	0.007			
	PRLR	0.002			
	BDNF	0.000			
	PTPN12	0.001			
	Overall	**0.002**			
Salvadoran Cordillera	*16S*	0.057	0.001		
	ND2	0.169	-		
	COI	0.141	-		
	PRLR	0.020	-		
	BDNF	0.005	-		
	PTPN12	0.010	-		
	Overall	**0.071**	**-**		
Guatemala	*16S*	0.064	0.008	0.001	
	ND2	0.138	0.084	0.016	
	COI	0.172	0.054	0.010	
	PRLR	0.016	0.009	0.008	
	BDNF	0.005	0.003	0.003	
	PTPN12	0.009	0.001	0.001	
	Overall	**0.066**	**0.032**	**0.007**	
Mexico	*16S*	0.071	0.026	0.024	0.000
	ND2	0.166	0.119	0.119	0.001
	COI	0.138	0.091	0.088	0.001
	PRLR	0.022	0.021	0.019	0.000
	BDNF	0.003	0.002	0.002	0.000
	PTPN12	0.010	0.005	0.004	0.001
	Overall	**0.069**	**0.052**	**0.048**	**0.001**

MATERIALS AND METHODS

Justification of Nomenclature

In the most comprehensive phylogeny of anoles published to date, Poe et al. (2017) applied a PhyloCode approach (Cantino and de Queiroz 2014) to define clade names under the crown clade *Anolis* Cope, 1864. Within the unranked clade-based taxonomy of anoles of Poe et al. (2017), the taxa discussed herein are beta anoles in the clade *Draconura* Wagler, 1830 (formerly the *auratus* group of Nicholson et al. 2012), which is part of the larger *Norops* clade. Most recently, Nicholson et al. (2018) showed the concordance between the clades of Poe et al. (2017) and the rank-based multi-genera approach to anole classification. In order to provide a valid taxonomy under the International Commission on Zoological Nomenclature (ICZN), Nicholson et al. (2018) converted Poe et al. (2017)'s clade names to a rank-based, multi-genera classification, which we follow here.

Taxon Sampling

Institutional abbreviations used here follow Sabaj (2016) and are as follows: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CM); Museum of Vertebrate Zoology Herpetology Collection, Berkeley, California (MVZ:Herp); Natural History Museum of Los Angeles County, Los Angeles, California (LACM); Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany (SMF); University of Florida, Florida Museum of Natural History, Gainesville, Florida (UF); University of Kansas Biodiversity Institute, Lawrence, Kansas (KU). Specimens from Josiah H. Townsend's field series are noted as JHT numbers.

Specimens of *N. crassulus* representing each of the four geographically discrete molecular clades were received from the KU and MVZ:Herp collections, and examined alongside samples collected by the authors and their collaborators (Appendix 1). From 2006 through 2015, JHT and various collaborators sampled localities in the Honduran departments of Copán, Cortés, Francisco Morazán, Intibucá, La Paz, Lempira, Ocotepeque, and Santa Bárbara for *N. crassulus* and *N. crassulus*-like anoles. Specimens were fixed in 10% formalin and preserved in 70% ethanol, with a tissue sample preserved in SED buffer (20% DMSO, 0.25 M EDTA, pH 7.5, NaCl saturated; Seutin et al. 1991; Williams 2007; Mulcahy et al. 2016). Forest formation definitions follow those of Holdridge (1967) and names of forest types that appear capitalized follow those defined by Townsend (2014). All GPS coordinates herein refer to WGS84 datum. Specimens from the Sierra de Agalta, Dept. Olancho, Honduras, a population previously assigned to "*N. crassulus*," were not included as part of this investigation as they are instead most closely related to *N. morazani;* a separate study is underway to determine the taxonomic status of that population.

Morphological Examinations

Morphometric and meristic data were recorded for each specimen following Köhler (2014). Sex was determined by the presence of hemipenes and/or a well-developed dewlap. Female *N. crassulus* possess a dewlap, but it is significantly reduced compared to males (McCranie and Köhler 2015). Measurements, counts, and descriptions were recorded following Köhler (2014), though some abbreviations were changed for clarity. Köhler (2014) provided complete definitions and photographic examples of all morphological characters taken. The first author recorded all characters to eliminate any potential inter-observer biases. In total, 103 specimens were examined, of which data from 100 were used in analyses. The three excluded specimens were considered juveniles or hatchlings. Comparative data for other Honduran *crassulus* subgroup anoles were taken from McCranie and Köhler (2015) and each species' original description.

Fifteen measurements were taken using either a stiff ruler (for snout-vent length and tail length) or digital calipers to the nearest 0.01 mm (all other measurements): snout-vent length (SVL), tail length (TL), head length (HL), head width (HW), snout length (SL), axilla-groin distance (AGD), vertical tail diameter (VTD), horizontal tail diameter (HTD), shank length (ShL), longitudinal diameter of the ear opening (LDE), vertical diameter of the ear opening (VDE), longitudinal diameter of the parietal scale (LDP), transverse diameter of the parietal scale (TDP), subdigital pad width (SPW), non-dilated subdigital pad width (NDPW).

Twenty-one scale counts were recorded: lamellae on the 4th toe (4TL, taken from both the left and right foot), ventral scales in one head length (VHL) and dorsal scales in one head length (DHL), ventral scales between the axilla and groin (VSAG) and dorsal scales between the axilla and groin (DSAG), scales at midbody (SMB), scales between the first (S1C) and second (S2C) canthals, enlarged supraocular scales (ESO), scales between the supraorbital semicircles (SOC), scales between the supraorbital semicircles and the interparietal plate (SIP), postrostrals (PRS), internasals (INS), supralabial scales to the level below the center of the eye (SLS), infralabial scales to the level below the center of the eye (ILS), loreal scales (LS), loreal scale rows (LSR), subocular scales in contact with supralabial scales (both counted and presented as SO/SPL), postmentals (PMS), sublabials (SLB), enlarged dorsal scale rows (EDS).

Twenty-two scale characters were recorded: condition of the terminal phalanx (CTP), condition of the axillary region (CAR), condition of the supradigital scales (CSD), condition of the enlarged supraocular scales (CEO), condition of the supraocular scales (CSO), condition of the supraorbital semicircles (CSS), condition of the prefrontal depression (CFD), condition of the parietal depression (CPD), relative size of the scales adjacent to the interparietal plate (SAP), condition of the snout scales (CSN), condition of the canthal ridge (CR), circumnasal condition (CNC), prenasal condition (PNC), condition of the supraciliary scales (SSC), size and condition of the scales anterior (SAE) and posterior (SPE) of the ear opening, condition of the outer postmentals (COP), condition of the ventral (VSC) and dorsal scales (DSC), condition of the dorsal (TDC), lateral (TLC), and ventral (TVC) caudal scales. All counts were recorded from the specimens' right side; however, where bilateral asymmetry in the character was apparent, both sides were recorded separately.

In male specimens with extended dewlaps, the number of gorgetal rows was recorded (GSR), and the dewlap size was approximated by noting its distal insertion relative to the eye and proximal insertion relative to the axilla. In male specimens with fully everted hemipenes, these organs were described largely following Klaver and Böhme (1986), as well as various descriptions of anole hemipenes in the literature (e.g., McCranie and Köhler 2015; Köhler et al. 2016). Following Köhler (2012), color of Honduran specimens was recorded in life based on photographs and also after approximately 30 months in alcohol. Color in preservative of specimens from other populations was also recorded.

Analyses

Statistical analyses of morphological data were performed in R 3.3.1 (R Core Team 2016), and all analyses were conducted on males and females separately to account for sexual size dimorphism. In total, 60 males and 40 females were included in these analyses. TL, VTD, and HTD were not included in the analyses because many specimens had incomplete tails, and GSR was not included due to the low number of male specimens with extended dewlaps. Any characters exhibiting no variation across specimens were also left out.

The remaining measurements (except SVL) were regressed against each specimen's SVL to account for variation in body size. As in other recent studies of anoles (e.g., Köhler et al. 2014a, 2014b, 2016), SL and SHL were also scaled against HL, and HL was scaled additionally against HW. Nonparametic Mann-Whitney U tests (MWU, equivalent to the Wilcoxon rank-sum test; Mann and Whitney 1947) were used to determine if any of 15 morphological measurements and 21 scale counts were significantly different between populations. Based on the molecular data presented by Hofmann and Townsend (2017), specimens from El Salvador and Guatemala were treated as one operational taxonomic unit (OTU), and specimens from the Lenca Highlands were treated as a second OTU. Because of the low sample size, specimens from a divergent population from Chiapas, Mexico were not included in the MWU analyses. Principal Component Analyses (PCA) were then performed separately on the 15 male and female morphological measurements to determine, in part, if variation in morphology could be attributed to populations. In these analyses, samples from the Lenca Highlands were considered one OTU, while specimens from all other populations of *N. crassulus* sensu lato were considered a second OTU. The data were log transformed prior to analysis and scaled to their standard deviation in order to normalize their distribution. PCAs were carried out using '*prcomp*' and plotted using the '*autoplot*' command in the package *ggfortify* (Tang et al. 2016). According to Kaiser's criterion, components with eigenvalues >1.0 were retained (Kaiser 1960).

RESULTS

Morphological Analyses

Some variation in selected morphological measurements, proportions, and scale counts was found among *N. crassulus* populations (Table 2). Thirteen characters in males and 11 in females were significantly different based on MWU analyses (Appendix 2). HW/SVL, HL/HW, SHL/SVL, SHL/HL, SPW/SVL, NDSPW/SVL, ESO, and INS were significant in both males and females. Additionally, SVL, VEO/SVL, LDPS/SVL, DS1H, SMB, S1C, SOSIP, ILS, and EDS were significant in either males or females. The first ten principal components explained 95% of the cumulative variance in both male and females (Appendix 3). In males and females, HW/SVL had the strongest positive loadings in PC1 (0.454 and 0.406, respectively). SL/SVL (0.536), ShL/SVL (0.461), and SL/HL (0.390) had the strongest positive loadings in PC2 for males, and HL/HW (0.448), ShL/SVL (0.395), and VEO/SVL (0.393) were the strongest in females. The two OTUs formed distinct clusters that overlapped somewhat in morphospace (Fig. 2). Coloration and pattern were variable across all specimens, as were dewlap coloration, size, and GSR. No combination of these traits reliably delimited specimens from any population. Based on the examination of seven specimens with fully everted hemipenes, hemipenial structure also appears highly conserved between all populations, largely agreeing with the description of McCranie and Köhler (2015: 52). However, specimens from Mexico appeared to have slightly broader lobes than others specimen examined, and a specimen from El Salvador (KU 184065) appeared to have a somewhat larger overall organ.

Molecular Evidence and Taxonomic Conclusion

Hofmann and Townsend (2017)'s previous analyses of mitochondrial and nuclear loci under concatenated and multispecies coalescent frameworks all unambiguously recovered the Lenca Highland population of *N. crassulus* as a lineage distinct from all other populations assigned to that name (Fig. 1). The genetic distances between this population and others assigned to *N. crassulus* (Table 1) were notably larger than those separating many recently described anoles from their closely related congeners for the mitochondrial loci 16S (5.7–7.1% compared to 3.2–4.4%; Köhler et al. 2016), ND2 (13.8–16.9% compared to 7.8–12.5%; Poe et al. 2015; Gray et al. 2016; Grisales-Martínez et al. 2017; Poe and Ryan 2017), and COI (13.8–17.2% compared to 7.3%; Poe et al. 2015).

We follow the unified species concept (de Queiroz 2007) in that we define species as separately evolving metapopulation lineages, with additional lines of evidence being relevant to species delimitation as "operational criteria." It is important that characters, such as morphology, distribution, and ecological niche, be considered in the delimitation of a species, with no one line of evidence necessarily weighted more heavily than another. Given the genetic distinctiveness, mid-Miocene divergence, allopatric distributions promoting long-term reproductive isolation, and subtle morphological differences, we conclude that the Lenca Highland population assigned to *N. crassulus* represents a species-level lineage distinct from populations in Guatemala, El Salvador, and Mexico. This population represents a separately evolving lineage that has undergone minimal phenotypic change, despite having diverged from their most recent common ancestor more

TABLE 2

Selected morphological character comparisons between *Norops caceresae*, sp. nov., and *N. crassulus*. Proportion data and averages ± standard deviations of measurements are rounded to the nearest 0.01. Averages ± standard deviations of count data are rounded to the nearest 0.1. Measurements are in millimeters (mm).

	N. caceresae, sp. nov.		*N. crassulus*					
	LENCA HIGHLANDS		SALVADORAN CORDILLERA		GUATEMALA		MEXICO	
	Male (n=12)	**Female (n=9)**	**Male (n=10)**	**Female (n=6)**	**Male (n=33)**	**Female (n=24)**	**Male (n=5)**	**Female (n=1)**
Maximum Snout-Vent Length (SVL)	57 (47.33 ± 7.20)	54 (49.22 ± 4.09)	49 (44.60 ± 3.03)	52 (45.67 ± 6.09)	55 (41.97 ± 5.39)	54 (44.00 ± 5.96)	47 (43.80 ± 4.66)	48
Complete TL/ SVL[1]	1.82–2.02 (1.93 ± 0.09)	1.60–2.00 (1.87 ± 0.14)	1.63–2.39 (2.15 ± 0.34)	2.11–2.26 (2.19 ± 0.06)	1.76–2.53 (2.17 ± 0.22)	1.54–2.44 (2.051 ± 0.27)	2.17–2.57 (2.407 ± 0.16)	1.94
Head Length/SVL	0.26–0.30 (0.28 ± 0.01)	0.25–0.28 (0.27 ± 0.01)	0.25–0.30 (0.27 ± 0.01)	0.25–0.29 (0.27 ± 0.01)	0.27–0.30 (0.29 ± 0.01)	0.24–0.31 (0.28 ± 0.02)	0.27–0.30 (0.28 ± 0.01)	0.27
Head Width/SVL	0.17–0.20 (0.18 ± 0.01)	0.17–0.18 (0.17 ± 0.01)	0.17–0.20 (0.18 ± 0.01)	0.17–0.21 (0.19 ± 0.02)	0.18–0.22 (0.20 ± 0.01)	0.16–0.21 (0.19 ± 0.01)	0.18–0.20 (0.19 ± 0.01)	0.17
Head Length/ Head Width	1.49–1.70 (1.58 ± 0.07)	1.50–1.70 (1.58 ± 0.07)	1.41–1.65 (1.48 ± 0.09)	1.35–1.56 (1.44 ± 0.08)	1.32–1.57 (1.45 ± 0.06)	1.32–1.60 (1.46 ± 0.07)	1.46–1.50 (1.48 ± 0.02)	1.54
Snout Length/SVL	0.13–0.15 (0.14 ± 0.01)	0.11–0.14 (0.13 ± 0.01)	0.12–0.14 (0.13 ± 0.01)	0.12–0.13 (0.12 ± 0.01)	0.12–0.15 (0.13 ± 0.01)	0.11–0.14 (0.13 ± 0.01)	0.12–0.14 (0.13 ± 0.01)	0.12
Snout Length/ Head Length	0.43–0.51 (0.48 ± 0.02)	0.43–0.532 (0.47 ± 0.03)	0.45–0.48 (0.47 ± 0.01)	0.45–0.48 (0.47 ± 0.01)	0.39-0.51 (0.46 ± 0.03)	0.43–0.53 (0.48 ± 0.03)	0.44–0.48 (0.45 ± 0.02)	0.46
Axilla-Groin Distance/ SVL	0.38–0.45 (0.41 ± 0.03)	0.39–0.50 (0.43 ± 0.03)	0.36–0.47 (0.41 ± 0.04)	0.36–0.455 (0.43 ± 0.04)	0.32–0.45 (0.39 ± 0.03)	0.37–0.47 (0.42 ± 0.03)	0.39–0.43 (0.41 ± 0.02)	0.42
Shank Length/ SVL	0.24–0.29 (0.26 ± 0.01)	0.22–0.27 (0.25 ± 0.02)	0.22–0.25 (0.24 ± 0.01)	0.22–0.25 (0.23 ± 0.01)	0.22–0.27 (0.24 ± 0.01)	0.21–0.25 (0.23–0.01)	0.22–0.26 (0.24 ± 0.01)	0.22
Shank Length/ Head Length	0.84–0.98 (0.93 ± 0.04)	0.79–0.94 (0.90 ± 0.06)	0.83–0.95 (0.87 ± 0.04)	0.79–0.95 (0.87 ± 0.05)	0.74–0.93 (0.84 ± 0.05)	0.74–0.97 (0.84 ± 0.05)	0.82–0.91 (0.86 ± 0.04)	0.82
Subdigital lamellae on Phalanges II-IV of Toe IV (Left and Right side averaged)	22–29 (25.8 ± 1.8)	23–28 (24.9 ± 1.3)	20–26 (23.2 ± 2.0)	20–26 (22 ± 1.6)	20–27 (23.4 ± 2.0)	18–28 (22.6 ± 2.1)	22–26 (23.7 ± 1.2)	20, 23
Subdigital lamellae on distal phalanx of Toe IV (Left and Right side averaged)	6–9 (6.9 ± 0.9)	5–8 (6.7 ± 0.8)	5–8 (7.0 ± 0.9)	4–8 (6.3 ± 1.1)	5–8 (6.2 ± 1.0)	4–8 (6.3 ± 0.9)	5–8 (6.5 ± 0.8)	6
Number of ventral scales in one head length	18–22 (19.7 ± 1.7)	16–22 (17.6 ± 2.2)	16–32 (20.4 ± 4.7)	18–22 (19.7 ± 2.0)	14–26 (20.55 ± 3.1)	14–22 (17.8 ± 2.5)	20–30 (25.2 ± 4.1)	20
Number of dorsal scales in one head length	22–28 (24.5 ± 2.3)	16–24 (20.9 ± 2.5)	20–30 (23.6 ± 3.0)	22–30 (24.3 ± 3.2)	16–32 (25.2 ± 3.4)	10–36 (23.8 ± 6.1)	20–30 (25.2 ± 4.1)	30
Number of ventral scales between the levels of axilla and groin	25–34 (29.3 ± 2.5)	26–33 (30.2 ± 2.5)	24–35 (30.8 ± 3.2)	28–31 (30.3 ± 3.9)	22–36 (29.8 ± 3.5)	23–40 (30.3 ± 4.2)	29–35 (31.8 ± 2.8)	27
Number of dorsal scales between the levels of axilla and groin	34–43 (38.6 ± 2.4)	34–46 (39.6 ± 3.5)	28-49 (39.4 ± 6.0)	36–45 (41.3 ± 4.1)	29-46 (35.5 ± 4.9)	32–63 (42.5 ± 8.8)	32-41 (36.8 ± 3.3)	51
Number of scales around midbody	88–106 (95.3 ± 6.5)	80–114 (91.6 ± 10.5)	84-106 (89.4 ± 12.7)	80–98 (88.3 ± 6.9)	66-120 (83.4 ± 11.9)	66–116 (84.8 ± 13.6)	60-76 (65.2 ± 6.3)	96
Number of scales between first canthals	7–9 (8.3 ± 0.7)	7–9 (8.2 ± 0.8)	5–9 (7.3 ± 1.3)	6–9 (7.3 ± 1.2)	6–10 (7.5 ± 0.9)	7–9 (7.9 ± 0.7)	7–9 (8.2 ± 0.8)	8

TABLE 2
(continued from previous page)

	N. caceresae, sp. nov.		*N. crassulus*					
	LENCA HIGHLANDS		SALVADORAN CORDILLERA		GUATEMALA		MEXICO	
	Male (n=12)	**Female (n=9)**	**Male (n=10)**	**Female (n=6)**	**Male (n=33)**	**Female (n=24)**	**Male (n=5)**	**Female (n=1)**
Number of scales between second canthals	5–7 (5.9 ± 0.7)	5–6 (5.8 ± 0.4)	5–7 (5.9 ± 0.6)	5–7 (5.7 ± 0.8)	4–7 (5.5 ± 0.7)	5–8 (5.8 ± 0.9)	5–6 (5.4 ± 0.5)	6
Number of scales between supraorbital semicircles	0–1 (0.9 ± 0.3)	1–2 (1.1 ± 0.3)	0–1 (0.8 ± 0.4)	0–1 (0.7 ± 0.5)	0–2 (0.9 ± 0.4)	0–2 (0.9 ± 0.4)	1 (1.0 ± 0.0)	0
Number of scales between interparietal plate and supraorbital semicircles	2–3 (2.8 ± 0.4)	2–4 (2.8 ± 0.8)	1–4 (2.6 ± 0.8)	2–3 (2.2 ± 0.4)	1–3 (2.3 ± 0.5)	1–3 (2.3 ± 0.5)	2–3 (2.2 ± 0.4)	2
Number of Postmentals	4–5 (4.1 ± 0.3)	4 (4.0 ± 0.0)	4–6 (4.3 ± 0.7)	3–6 (4.8 ± 1.3)	4–5 (4.1 ± 0.3)	4–6 (4.1 ± 0.4)	4 (4.0 ± 0.0)	4
Number of Postrostrals	5–6 (5.4 ± 0.5)	5–7 (5.4 ± 0.7)	5–6 (5.3 ± 0.5)	5–7 (5.8 ± 0.8)	4–10 (5.4 ± 1.0)	4–6 (5.3 ± 0.6)	5–6 (5.2 ± 0.4)	5
Number of Internasals	6–8 (7.3 ± 0.6)	6–9 (7.1 ± 0.9)	5–8 (6.3 ± 0.8)	6–7 (6.3 ± 0.5)	5–9 (6.5 ± 1.1)	4–8 (6.1 ± 0.9)	6–8 (7.2 ± 0.8)	7
Number of Supralabials to level below center of eye	5–7 (6.0 ± 0.7)	4–6 (5.7 ± 0.5)	6–7 (6.5 ± 0.5)	5–7 (6.0 ± 0.63	5–7 (6.1 ± 0.6)	5–7 (6.0 ± 0.6)	5–6 (5.8 ± 0.4)	6
Number of Infralabials to level below center of eye	5–8 (5.8 ± 0.8)	4–6 (5.2 ± 0.7)	5–7 (6.0 ± 0.7)	5–7 (6.0 ± 0.6)	4–7 (5. 7 ± 0.6)	5–7 (5.8 ± 0.7)	5–6 (5.8 ± 0.4)	7
Number of enlarged supraocular scales	5–10 (7.1 ± 1.4)	5–9 (6.2 ± 1.4)	3–9 (5.2 ± 1.7)	3–6 (4.0 ± 1.3)	3–7 (5.3 ± 1.3)	2–8 (5.0 ± 1.5)	5–6 (5.6 ± 0.5)	6
Number of Suboculars in contact with number of supralabials (SO/SL)	2–3/1–3 (2.2 ± 0.4/ 2.5 ± 0.7)	1–3/1–3 (2.1 ± 0.6/ 2.2 ± 0.7)	1–3/1–3 (2.3 ± 0.7/ 2.0 ± 0.1)	2/1–2 (2.0 ± 0.0/ 1.5 ± 0.5)	1–4/1–4 (2.5 ± 0.7/ 2.3 ± 0.8)	2–3/1–3 (2.5 ± 0.5/ 2.2 ± 0.5)	1–3 /1–2 (2.0 ± 1.0/ 1.6 ± 0.5)	2/2
Number of Loreal scales	17–24 (19.5 ± 2.3)	13–27 (18.3 ± 4.1)	17–30 (23.6 ± 4.1)	19–26 (22.2 ± 2.5)	12–36 (19.0 ± 4.9)	13–25 (17.5 ± 3.1)	18–23 (19.4 ± 2.1)	21
Number of Loreal scale rows	4–5 (4.1 ± 0.3)	3–5 (4.0 ± 0.9)	4–5 (4.7 ± 0.5)	4–6 (4.8 ± 0.8)	3–6 (4.2 ± 0.6)	3–5 (4.1 ± 0.7)	4–5 (4.6 ± 0.5)	5
Number of Sublabials	2–4 (2.4 ± 0.7)	2–4 (2.9 ± 0.9)	2–5 (2.9 ± 1.1)	2 (2.0 ± 0.0)	2–5 (2.7 ± 0.9)	2–8 (2.8 ± 1.4)	2–4 (2.8 ± 0.8)	2
Number of Enlarged Dorsal Scale Rows	12–19 (17.2 ± 1.9)	12–20 (16.7 ± 2.9)	12–16 (13.5 ± 1.4)	12–15 (12.5 ± 1.2)	13–19 (15.2 ± 1.4)	12–20 (15.4 ± 2.3)	12–17 (14.4 ± 2.1)	14
Number of Gorgetal scale rows[2]	6–7 (6.3 ± 0.5)	-	-	-	6–8 (6.7 ± 1.0)	-	5–7 (6.2 ± 0.8)	-

Note.[1] n = 5 (male), 4 (female) (Salvadoran Cordillera); 24, 16 (Guatemala); 7, 6 (Lenca Highlands); 5, 1 (Mexico). [2] n = 0 (Salvadoran Cordillera); 7 (Guatemala); 11 (Lenca Highlands); 5 (Mexico).

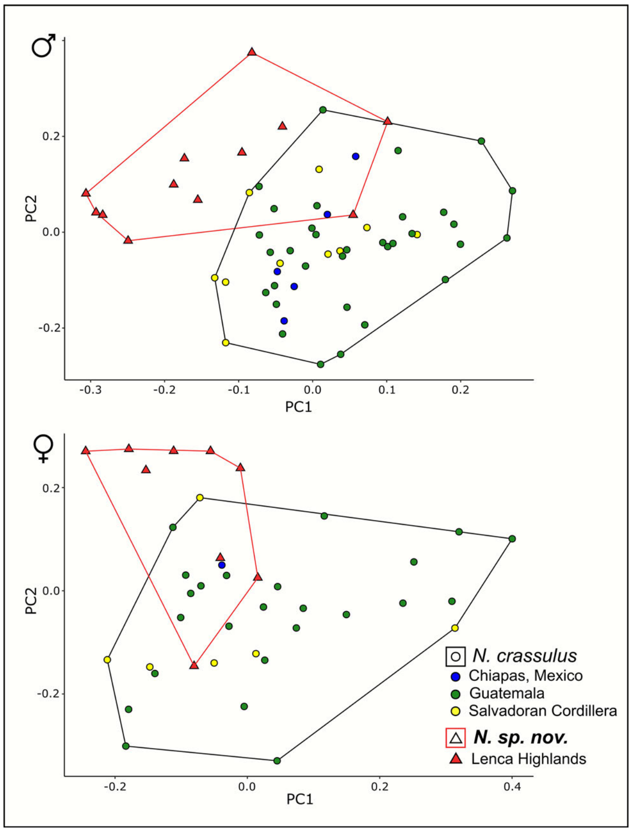

Fig. 2.—Plots of the first two principal components for males (**A**) and females (**B**). Colors correspond to lineages as in Figure. 1.

than 13 million years ago (Fig. 1; Hofmann and Townsend 2017). As the type locality of *N. crassulus* is Cobán, Alta Verapaz, Guatemala (Cope 1864; Stuart 1942) the name *N. crassulus* sensu stricto is restricted to those populations occurring in the highlands of Guatemala, El Salvador, and Mexico, with the understanding that further taxonomic investigation of the populations in Chiapas, Mexico, remains necessary and may lead to the recognition of additional taxa. As the Lenca Highland anoles previously assigned to *N. crassulus* are not conspecific with that taxon, and no applicable names are available in synonymy, we describe this population as a new species below.

SYSTEMATICS

Class Reptilia Laurenti, 1768
Order Squamata Oppel, 1811
Family Dactyloidae Fitzinger, 1843
Subfamily Anolinae Cope, 1864
Genus ***Norops*** Wagler, 1830

Norops caceresae, **new species**

English Common Name: Berta's Anole
Spanish Common Name: Pichete de Berta
(Figs. 3–5)

Anolis crassulus—Hahn, 1971:111; Meyer and Wilson 1971:106; 1973:16; Wilson 1983:125; Wilson and Townsend 2007:135; Townsend and Wilson 2009:64; Wilson and Johnson 2010:125 (in part); Townsend and Wilson 2010:474 (in part).

Norops crassulus—McCranie et al. 1992:208; Wilson and McCranie 1994:148; 2002:91; 2003a:24 (in part); 2003b:37; Köhler and Obermeier 1998:127 (in part); Köhler 2008:104 (in part); Solís et al. 2014:129 (in part); Townsend 2014:239 (in part); Johnson et al. 2015:81 (in part); McCranie 2015:368 (in part); McCranie and Köhler 2015:49 (in part).

N. crassulus (Honduras)—Köhler et al. 1999:286.

A. crassulus (Honduras)—Hofmann and Townsend 2017:8.

Holotype.—CM 161315 (field number JHT 3914), Figures 3 and 4, an adult male, from near Río Agua Negra, 14.459°N, 88.385°W, 1,940 m above sea level, Reserva Biológica Opalaca, Departamento de Intibucá, Honduras (Fig. 6), collected on 28 May 2015 by Thomas J. Firneno Jr., Michael W. Itgen, Josiah H. Townsend, and Kayla D. Weinfurther.

Paratypes.—(*n* = 22; 12 males, 10 females); CM 161303–161305, 161308, MVZ:Herp:286121–286122, KU 348836, KU 348838 [JHT 3739, 3741], (field numbers JHT 3738–39, 3741–43, 3764, 3767, 3781), adult males, and CM 161301–161302, 161306–161307, MVZ:Herp:286123–286124, KU 348835, KU 348837 [JHT 3737, 3740] (field numbers JHT 3735–37, 3740, 3766, 3768–70), adult females, from near El Rodeo, 14.441°N, 88.145°W, 2100 m above sea level, Refugio de Vida Silvestre Mixcure, Departamento de Intibucá, Honduras, collected 23 May 2015 by Thomas J. Firneno Jr., Michael W. Itgen, Josiah H. Townsend, and Kayla D. Weinfurther; CM 161310, 161312–161314 (field numbers JHT 3887, 3906, 3910–11), adult males, CM 161309 (field number JHT 3822), an adult female, and CM 161311 (field number JHT 3888), a subadult female, with the same collection data as the holotype.

Referred specimens.—(*n* = 78); KU 219977, from 9.8 km SW of Siguatepeque, Depto. de Comayagua, Honduras; UF 166190–91, and KU 194268–70, from Zacate Blanco, Depto. de Intibucá, Honduras; SMF 86963–67, from near El Rodeo, Depto. de Intibucá, Honduras; KU 219950–53, from 18.1 km NW of La Esperanza, Depto. de Intibucá, Honduras; KU 194271, from 11 km NW of La Esperanza, Depto. de Intibucá, Honduras; UF 103410–11, from 17 km NE of La Esperanza, Depto. de Intibucá, Honduras; LACM 47683–85, from 2.4 km ENE of La Esperanza, Depto. de Intibucá, Honduras; LACM 47686–90, 4.8 km ENE of La Esperanza, Depto. de Intibucá, Honduras; LACM 47691, from 12.9 km ENE of La Esperanza, Depto. de Intibucá, Honduras; UF 121773, about 10 km SE of La Esperanza, Depto. de Intibucá, Honduras; CM 59118–19 and LSUMZ 38816–24, from La Esperanza, Depto. de Intibucá, Honduras; KU 219954, from San Pedro La Loma, Depto. de Intibucá, Honduras; FMNH 283624–27, from Santa Catarina, Depto. de Intibucá, Honduras; UF 166192, from Cerro El Pelón, Depto. de Intibucá, Honduras; UF 166185–166189

Fig. 3.—Dorsal and ventral body views of CM 161315, the holotype of *Norops caceresae*, sp. nov.

(but see *Remarks* for UF 166189) from near Guajiquiro, Depto. de La Paz, Honduras; KU 184084–87, from Cantón Palo Blanco, Depto. de La Paz, Honduras; KU 1584072–77, from Cantón El Zancudo, Depto. de La Paz, Honduras; SMF 78092 from Opatoro, Depto. de La Paz, Honduras; KU 219955–56, 219978–81 from mountains S of San Pedro de Tutule, Depto. de La Paz, Honduras; KU 194300–04, from about 5 km S of Santa Elena, Depto. de La Paz, Honduras; FMNH 236387, KU 209323–26, and 219957–60, from Narantojos, Depto. de Lempira, Honduras.

Diagnosis.—A medium-sized species (maximum recorded snout-vent length 57 mm in males: KU 348838, CM 161310, CM 161315; 54 mm in females: KU 348837, CM 161307) of beta anole in the genus *Norops* endemic to southwestern Honduras. *Norops caceresae* can be differentiated from all other anoles in Honduras, except those of the *N. crassulus* species subgroup, by the combination of having enlarged middorsal scales, strongly keeled ventral scales, two or fewer scales separating the supraorbital semicircles, four to seven loreal scale rows, suboculars and supralabials in contact, heterogeneous lateral body scales, enlarged postcloacal scales in males, and an orange-to-red male dewlap (in life). *Norops caceresae* can be diagnosed from the other species of the *Norops crassulus* species subgroup, except *N. crassulus* sensu stricto, as follows

Fig. 4.—Dorsal, lateral, and ventral views of the head of CM 161315, the holotype of *Norops caceresae*, sp. nov.

(known distributions in parentheses): from *N. amplisquamosus* McCranie et al., 1993 (northwestern Cortés, Honduras), *N. heteropholidotus* (Mertens, 1952) (northwestern El Salvador, southeastern Guatemala, and southwestern Honduras), *N. muralla* (Köhler et al., 1999) (northwestern Olancho, Honduras), *N. sminthus* (Francisco Morazan and southern Comayagua, Honduras), and *N. wermuthi* Köhler and Obermeier, 1998 (northern Nicaragua and extreme southeastern Honduras) by its strongly keeled ventral scales (versus smooth to weakly keeled); from *N. anisolepis* (Chiapas, Mexico) by its larger size (maximum SVL 57 mm in males, 54 mm in females; versus 47 mm in male, 48 mm in female *N. anisolepis*) and its orange-to-red male dewlap (versus bright pink male dewlap in *N. anisolepis*); from *N. haguei* (Stuart, 1942) (Alta Verapaz, Guatemala) by its larger dorsal scales (34–43 between level of axilla and groin, approximately equal to or slightly smaller in size than ventrals; versus 41–57, dorsals much smaller than ventrals in *N. haguei*); from *N. morazani* (northern Francisco Morazán, Honduras) by having a hemipenis with an undivided asulcate processus (versus divided asulcate processus in *N. morazani*), and having 6–9 scales separating the nasals (2–4 in *N. morazani*); and from *N. rubribarbaris* Köhler et al., 1998 (Santa Bárbara, Honduras) by having a TL/SVL 1.82–2.02 in males, 1.60–2.00 in females (versus 2.16–2.54 in males, 2.19–2.21 in females of *N. rubribarbaris*), and having 12–20 rows of enlarged dorsal scales (versus 8–11 in *N. rubribarbaris*).

Norops caceresae is most similar in external morphology to *N. crassulus* sensu stricto (highlands of central Guatemala, southwestern El Salvador, and Chiapas, Mexico). *Norops caceresae* is distinguished from all other populations assigned to *N. crassulus* by the following: (1) a longer head relative to width: HL/HW 1.49–1.70 (1.58 ± 0.07) in males, 1.50–1.70 (1.58 ± 0.07) in females (versus 1.32–1.65 [1.46 ± 0.06] in males, 1.32–1.56 [1.46 ± 0.07] in females of *N. crassulus*); (2) a shorter tail relative to snout–vent length: complete TL/SVL 1.79–2.02 (1.91 ± 0.01) in males, 1.60–2.00 (1.87 ± 0.14) in females (versus 1.62–2.37 [2.20 ± 0.24] in males, 1.54–2.44 [2.07 ± 0.24] in females of *N. crassulus*) (3) a longer shank relative to snout-vent length: ShL/SVL: 0.24–0.29 (0.26 ± 0.01) in males, 0.22–0.27 (0.25 ± 0.02) in females (versus 0.22–0.27 [0.24 ± 0.01] in males, 0.21–0.25 [0.23 ± 0.01] in females of *N. crassulus*); (4) a longer shank relative to head length: ShL/HL: 0.84–1.13 (0.94 ± 0.07) in males, 0.79–0.94 (0.92 ± 0.06) in females (versus 0.74–0.95 [0.83 ± 0.12] in males, 0.74–0.97 [0.84 ± 0.05] in females of *N. crassulus*); (5) a slightly higher average number of lamellae on Phalanges II-IV of the 4th toe: 25.7 ± 1.8 in males, 24.9 ± 1.3 in females (versus 23.3 ± 1.9 in males, 22.5 ± 2.0 in females of *N. crassulus*).

Description of the holotype.—Adult male (Figs. 3-4), medium sized, hemipenes everted, right thigh with skin and thigh muscle removed; tail complete; SVL 57 mm, tail length 114 mm, tail slightly laterally compressed, vertical diameter 3.46 mm, horizontal diameter 2.25 mm, twice as long as SVL; head length (HL) 15.87 mm, 27.8% of SVL; head width 9.66 mm, head 1.64 times as long as wide; snout 7.32 mm, 46.1% of head length, 12.8% of SVL; axilla-groin distance 21.64 mm, 38.0% of SVL; shank length 15.49 mm, 27.2% of SVL, 97.6% of HL; dilated subdigital pad width 1.01 mm, non-dilated 0.46 mm; when the hind limb is adpressed, the longest digit reaches approximately to the middle of the eye.

Scales on dorsal surface of snout large, irregular, keeled; seven scales between nasals, keeled; one scale separates nasal from rostral; prenasal divided in vertical series, the lower in contact with the rostral and first supralabial and

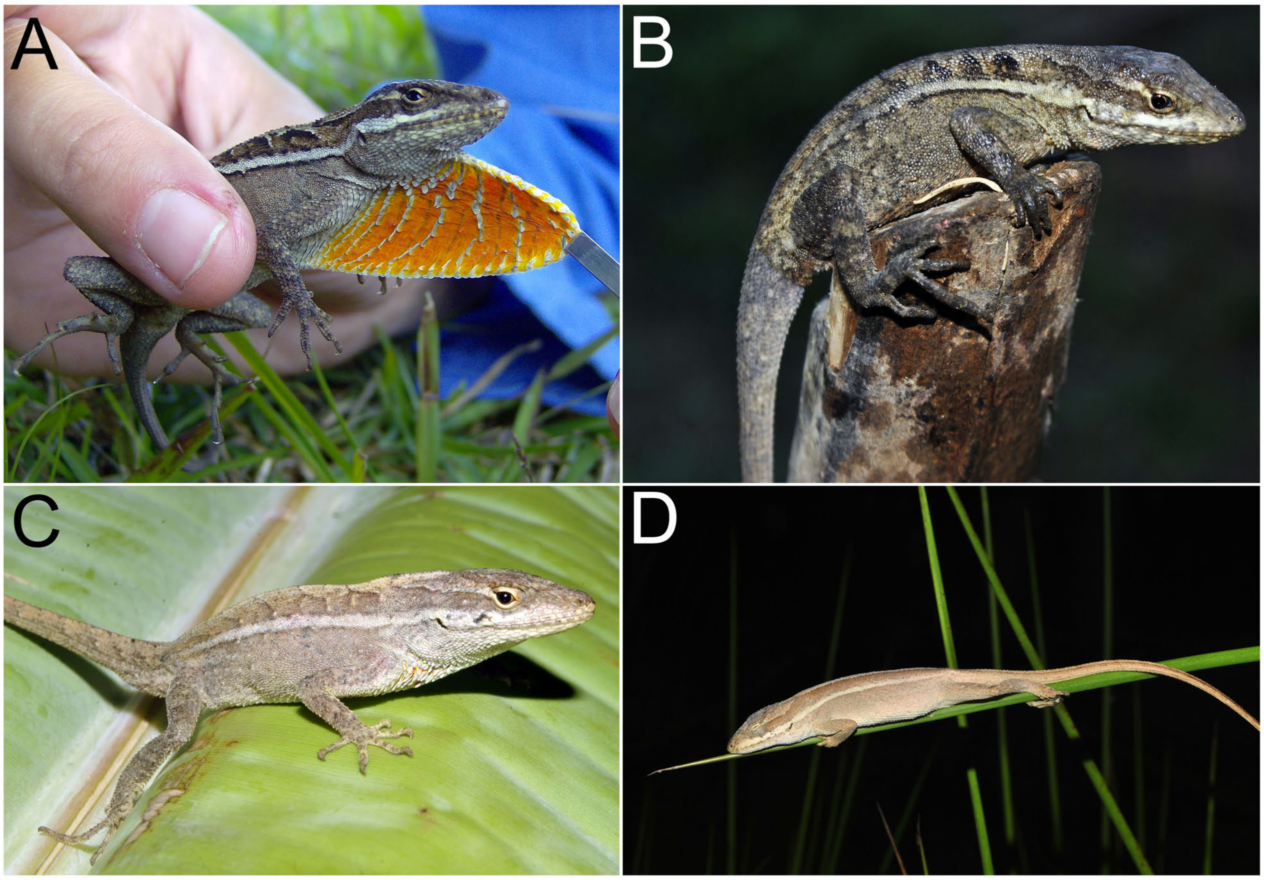

Fig. 5.—Adult male examples of *Norops caceresae*, sp. nov., in life. **A,** adult male from El Rodeo (14.460°N, 88.1585°W), 2,160 m elevation, Departamento de Intibucá, Honduras, showing the typical coloration of the male dewlap (JHT 2913). **B-D,** In situ from Yamaranguila (14.364°N, 88.263°W), 2,060 m elevation, Departamento de Intibucá (not collected). Photo A by César Cerrato-Mendoza; photos B–D by Josue Ramos Galdamez.

the higher in contact with neither; six postrostrals; distinct frontal depression with scales keeled radially; well-developed supraorbital semicircles consisting of six enlarged, irregular scales, three smooth and three with weak keels; one keeled scale separates supraorbital semicircles at their closest point; shallow parietal depression, with scales rugose, irregular; interparietal separated from supraorbital semicircles by three scales; scales on the posterior portion of the head irregular, rugose to weakly keeled; six moderately enlarged, keeled, supraocular scales; two elongate, keeled superciliaries; distinct canthal ridge, nine scales between first canthals, six between second; 22 weakly keeled loreal scales in four rows; 6/5 keeled suboculars, two in contact with the posterior-most supralabial; 6/6 supralabials to the level below center of eye; mental wider than long, completely divided by medial suture, bordered by 4 postmentals with the outer pair greatly enlarged; 6/5 infralabials to the level below center of eye, longest approximately equal to longest supralabial; chin scales smooth to weakly keeled, juxtaposed, grading posteriorly into larger, weakly keeled, imbricate throat scales; middorsal scales of the neck weakly elevated, forming indistinct crest; scales anterior to the ear opening keeled and distinctly larger than those posterior to the ear opening, which are granular; dorsum of body covered in keeled, subimbricate to imbricate scales, with approximately 12 irregular, enlarged medial dorsal scale rows, largest scales 0.73 x 0.79 mm, posterior edge rounded or weakly pointed, approximately 24 enlarged dorsal scales in one head length, 37 between the level of the axilla and groin; dorsals grade into subimbricate, heterogeneous lateral scales, then further into granular, mostly homogeneous scalation; ventrals strongly keeled, imbricate, pointed, the largest of which are slightly larger than dorsals (0.9 x 0.9 mm), approximately 20 ventrals in one head length, 29 between the axilla and groin; 92 scales at midbody; caudal scales strongly keeled, imbricate; dorsal caudal scales slightly enlarged, three scales per caudal section; postcloacals enlarged; scales on limbs strongly keeled, imbricate, pointed on forelimbs and upper half of hindlimbs, ends grading to rounded on the shank of the hindlimb; scales of fingers and toes distinctly keeled, multicarinate and parallel; distal phalanx of toes narrower

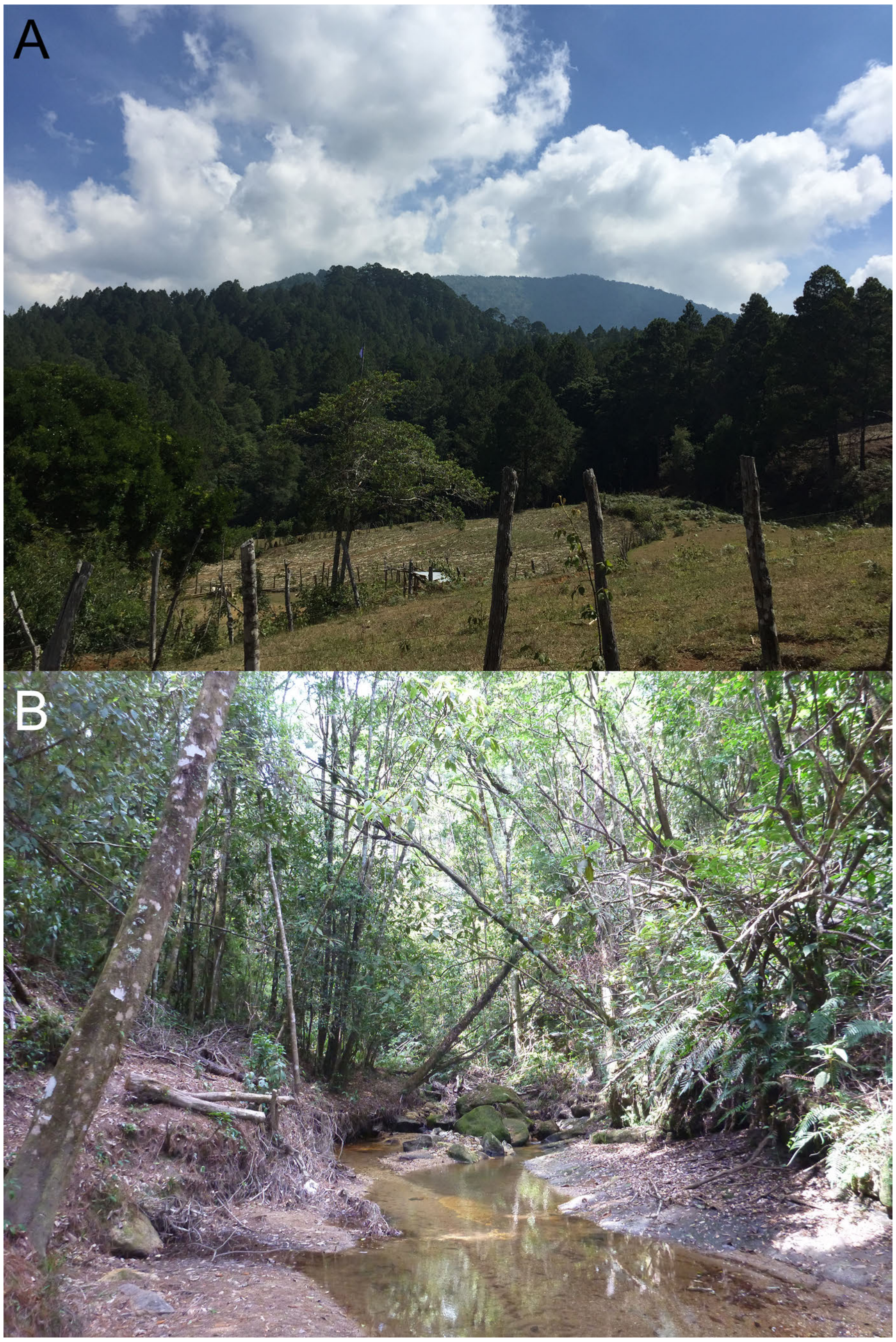

Fig. 6.—Type locality habitat of *Norops caceresae*, sp. nov. **A,** photograph of Reserva Biológica Opalaca, Departamento de Intibucá, Honduras; **B,** typical habitat of *Norops caceresae.* The holotype and some paratypes were collected while sleeping on low vegetation at night along this stream; photos by Josiah Townsend.

than and raised above dilated subdigital pad, 29/26 lamellae under phalanges II to IV of fourth toe, 8/9 lamellae under the distal phalanx; axillary pocket absent; dewlap large, six gorgetal rows consisting of 6–8 large, keeled gorgetals, anterior position below the anterior eye opening, posterior position extends to 7 mm beyond the axilla.

The completely everted hemipenis is a medium-sized, partially-bilobed organ (lobes connected by thin tissue through the apex); lobes are somewhat calyculate; an undivided, nub-like asulcal processus is evident approximately where the two lobes meet, halfway down the apex; truncus has transverse folds and is approximately equal in length

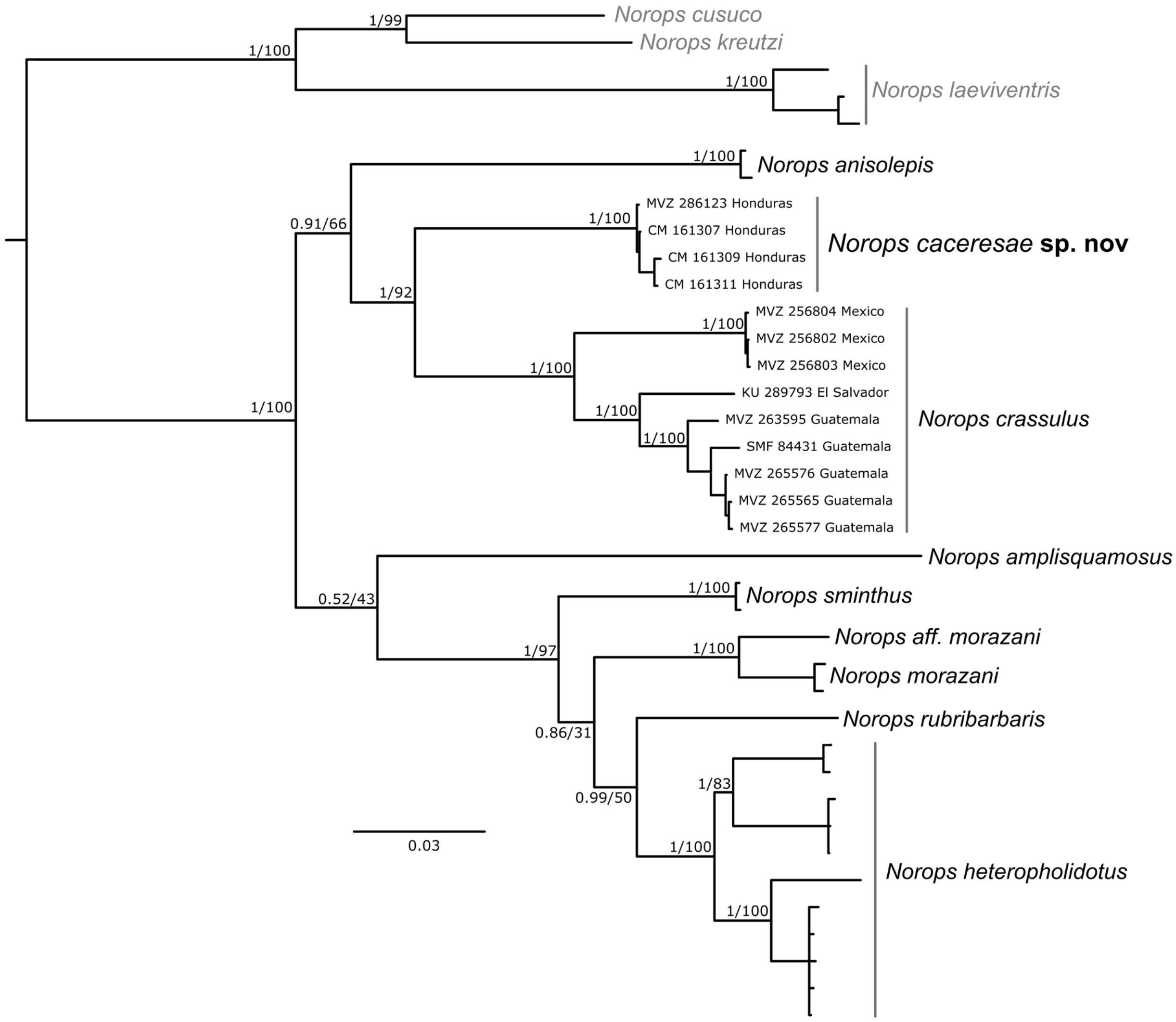

Fig. 7.—Phylogeny of the *Norops crassulus* species subgroup based on three mitochondrial (16S, ND2, COI) and three nuclear loci (PRLR, BDNF, PTPN12) showing the phylogenetic placement of *Norops caceresae*, sp. nov., re-annotated from Hofmann and Townsend (2017: fig. S1). Nodes are labelled with Bayesian posterior probabilities (left) and maximum likelihood bootstrap support values (right).

to the length of each lobe; well-developed sulcal lips surround the sulcus spermaticus, which opens into a broad area covering the apex between lobes.

After approximately 30 months in preservative, the coloration was recorded as follows: dorsal surfaces of head and body with Hair Brown (277) ground color, with one pair of well-defined and one pair of poorly-defined Vandyke Brown (281) scallops edged in Pratt's Payne's Gray (293), with intervening middorsal area Pratt's Payne's Gray (293); lateral surfaces of head Hair Brown (277) with supralabial region Dark Pearl Gray (290) and a Dark Pearl Gray (290) spot directly posterior of eye; infralabial region speckled Vandyke Brown (281) and Pearl Gray (262); dorsolateral surfaces with broad Pearl Gray (262) line originating just anterior of the ear opening and extending to the level of the adpressed elbow; lateral surfaces of body Glaucous (272); ventral surface Pearl Gray (262) with Smoke Gray (266) suffusions; dorsal surfaces of limbs Glaucous (272) with Hair Brown (277) suffusions; hind limbs with paired Sepia (279) crossbands on the medial portions of the calves; ventral areas of limbs Pearl Gray (262) with Smoke Gray (266) and Grayish Horn Color (268) suffusions more apparent than on ventral surface of body; dewlap extended in preservation, but color completely faded to Pale Buff (1).

Variation in paratypes.—Slight variation in meristic characters is apparent in some paratypes. A median suture only partially divides the mental in CM 161302, CM 161310, MVZ:Herp:286123, opposed to completely dividing it in all other paratypes. In most specimens, the mental is in contact posteriorally with four postmentals, two greatly enlarged outer and two smaller, longer than broad inner; in one male MVZ:Herp:286122, one of the postmentals is divided, creating a fifth postmental. Most paratypes have at most a single scale separating the supraorbital semicircles at the narrowest point; in one female, CM 161307, there are two. Between two and three scales separate the interparietal plate and the supraorbital semicircles; in two females, KU 348835 and CM 161307, there are four. Most paratypes have between two and four sublabials; in one subadult female, CM 161311, and one adult male, CM 161313, a small scale separates the outer left postmental from the infralabial, leaving only a single sublabial. In two males (CM 161303 and 161305) and two females (KU 348837, MVZ:Herp:286124), the circumorbital scales are incomplete, leaving some of the enlarged supraoculars in contact with the supraocular semicircles. Variation in the size of the scales around the midbody is evident, with females exhibiting wider variation (80–114, 91.6 ± 10.5) than males (86–106, 94.6 ± 6.8). Females exhibited larger dorsal scales relative to head length, as evidenced by their count of dorsal scales in one head length (16–24, 20.9 ± 2.5) compared to males (20–28, 24.2 ± 2.5). In six male paratypes (CM 161310, CM 161313–161314, KU 348838, MVZ:Herp:286121–286122), the dewlap extends from under approximately the anterior edge of the eye to 5–8 mm past the axilla; in two other male paratypes (CM 161304–161305) it extends 3 mm past the axilla, and in two additional male paratypes (CM 161303, KU 348836) it extends from under approximately the middle of the eye to 2 mm past the axilla.

Variation in color and dorsal pattern are evident in preserved male and female paratypes. Adult males typically exhibited a dorsal coloration and pattern similar to that of the holotype, with a gray-brown to yellow-brown ground color and well-defined pale dorsolateral lines extending from the side of the head onto the body. Dorsal ground color between these dorsolateral lines is typically darker than the ground color on the lateral portions of the body. In most adult male paratypes, this line was more evident than in the holotype, typically 2–8 dorsal scales wide and terminating one-third to two-thirds the distance between the limbs. All male paratypes possess a dorsal pattern consisting of dark brown, paired scallops or chevrons, with well-defined chevrons in the general shape of equilateral triangles having the base formed by the dorsolateral stripe and the vertices contacting the middorsal line. In some individuals (e.g., CM 161303, CM 161312), these scallops are relatively pale and only apparent on the anterior half of the body, while in others (e.g., KU 348836) they are dark, outlined with pale cream lines, and possess a pale spot in the center of each chevron. Most female paratypes exhibit a similar coloration and pattern to that of males, although in some females (e.g., CM 161306) the dorsolateral stripes are poorly defined, and pattern is reduced to the outlines of chevrons on the anterior half of the body. In other females, the scallops or chevrons only extend from the dorsolateral stripe to about halfway to the middorsal line (e.g., KU 348835). In one female (CM 161311), the dorsolateral stripes and dorsal scalloping are absent and replaced by a broad, cream-colored middorsal stripe that is 2–4 enlarged middorsal scales in width at midbody.

The dewlap coloration in life of two adult males (Fig. 5A, JHT 2913; MVZ:Herp:286122) from El Rodeo, Departamento de Intibucá, Honduras, were both Medium Chrome Orange (75) to Spectrum Orange (9), with Light Chrome Orange (76) around the margins, and Pale Buff (1) to Smoky White (261) marginal, gorgetal, and sternal dewlap scales.

Illustrations.—Figs. 3–5; McCranie and Köhler 2015: 54, fig. 16A (adult male) and 16B (adult male head and dewlap) (as *Norops crassulus*). Note that Köhler 2014: 247, fig. 27(I), 248, fig. 28(C), and McCranie and Köhler 2015: 53, fig. 15, are of specimens from Olancho, Honduras, representing *N.* aff. *N. morazani* (Hofmann and Townsend 2017).

Distribution.—*Norops caceresae* occurs at moderate and intermediate elevations (1,200–2,260 m) in the departments of Comayagua, Intibucá, La Paz, and Lempira in southwestern Honduras. Its known distribution is bordered to the west by the Río Ulúa and the south by Río Lempa.

Natural History.—*Norops caceresae* inhabits both intact and disturbed Mixed Transitional Cloud Forest, Broadleaf Cloud Forest, and Mixed Cloud Forest between 1,200 and 2,260 m elevation. This diurnal species appears most abundant near forest edges and along streams and is locally abundant in the matrix of traditional agriculture and forest patches that typifies much of the Lenca Highlands (Fig. 6). At night, *N. caceresae* can be encountered asleep on low vegetation, typically >1.5 m above the ground. We have observed this species in sympatry with *N. heteropholidotus* around a large stream through relatively intact Mixed Cloud Forest in the Cordillera de Opalaca in western Intibucá, Honduras, and with *N. heteropholidotus* and *N. laeviventris* (Wiegmann, 1834) in and around small Mixed Cloud Forest fragments at Cerro San Pedro La Loma in eastern Intibucá.

Phylogenetic relationships.—An updated phylogeny of the *Norops crassulus* subgroup is presented in Figure 7. *Norops caceresae* is monophyletic in both mtDNA and nDNA analyses, as well as in concatenated and multispecies coalescent frameworks (Hofmann and Townsend 2017). Sequences of the mtDNA loci 16S, ND2, and COI, as well as the nDNA loci PRLR, BDNF, and PTPN12, for *N. caceresae* (generated by Hofmann and Townsend 2017) are available on GenBank (Appendix 4). Intraspecific distances at each of these loci are: 0.5% (16S); 0.8% (ND2); 0.7% (COI); 0.2% (PRLR); 0.0% (BDNF); 0.1% (PTPN12). From populations of its closest relative, *N. crassulus* sensu stricto, it is 5.7–7.1% divergent at 16S, 13.8–16.9% at ND2, 13.8–17.2% at COI, 1.6–2.2% at PRLR, 0.3–0.5% at BDNF, and 0.9–1.0% at PTPN12. *Norops caceresae* is a member of the "*crassulus*" clade (containing *N. anisolepis* and all *N. crassulus* populations from Mexico, El Salvador, and Guatemala; sensu Hofmann and Townsend 2017) of the *Norops crassulus* species subgroup in the genus *Norops*.

Etymology.—The eponym *caceresae* is a noun in the genitive case, and is given in honor of Berta Isabel Cáceres Flores of La Esperanza, Departamento de Intibucá, Honduras (approximately 25 km from the type locality). Berta Cáceres was a community leader and environmental activist who cofounded the Consejo Cívico de Organizaciones Populares e Indígenas de Honduras (COPINH: Civic Council of Popular and Indigenous Organizations of Honduras), and, in the face of threats against her and her family and the murders of friends and colleagues, led grassroots efforts to unite communities against environmentally destructive actions and the privatization of native lands in Honduras. She was awarded the Goldman Prize for Conservation in 2015, and continued her work organizing and fighting for indigenous rights and environmental justice until she was assassinated in her home in La Esperanza on 3 March 2016. We name this species as a small gesture to honor Berta and to raise awareness for COPINH and their work, while continuing to draw attention to the plight of indigenous and environmental activists in Honduras, dozens of whom have been murdered over the past decade.

Remarks.—Phylogenetic analyses of the *Norops crassulus* subgroup revealed an unexpected cryptic sister lineage to *N. rubribarbaris* (= *N.* aff. *N. rubribarbaris*; Hofmann and Townsend 2017) comprised of two samples from Dept. La Paz, near Guajiquiro. Of the two samples, only 16S and COI sequences were available, and no viable tissue remained to sequence additional loci. Only one of these samples, UF 166189, has been accessioned, and was part of the series of *N. crassulus* examined by McCranie and Köhler (2015); the other sample was deposited but not accessioned and is presumed lost. UF 166189 is a juvenile anole with enlarged middorsals, keeled ventrals, and heterogeneous lateral scalation, a brown dorsum with a dark middorsal line, a white venter with some dark mottling, and mottling on the limbs. These samples suggest a cryptic lineage potentially exists in sympatry with the newly described species, warranting further investigation.

DISCUSSION

With the description of *N. caceresae,* the *Norops crassulus* species subgroup now consists of 11 species: *N. ampliquamosus, N. anisolepis, N. caceresae, N. crassulus, N. haguei, N. heteropholidotus, N. morazani, N. muralla, N. rubribarbaris, N. sminthus,* and *N. wermuthi.* Hofmann and Townsend (2017) showed that this subgroup is monophyletic with respect to other *Norops* and contains several cryptic lineages in need of further study.

Norops caceresae is endemic to an area less than 10,000 km^2, inhabiting areas above 1,200 m elevation that are associated with Mixed Transitional Cloud Forest, Broadleaf Cloud Forest, and Mixed Cloud Forest. This species is under some degree of threat from anthropogenic habitat destruction, but appears to be tolerant of anthropogenic disturbance and able to utilize edges and fence-lines associated with agricultural clearings. This anole is relatively abundant where found, and under no direct threat from human exploitation. Following the IUCN Red List criteria (2001), we would consider this species to be Least Concern/Near Threatened.

Norops caceresae is notably conserved in external morphology relative to its sister taxon, *N. crassulus.* Cryptic species are a critical, yet poorly-reflected consideration in both biodiversity conservation and the exploration of ecological and evolutionary processes (Bickford et al. 2007; Jörger and Schrödl 2013; Fišer et al. 2018). Many cryptic species are discovered—often incidentally through broader phylogenetic studies—but left unnamed, masking them from studies that rely on Linnean binomials as hypotheses or variables (Fišer et al. 2018; Struck et al. 2018). Therefore, it is important that such genetically-distinct lineages are thoroughly examined through integrative taxonomy, in an effort to better understand natural processes. Recent reviews by Fišer et al. (2018) and Struck et al. (2018) have summarized the mechanisms for the formation of cryptic species: recent divergence, phylogenetic niche conservatism (stasis), convergence, and parallelism. As the age and relatedness of the externally-similar members of the *Norops crassulus* species group belie a recent divergence or convergent evolution (Hofmann and Townsend 2017), phylogenetic niche conservatism seems the most likely means of speciation across these taxa. Allopatric speciation caused by complex geologic history is one of the dominant drivers of the herpetofaunal biodiversity in the Chortís Highlands and can lead to morphological stasis, as is well-documented in Plethodontid salamanders (Rovito et al. 2012; Rovito 2017; Townsend et al. 2011).

The elevated region that spreads across the departments of La Paz, Intibucá, and Lempira, geologically linked and referred to collectively as the Lenca Highlands, has previously been recognized as being unstudied in terms of herpetofauna diversity (McCranie 2007). Recent focus on fieldwork in the Lenca Highlands has begun to address this deficiency (McCranie 2014) and has begun to reveal previously overlooked endemic diversity. In addition to the description of *N. caceresae*, Luque-Montes et al. (2018) recently described a new species of true frog, *Rana lenca*, from this region, based on populations previously referred to as hybrids between the lowland species *Rana brownorum* Sanders, 1973 and *R.* cf. *R. forreri* Boulenger, 1883, and the description of a new species of *Bolitoglossa* (Itgen et al. in preparation) endemic to the Lenca Highlands is also underway. These three taxa will join the salamanders *B. celaque* McCranie and Wilson, 1993, *B. heiroreias* Greenbaum, 2004, *B. synoria* McCranie and Köhler, 1999, and *Oedipina chortiorum* Brodie et al., 2012, the treefrog *Exerodonta catracha* (Porras and Wilson, 1987), and the lizards *Abronia montecristoi* Hidalgo, 1983, *A. salvadorensis* Hidalgo, 1983, and *N. heteropholidotus* as part of the endemic herpetofauna of the Lenca Highlands and adjacent areas.

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APPENDIX 1

Specimens examined. An asterisk ("*") following a museum voucher number indicates the specimen was also included in the molecular analyses of Hofmann and Townsend (2017). If an asterisk follows a series (e.g. "A–D"*) or country name, all specimens were used in molecular analyses.

Norops caceresae, sp. nov. (23 specimens): **HONDURAS*: Intibucá**: Refugio de Vida Silvestre Mixcure, El Rodeo: CM 161301–161308; KU 348835–348838, MVZ:Herp:286121–286124; Reserva Biológica Opalaca, Río Agua Negra: CM 161309–161315.

Norops crassulus (81 specimens): **EL SALVADOR: Santa Ana**: Volcan de Santa Ana, Lago Sur: KU 184063–184071, KU 184078–184083; Finca El Milagro: KU 289793*. **GUATEMALA: Alta Verapaz**: Tactic: KU 190610; near Caquipec Mines, 20 km E and 6 km S Coban: MVZ:Herp:143408–143409; 25 km NW (by road) Senahu, Finca Volcan: MVZ:Herp:159923. **Baja Verapaz**: vicinity Union Barrios: KU 190619; 1.9 km NNW La Union Barrios: KU 190611–190613; 3 km NW Purulha: KU 190614–190616; 3 km N Niño Perdido: KU 190623; "156.5 km" [likely in error] ESE of Purulha, Cerro Quisis: MVZ:Herp:160512–160513, 160516–160517; 2.5 mi NE of Chilasco, Finca San Jorge: MVZ:Herp:160518–160523, 160529–160530, 160532, 160534–160538; 5 km ENE of Chilasco, Finca San Jorge: MVZ:Herp:160539–160540; 5 km ESE of Purulha, Finca Mirador: MVZ:Herp:160524–160526; 6.5 km ESE of Purulha, Finca Mirador: MVZ:Herp:160548. **Chimaltenango**: Cerro Balamjuyu, 12.5 km SW (by rd) highway from Patzitzia to Patzún: MVZ:Herp:270039*. **El Quiche**: 3.3 km NE (by road) of Laj Chimel on road to San Pablo el Baldío: MVZ:Herp:265576*; 3.5 km NE (by road) of Laj Chimel on road to San Pablo el Baldío: MVZ:Herp:265564–265565*, 265577–265578*; 4.9 km NE (by road) of Laj Chimel on road to San Pablo el Baldío: MVZ:Herp:265579–265580*. **Huehuetenango**: 3 km NNW of San Mateo Ixtatan: MVZ:Herp:160563–160566; 2 km W San Mateo Ixtatan: MVZ:Herp:171455–171456, 171554–171557; 4 km W San Mateo Ixtatan: MVZ:Herp:171553. **Jalapa**: Cerro Miramundo, ~1 km S of Mataquescuintla-Miramundo: MVZ:Herp:263595*. **Zacapa**: Sierra de las Minas, 7.8 km NNW San Lorenzo: KU 190619–190621; 3.4 km WSW San Lorenzo: KU 190622. **MEXICO***: **Chiapas**: Cerro Boqueron, 0.8 km WSW (by air) of Ejido Boqueron, Municipio Motozintla: MVZ:Herp:256801–256806.

APPENDIX 2

Mann-Whitney U test summary statistics and P-values. **Boldface** values are significant (p<0.05).

	Male		Female	
	U	p-value	U	p-value
SVL	175	0.0917	**73**	0.0394
HL/SVL	232.5	0.6101	143.5	0.7895
HW/SVL	**416**	0.0013	**232**	0.0013
HL/HW	**38.5**	<0.0001	**27**	0.0003
SL/SVL	199.5	0.2363	155.5	0.5042
SL/HL	210	0.3329	150	0.6286
AG/SVL	196	0.2099	114	0.4943
SHL/SVL	**42.5**	<0.0001	**57**	0.0097
SHL/HL	**53.5**	<0.0001	**557**	0.0098
LEO/SVL	230	0.5745	146	0.7247
VEO/SVL	236	0.6603	**67.5**	0.0251
LDPS/SVL	**390**	0.0072	160	0.4124
TDPS/SVL	260	0.9759	134.5	1.0000
SPW/SVL	**407**	0.0023	**194.5**	0.0468
NDSPW/SVL	**360**	0.0302	**194**	0.0464
VS1H	295	0.4409	157.5	0.4497
DS1H	285	0.5778	**196.5**	0.0381
VSAG	292	0.4931	126	0.7760
DSAG	168.5	0.0689	157	0.4722
SMB	**104.5**	0.0018	89.5	0.1326
S1C	**125.5**	0.0045	96.5	0.1799
S2C	205	0.2323	127.5	0.7994
ESO	**92.5**	0.0005	**69**	0.0260
SOS	243	0.6453	100.5	0.1070
SOSIP	**142**	0.0080	86	0.0558
PR	233.5	0.5609	140.5	0.8498
IN	**133.5**	0.0079	**60.5**	0.0074
SLS	294	0.4167	169.5	0.1627
ILS	265	0.8761	**195**	0.0283
LS	254	0.9430	144	0.7759
LSR	316	0.1539	157.5	0.4289
SO	328	0.1087	168	0.2021
SL	206.5	0.2620	113	0.3894
PMS	267	0.7486	148.5	0.4551
SLB	308.5	0.2596	103.5	0.2253
EDS	**78**	0.0002	81.5	0.0745

APPENDIX 3

Principal component scores for the first ten PCs from male and female morphological measurement analyses.

Male	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**
Standard Deviation	1.940	1.544	1.343	1.177	1.125	0.972	0.900	0.878	0.807	0.752
Proportion of Variance	0.251	0.159	0.120	0.092	0.084	0.063	0.054	0.051	0.043	0.038
Cumulative Proportion	0.251	0.410	0.530	0.623	0.707	0.770	0.824	0.875	0.919	0.956
SVL	-0.427	-0.043	-0.189	-0.079	0.061	-0.012	0.053	-0.217	0.096	0.123
HL/SVL	0.232	0.290	0.460	-0.101	0.280	-0.028	0.293	-0.059	0.129	0.213
HW/SVL	0.454	0.057	0.075	-0.204	-0.042	0.058	0.334	-0.010	0.041	-0.237
HL/HW	-0.361	0.155	0.266	0.231	0.259	-0.085	-0.169	-0.034	0.044	0.449
SL/SVL	0.100	0.536	-0.095	-0.245	0.343	0.136	-0.031	-0.069	-0.106	0.034
SL/HL	-0.061	0.390	-0.451	-0.257	0.187	0.172	-0.257	-0.036	-0.208	-0.111
AG/SVL	-0.052	0.123	-0.404	0.354	0.287	-0.013	0.289	0.350	0.446	-0.007
SHL/SVL	-0.190	0.461	0.210	-0.108	-0.376	-0.084	0.239	-0.011	0.218	-0.020
SHL/HL	-0.323	0.285	-0.063	-0.098	-0.532	-0.064	0.062	0.029	0.138	-0.145
LEO/SVL	0.114	0.213	-0.035	0.465	-0.325	0.380	0.097	0.072	-0.492	0.326
VEO/SVL	0.156	0.207	-0.041	0.603	-0.001	0.141	-0.196	-0.166	0.220	-0.430
LDPS/SVL	0.268	-0.047	-0.103	-0.201	-0.214	0.413	-0.319	0.268	0.522	0.430
TDPS/SVL	0.197	0.216	0.165	0.025	-0.087	-0.560	-0.537	0.367	-0.097	-0.054
SPW/SVL	0.215	0.018	-0.426	0.015	-0.120	-0.440	0.307	0.116	-0.188	0.338
NDSPW/SVL	0.277	0.042	-0.174	0.069	-0.141	-0.264	-0.162	-0.752	0.204	0.230
Female	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**
Standard Deviation	2.122	1.485	1.377	1.265	1.069	0.977	0.839	0.801	0.714	0.642
Proportion of Variance	0.300	0.147	0.126	0.107	0.076	0.064	0.047	0.043	0.034	0.027
Cumulative Proportion	0.300	0.447	0.574	0.680	0.756	0.820	0.867	0.910	0.944	0.971
SVL	-0.392	-0.004	0.191	0.060	-0.213	-0.039	0.043	-0.101	-0.216	0.010
HL/SVL	0.335	0.286	0.218	-0.151	-0.112	0.347	0.230	-0.047	-0.194	-0.021
HW/SVL	0.406	-0.155	-0.093	-0.176	0.018	0.225	0.187	0.234	-0.012	0.223
HL/HW	-0.213	0.448	0.314	0.089	-0.119	0.022	-0.034	-0.321	-0.160	-0.304
SL/SVL	0.271	-0.060	0.555	0.035	0.028	0.251	-0.078	-0.076	0.078	0.034
SL/HL	0.031	-0.353	0.509	0.198	0.147	0.003	-0.334	-0.043	0.319	0.079
AG/SVL	-0.220	-0.051	0.294	0.180	-0.408	-0.057	0.069	0.669	-0.195	0.238
SHL/SVL	-0.081	0.395	0.227	-0.486	0.285	0.117	0.020	0.253	0.045	0.044
SHL/HL	-0.341	0.135	0.039	-0.330	0.349	-0.171	-0.175	0.269	0.199	0.058
LEO/SVL	0.084	0.230	-0.071	-0.257	-0.672	-0.103	-0.157	-0.105	0.580	0.162
VEO/SVL	0.152	0.393	-0.142	0.268	0.120	-0.001	-0.540	-0.079	-0.259	0.587
LDPS/SVL	0.305	0.136	0.129	0.044	-0.032	-0.606	0.231	0.070	-0.222	0.029
TDPS/SVL	0.333	0.144	0.150	0.103	0.151	-0.511	-0.006	0.082	0.187	-0.219
SPW/SVL	-0.098	-0.301	0.192	-0.456	-0.003	-0.274	0.150	-0.442	-2.170	0.458
NDSPW/SVL	0.187	-0.228	-0.032	-0.397	-0.215	-0.057	-0.603	0.121	-0.409	-0.397

APPENDIX 4

GenBank accession numbers for sequence data of *Norops caceresae*, sp. nov., generated by Hofmann and Townsend (2017). Sequences with JHT field numbers refer to specimens not accessioned.

Museum ID	*16S*	*ND2*	*COI*	*PRLR*	*BDNF*	*PTPN12*
UF 166186	KU688065	–	KU687954	–	–	–
UF 166188	KU688066	–	KU687955	–	–	–
UF 166190	KU688060	–	KU687949	–	–	–
UF 166191	KU688061	–	KU687950	–	–	–
[JHT 2891]	KU688062	–	KU687951	–	–	–
[JHT 2892]	KU688063	–	KU687952	–	–	–
[JHT 2894]	MF094466	–	MF094513	–	–	–
[JHT 2895]	KU688067	–	KU687956	–	–	–
MVZ:Herp:286123	MF094468	MF094560	MF094515	MF094598	MF094634	MF094661
CM 161307	MF094469	MF094561	MF094516	MF094599	MF094635	MF094662
CM 161309	MF094471	–	MF094518	MF094601	MF094637	MF094664
CM 161311	MF094472	MF094562	MF094519	MF094602	MF094638	MF094665