

Morphological variation in Central American leaf-litter anoles: *Norops humilis*, *N. quaggulus* and *N. uniformis*

GUNTHER KÖHLER, SARAH ALT, CHRISTOPH GRÜNFELDER, MATTHIAS DEHLING & JAVIER SUNYER

Abstract. Pholidosis, morphometrics, and hemipenis morphology were studied in the Central American anole species *Norops humilis*, *N. quaggulus*, and *N. uniformis*. Head scalation illustrations of each species and a distribution map are provided. In hemipenis morphology, the three taxa are distinct. However, very little differentiation in pholidotic and morphometric characters is documented. Interspecific variation was observed in several characters but with overlap of the documented ranges. A discriminant function analysis based on five pholidotic characters yielded a scatter diagram that showed large overlap between the clusters of the three taxa.

Key words. Reptilia, Squamata, Iguanidae, *Norops humilis*, *N. quaggulus*, *N. uniformis*, distribution, morphological variation, hemipenis morphology.

Resumen. Se estudia la folidosis, morfometría y morfología del hemipene de los anolis centroamericanos *Norops humilis*, *N. quaggulus* y *N. uniformis*. Se proveen ilustraciones de las escamas de la cabeza así como un mapa de distribución para estas especies. Las tres especies son distintivas en cuanto a la morfología del hemipene aunque se documenta muy poca diferencia en caracteres morfométricos y de folidosis. Se observa variación interespecífica en ciertos caracteres pero existe solapamiento de los rangos documentados. Un análisis de función discriminante basado en cinco caracteres de folidosis produjo un diagrama disperso que muestra gran solapamiento entre los rangos de los tres taxa.

Introduction

In 1863, W. PETERS described *Anolis humilis* based on two female syntypes (now ZMB 500, 55223) from “Veragua” [probably western Panama; see SAVAGE 1970]. COPE (1885) described *Anolis quaggulus* (based on an adult male [now USNM 24979 according to COCHRAN 1961] from “San Juan river, Nicaragua”) and *Anolis uniformis* (based on “many specimens from Guatemala from Henry Hague, and one from Yucatan from Arthur Scott” [COPE 1885:393]). In 1935, STUART named *Anolis ruthveni* (based on an adult male from “about two miles north of Santa Teresa, El Peten, Guatemala”). In his monograph of Costa Rican lizards, TAYLOR (1956) described another taxon related to this cluster of species: *Anolis humilis marsupialis* based on a series of seven specimens from

“about 15 km WSW of San Isidro del General along the Dominical Road” (probably Puntarenas Province, or near the boundary of this province in San José Province).

BARBOUR (1934) and most subsequent authors (e.g., STUART 1948, 1963, PETERS & DONOSO-BARROS 1970) placed *quaggulus* in the synonymy of *humilis*, and *ruthveni* in the synonymy of *uniformis*, respectively. Also, these authors considered *uniformis* as a subspecies of *humilis*, a view considered valid until MEYER & WILSON (1972) presented evidence for species status of *uniformis*, mostly based on differences in male dewlap coloration. Subsequent authors (e.g., FITCH & SEIGEL 1984, SAVAGE & VILLA 1986, KÖHLER 2000) followed the conclusion that *humilis* and *uniformis* represent two separate species. Recently, KÖHLER et al. (2003) resurrected *quaggulus* as a valid species distinct from

humilis, mostly based on differences in hemipenial morphology, and they also concluded that *Anolis humilis marsupialis* remains in the synonymy of *N. humilis*.

Here, we report upon the results of our study on the interspecific variation in pholidosis, morphometrics, and hemipenis morphology of the small leaf litter anoles currently assigned to the species *Norops humilis*, *N. quaggulus*, and *N. uniformis*.

Materials and methods

The species descriptions are based on specimens examined by the authors (see Appendix). The distribution map is based on specimens examined by the authors (closed symbols) and on additional records (open symbols) taken from LEE (1996), and SAVAGE (2002). Measurements and scalation data were taken from 37 *Norops humilis* (27 males, 10 females), 45 *N. quaggulus* (26 males, 19 females), and 29 *N. uniformis* (19 males, 10 females). Abbreviations for museum collections follow those of LEVITON et al. (1985). Nomenclature of scale characters follows that of KÖHLER (2003). Terminology for hemipenial morphology follows that of MYERS et al. (1993) and SAVAGE (1997). All measurements were made using precision calipers and were rounded to the nearest 0.1 mm. Head length was measured from the tip of the snout to the anterior margin of the ear opening. Snout length was measured from the tip of the snout to the anterior border of the orbit. Head width was determined as the distance between the oral ricti. Dorsal scales were counted at the middle portion of the trunk along a paravertebral line, and ventral scales were counted at the middle portion of the trunk along the midline. Tail height and width were measured at the point reached by the heel of the extended hind leg. Subdigital lamellae were counted on phalanges ii to iv of the 4th toe. Abbreviations used are SVL (snout-vent length), HL (head length) and HW (head width). Statistics were performed using the computer program Statistica ver-

sion 6.1. To assess whether the means of two groups are statistically different t-tests were performed ($p < 0.005$). Discriminant Function Analyses were used to test if the taxa in question could be differentiated by a combination of several pholidotic characters.

Results

Interspecific variation is most evident in hemipenis morphology with each species having a distinct hemipenis shape and surface ornamentation. The hemipenis of *Norops humilis* is a medium-sized organ with well-developed elongate lobes and with a strongly calyculate surface on both the truncus and the lobes. In *N. quaggulus*, the hemipenis is relatively small with short and stout lobes and without a strongly calyculate surface on either the truncus or the lobes. *Norops uniformis* has a medium-sized bilobate hemipenis with the sulcus spermaticus bifurcating at base of apex and the branches continuing to tips of lobes; an asulcate ridge is present; the lobes are strongly calyculate and the truncus bears transverse folds. In our material, intraspecific variation in hemipenis morphology is restricted to size differences of the organ with smaller individuals having smaller hemipenes.

In contrast to the documented interspecific differences in hemipenis morphology, very little differentiation in pholidotic and morphometric characters could be documented. See Table 1 for variation in selected measurements and proportions and scale characters. Interspecific variation was observed in several characters but with large overlap of the documented ranges. Statistically significant differences ($p < 0.005$) were observed between *Norops uniformis* and the other two species in the following characters: (1) number of supralabials to level below centre of eye; (2) number of postrostrals; (3) number of dorsal scales between levels of axilla and groin; (4) number of ventral scales between levels of axilla and groin. Statistically significant differences between

N. quaggulus and *N. humilis* were observed in the number of postrostrals. *Norops uniformis* usually has 1-3 pale vertical lines in the flank region (lines can be broken), a character absent in *N. humilis* and *N. quaggulus* (Figures 1-3). *Norops quaggulus* differs from the other two species by usually having three large elongate scales in the anterior supraciliar region (only two such scales present in *N. humilis* and *N. uniformis*).

A discriminant function analysis based on three pholidotic characters (number of dorsal scales between levels of axilla and groin [DAG], number of ventral scales between levels of axilla and groin [VAG], and number of supralabial scales to level of centre of eye [supralabials]) yielded a scatter diagram (not shown) that correctly classified 59.5% of the specimens. A discriminant function analysis

based on five pholidotic characters (those above plus number of postrostral scales [postrostrals] and number of scales around midbody [SAM]) yielded a scatter diagram (Fig. 4) that correctly classified 71.8% of the specimens. The first and second discriminant functions classified 71.1% of the *N. quaggulus* specimens (group 1), 63.9% of the *N. humilis* specimens (group 2), and 82.8% of the *N. uniformis* specimens (group 3). Accordingly, the polygons of the three species largely overlap. The first function is $DS = -0.50732$ (supralabials) + 0.56861 (postrostrals) + 0.28199 (SAM) + 0.41253 (DAG) + 0.22297 (VAG). The second function is $DS = 0.37570$ (supralabials) + 0.49129 (postrostrals) + 0.65182 (SAM) - 0.16661 (DAG) - 0.59379 (VAG).

Key to *Norops humilis*, *N. quaggulus* and *N. uniformis*

- 1a Usually 22-32 dorsal scales between levels of axilla and groin, rarely up to 36; 6-10, mean 7.6, supralabial scales; flank usually with 1-3 pale vertical lines (lines can be broken); dewlap in adult males (in life) rose with purple spots *Norops uniformis*
- 1b Usually 30-39 dorsal scales between levels of axilla and groin, rarely few as 23; 5-8, mean 6.5, supralabial scales; flank without pale vertical lines or broken lines; dewlap in adult males (in life) different as above 2
- 2a Usually two large elongate scales in the anterior supraciliar region (Figure 5a); postaxillary pocket usually relatively wide, and shallow; hemipenis relatively large with well-developed elongate lobes and with a strongly calyculate surface on both the truncus and the lobes; maximum SVL 46.2 mm in males and 50.0 mm in females *Norops humilis*
- 2b Usually three large elongate scales in the anterior supraciliar region (Figure 5b); postaxillary pocket usually narrow, tube-like and deep; hemipenis relatively small with short and stout lobes and without a strongly calyculate surface on either the truncus or the lobes; maximum SVL 37.0 mm in males and 41.0 mm in females *Norops quaggulus*

Norops humilis (PETERS, 1863)

Anolis humilis PETERS, 1863: 138; type locality: Veragua, Panama.

Anolis humilis marsupialis TAYLOR, 1956: 97; type locality: 75 km WSW San Isidro de General, Costa Rica.

Geographic distribution: Central Costa Rica to Panama east of the Canal Zone (Fig. 9).

Diagnosis: *Norops humilis* can be distinguished from all other Central American species of *Norops*, except *N. compressicauda*, *N. quaggulus*, *N. tropidonotus*, *N. uniformis*, and *N. wampuensis*, by having a deep tube



Fig. 1. Adult Male of *Norops humilis* from Fortuna, Chiriquí, Panama.



Fig. 2. Adult Male of *Norops quaggulus* from Parque Nacional Saslaya, Nicaragua.

like axillary pocket. *Norops compressicauda*, *N. tropidonotus* and *N. wampuensis* have the scales anterior to the ear opening distinctly larger than those posterior to the ear opening (these scales more or less subequal in *N. humilis*). *Norops uniformis* has usually 1-3 pale vertical lines in the flank region (absent in *N. humilis*) and a rose male dewlap with a large central purple spot (male dewlap reddish orange with yellow margin in *N. humilis*). *Norops quaggulus* has usually three large elongate scales in the anterior supraciliar region (usually two such scales in *N. humilis*). Also, in *N. quaggulus* the hemipenis is relatively small with short and stout lobes and without a strongly calyculate surface on either the truncus or the lobes (the hemipenis of *N. humilis* is relatively large with well-developed elongate lobes and with a strongly calyculate surface on both the truncus and the lobes).

Description: Maximum SVL 43.9 mm in males, 48.0 mm in females; tail length / SVL ratio 1.33-1.70; HL / SVL 0.24-0.33 in males, 0.23-0.30 in females; HL / HW 1.39-1.62 in males, 1.38-1.65 in females; shank length / SVL 0.24-0.31; shank length / HL 0.78-1.19; longest toe of adpressed hind limb usually reaching to a point between posterior and anterior border of eye; tail slightly to distinctly laterally compressed in cross section, tail height / width ratio 1.13-1.47.

Scales on snout strongly keeled; 6-9 post-

rostrals (Fig. 6); 6-10 scales between nasals; usually 2 scales between circumnasal and rostral; scales in distinct frontal depression strongly keeled; supraorbital semicircles poorly to moderately developed, composed of keeled scales; 1-3, rarely 4, rows of scales separating supraorbital semicircles at narrowest point; 2-5 rows of scales separating supraorbital semicircles and interparietal at narrowest point; supraorbitals composed of 6-8 distinctly enlarged, strongly keeled scales; 1-2 enlarged supraorbitals in contact with supraorbital semicircles; supraorbitals decreasing abruptly in size laterally; 2-3 rows of granular scales between enlarged supraoculars and superciliaries at level of mid-orbit; usually 2 elongated superciliaries, the anterior one about two times the length of the following one; interparietal scale not well developed, only slightly enlarged relative to adjacent scales, surrounded by scales of moderate size; canthal ridge distinct, composed of 3-4 large scales; 7-12 scales present between second canthals; 7-13 scales present between posterior canthals; loreal region slightly concave, 22-46 strongly keeled loreal scales in a maximum of 4-8 horizontal rows; keeled subocular scales usually arranged in a single row; subocular series either in contact with supralabials or separated by one complete scale row; 5-8 supralabials to level below centre of eye; mental completely divided medially, bordered posteriorly by 5-8 postmentals; 5-8 infralabials to level below



Fig. 3. Adult Male of *Norops uniformis* from the Cockscomb Basin Wildlife Sanctuary, Stann Creek, Belize.

centre of eye; keeled granular scales present on chin and throat; lateral head scales anterior to the ear opening about the same size as those posterior to the ear opening; ear opening usually vertically oval.

Dorsum of body with keeled, subimbricate scales, 17-30 dorsal scales in one head length, 23-43 dorsal scales between levels of axilla and groin; 7-11 median rows of dorsal scales enlarged, dorsals abruptly larger than the smaller, keeled and homogeneous laterals; ventrals at midbody distinctly keeled, mucronate and subimbricate, 23-52 ventral scales in one head length, 32-57 ventral scales between levels of axilla and groin.

Dorsal, lateral and ventral caudal scales strongly keeled, without whorls of enlarged scales, although an indistinct division in segments is discernible; dorsal medial caudal scales slightly enlarged, not forming a crest; limb scales strongly keeled, imbricate; digital pads dilated, about two times as wide as non-dilated distal portion of toe; distal phalanx narrower than and raised from, dilated pad; 16-23 lamellae under phalanges ii-iv of fourth toe.

The completely everted hemipenis (SMF 80845) is a moderate-sized organ with well-developed elongate lobes (length of lobes equal to or slightly greater than length of truncus); both the truncus and the lobes have a strongly calyculate surface; sulcus spermaticus bifurcates at the base of the apex and the branches continue to the tip of the lobes.

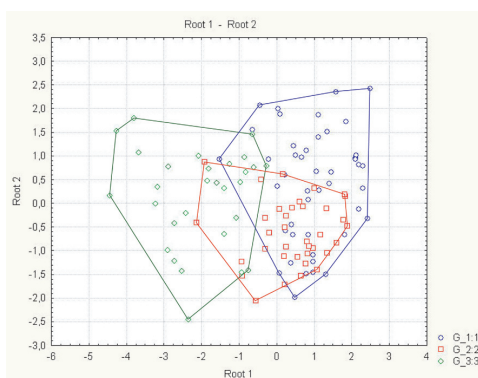


Fig. 4. Discriminant function analysis of Central American leaf litter anoles: 1) *Norops quaggulus*; 2) *Norops humilis*; 3) *Norops uniformis*. See text for details.

Norops quaggulus (COPE, 1885)

Anolis quaggulus COPE, 1885: 391; type locality: Río San Juan, Nicaragua.

Geographic distribution: Eastern Honduras to central Costa Rica (Fig. 9).

Diagnosis: *Norops quaggulus* can be distinguished from all other Central American species of *Norops*, except *N. compressicauda*, *N. humilis*, *N. tropidonotus*, *N. uniformis*, and *N. wampuensis*, by having a deep tube like axillary pocket. *Norops compressicauda*, *N. tropidonotus* and *N. wampuensis* have the scales anterior to the ear opening distinctly larger than those posterior to the ear opening (these scales more or less subequal in *N. quaggulus*). *Norops uniformis* has usually 1-3 pale vertical lines in the flank region (absent in *N. quaggulus*) and a rose male dewlap with a large central purple spot (male dewlap reddish orange with yellow margin in *N. quaggulus*). *Norops humilis* has usually two large elongate scales in the anterior supraciliar region (usually three such scales in *N. quaggulus*). Also, in *N. humilis* the hemipenis is relatively large with well-developed elongate lobes and with a strongly calyculate surface on both the truncus and

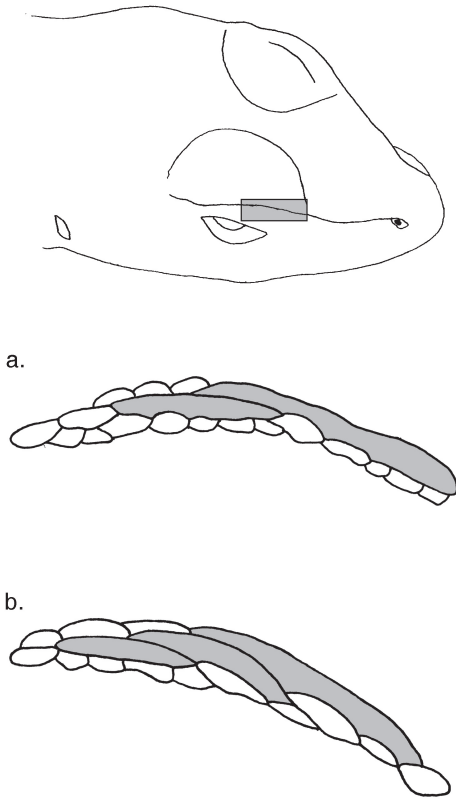


Fig. 5. Superciliary region of a) *Norops humilis* (SMF 85104) and b) *Norops quaggulus* (SMF 77480).

the lobes (the hemipenis of *N. quaggulus* is relatively small with short and stout lobes and without a strongly calyculate surface on either the truncus or the lobes).

Description: Maximum SVL 40.4 mm in males, 43.7 mm in females; tail length / SVL ratio 1.29-1.73; HL / SVL 0.23-0.33 in males, 0.22-0.30 in females; HL / HW 1.39-1.66 in males, 1.37-1.63 in females; shank length / SVL 0.24-0.30; shank length / HL 0.82-1.20; longest toe of adpressed hind limb usually reaching to a point between posterior and anterior border of eye; tail slightly to distinctly laterally compressed in cross section, tail height / width ratio 0.81-1.74.

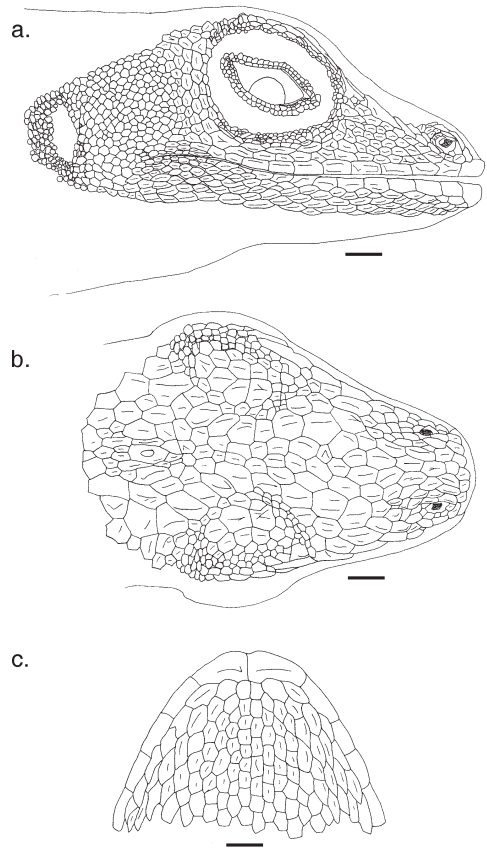


Fig. 6. Head of *Norops humilis* (SMF 80847). a) lateral view; b) dorsal view; c) ventral view. Scale bars equal 1.0 mm.

Scales on snout strongly keeled; 7-10 postrostrals (Fig. 7); 7-11 scales between nasals; usually 2 scales between circumnasal and rostral; scales in distinct frontal depression strongly keeled; supraorbital semicircles poorly to moderately developed, composed of keeled scales; 1-4 rows of scales separating supraorbital semicircles at narrowest point; 2-5 rows of scales separating supraorbital semicircles and interparietal at narrowest point; supraorbitals composed of 6-8 distinctly enlarged, strongly keeled scales; 1-2 enlarged supraorbitals in contact with supraorbital semicircles; supraorbitals

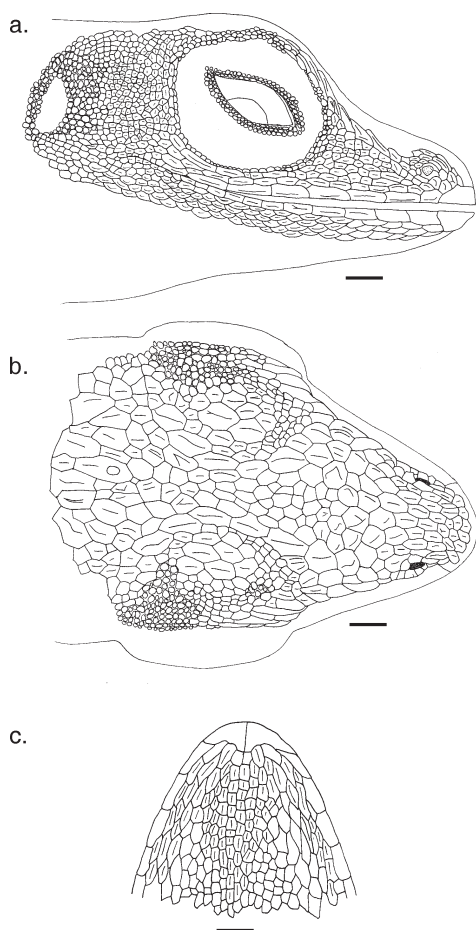


Fig. 7. Head of *Norops quaggulus* (SMF 77480). a) lateral view; b) dorsal view; c) ventral view. Scale bars equal 1.0 mm.

decreasing abruptly in size laterally; 2-3 rows of granular scales between enlarged supraoculars and superciliaries at level of mid-orbit; usually 3 elongated superciliaries, the anterior one largest; interparietal scale not well developed, only slightly enlarged relative to adjacent scales, surrounded by scales of moderate size; canthal ridge distinct, composed of 3-4 large scales; 7-12 scales present between second canthals; 8-15 scales present between posterior canthals; loreal region slightly con-

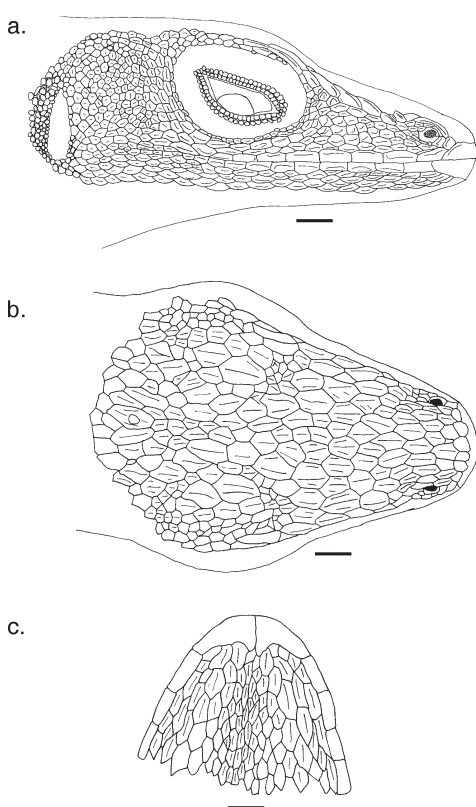


Fig. 8. Head of *Norops uniformis* (SMF 83957). a) lateral view; b) dorsal view; c) ventral view. Scale bars equal 1.0 mm.

cave, 26-52 strongly keeled loreal scales in a maximum of 5-9 horizontal rows; keeled subocular scales usually arranged in a single row; subocular series either in contact with supralabials or separated by one complete scale row; 5-8 supralabials to level below centre of eye; mental completely divided medially, bordered posteriorly by 4-8 postmentals; 5-10 infralabials to level below centre of eye; keeled granular scales present on chin and throat; lateral head scales anterior to the ear opening about the same size as those posterior to the ear opening; ear opening usually vertically oval.



Fig. 9. Distribution of *Norops humilis* (squares) and *N. quaggulus* (triangles). Red symbols represent localities from where we have examined adult males with everted hemipenes; black symbols represent localities from where we have examined specimens of the respective species but not males with everted hemipenes; white symbols represent literature records. A single symbol can represent two or more nearby localities.

Dorsum of body with keeled, subimbricate scales, 19-29 dorsal scales in one head length, 26-42 dorsal scales between levels of axilla and groin; 7-11 median rows of dorsal scales enlarged, dorsals abruptly larger than the smaller, keeled and homogeneous laterals; ventrals at midbody distinctly keeled, mucronate and subimbricate, 26-44 ventral scales in one head length, 35-56 ventral scales between levels of axilla and groin.

Dorsal, lateral and ventral caudal scales strongly keeled, without whorls of enlarged scales, although an indistinct division in segments is discernible; dorsal medial caudal scales slightly enlarged, not forming a crest;

limb scales strongly keeled, imbricate; digital pads dilated, about two times as wide as non-dilated distal portion of toe; distal phalanx narrower than and raised from, dilated pad; 16-22 lamellae under phalanges ii-iv of fourth toe.

The completely everted hemipenis (SMF 79824) is a relatively small organ with short and stout lobes (length of lobes less than half the length of truncus); the truncus and lobes are not calyculate, but tiny papillae are present in many specimens, and these papillae are frequently black; the sulcus spermaticus bifurcates at the base of the apex and the branches continue to the tip of the lobes.

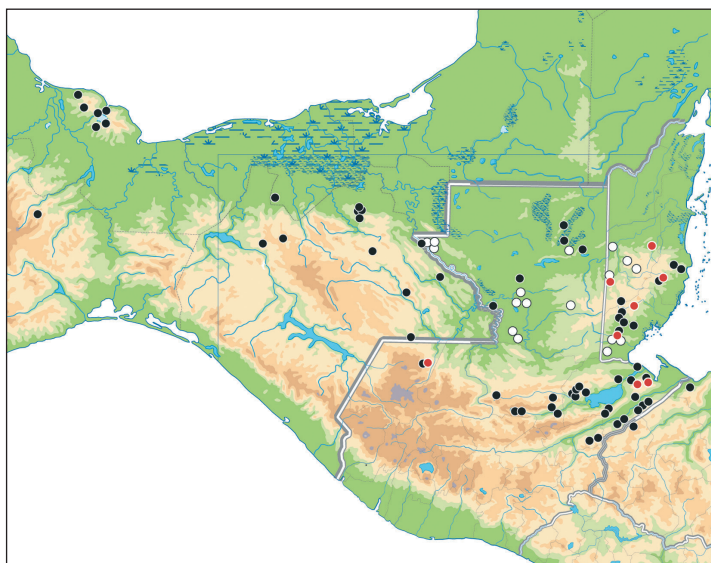


Fig. 10. Distribution of *Norops uniformis* (circles). Red symbols represent localities from where we have examined adult males with everted hemipenes; black symbols represent localities from where we have examined specimens of the respective species but not males with everted hemipenes; white symbols represent literature records. A single symbol can represent two or more nearby localities.

Norops uniformis (COPE, 1885)

Anolis uniformis COPE, 1885: 392; type locality: Yucatán.

Anolis ruthveni STUART, 1935: 310: 1; type locality: 2 mi. north of Santa Teresa, El Petén, Guatemala.

Geographic distribution: Southern Mexico including the Yucatán Peninsula to western Honduras (Fig. 10).

Diagnosis: *Norops uniformis* can be distinguished from all other Central American species of *Norops*, except *N. compressicauda*, *N. humilis*, *N. quaggulus*, *N. tropidonotus*, and *N. wampuensis*, by having a deep tube like axillary pocket. *Norops compressicauda*, *N. tropidonotus* and *N. wampuensis* have the scales anterior to the ear opening distinctly larger than those posterior to the ear opening (these scales more or less subequal in *N. uniformis*).

Norops humilis and *N. quaggulus* lack pale vertical lines in the flank region (usually present in *N. uniformis*) and have a reddish orange dewlap with yellow margin (male dewlap rose with a large central purple spot in *N. uniformis*).

Description: Maximum SVL 40.3 mm in males, 40.5 mm in females; tail length / SVL ratio 1.22-1.57; HL / SVL 0.24-0.38 in males, 0.22-0.30 in females; HL / HW 1.47-1.76 in males, 1.45-1.64 in females; shank length / SVL 0.25-0.31; shank length / HL 0.73-1.15; longest toe of adpressed hind limb usually reaching to a point between posterior and anterior border of eye; tail slightly to distinctly laterally compressed in cross section, tail height / width ratio 1.27-2.05.

Scales on snout strongly keeled; 5-8 postrostrals (Fig. 8); 6-10 scales between nasals; usually 2 scales between circumnasal and rostral; scales in distinct frontal depression strongly keeled; supraorbital semicircles poorly to moderately developed, com-

		<i>N. humilis</i> ♂ 27 ♀ 10	<i>N. quaggulus</i> ♂ 26 ♀ 19	<i>N. uniformis</i> ♂ 19 ♀ 10
maximum SVL	males	43.9	40.4	40.3
	females	48	43.7	40.5
tail length / SVL	males	1.48-1.70 (1.61±0.06)	1.35-1.73 (1.53±0.10)	1.28-1.57 (1.43±0.11)
	females	1.33-1.50 (1.43±0.07)	1.29-1.49 (1.40±0.08)	1.22-1.35 (1.30±0.06)
tail diameter vertical / horizontal	males	1.30-1.47 (1.24±0.09)	0.81-1.74 (1.25±0.16)	1.31-2.05 (1.52±0.21)
	females	1.13-1.21 (1.15±0.04)	1.13-1.54 (1.25±0.17)	1.27-1.48 (1.35±0.09)
axilla-groin distance / SVL	males	0.25-0.43 (0.40±0.04)	0.35-0.44 (0.39±0.02)	0.32-0.45 (0.38±0.03)
	females	0.34-0.46 (0.40±0.05)	0.31-0.46 (0.39±0.06)	0.37-0.44 (0.40±0.03)
HL / SVL	males	0.24-0.33 (0.27±0.02)	0.23-0.33 (0.27±0.02)	0.24-0.38 (0.29±0.03)
	females	0.23-0.30 (0.26±0.03)	0.22-0.30 (0.26±0.03)	0.22-0.30 (0.27±0.03)
HL / HW	males	1.39-1.62 (1.54±0.06)	1.39-1.66 (1.54±0.06)	1.47-1.76 (1.57±0.07)
	females	1.38-1.65 (1.50±0.11)	1.37-1.63 (1.51±0.11)	1.45-1.64 (1.54±0.09)
snout length/ SVL	males	0.17-0.21 (0.19±0.01)	0.18-0.24 (0.20±0.02)	0.18-0.28 (0.21±0.02)
	females	0.17-0.21 (0.19±0.01)	0.17-0.22 (0.19±0.02)	0.01-0.21 (0.18±0.09)
snout length/ HL	males	0.61-0.82 (0.74±0.06)	0.67-0.86 (0.76±0.05)	0.64-0.84 (0.73±0.05)
	females	0.61-0.80 (0.73±0.08)	0.62-0.83 (0.73±0.08)	0.40-0.77 (0.69±0.16)
shank length/SVL	males	0.24-0.31 (0.27±0.02)	0.24-0.30 (0.27±0.01)	0.27-0.31 (0.28±0.01)
	females	0.24-0.28 (0.26±0.02)	0.24-0.30 (0.26±0.03)	0.25-0.29 (0.27±0.03)
shank length/HL	males	0.78-1.14 (0.99±0.10)	0.82-1.20 (1.00±0.09)	0.73-1.15 (0.97±0.10)
	females	0.90-1.19 (0.99±1.12)	0.84-1.10 (1.00±0.07)	0.94-1.15 (1.00±0.09)
subdigital lamellae of 4th toe		16-22 (19.00±2.43)	16-23 (19.57±1.64)	16-23 (19.93±1.75)
number of scales between SS		1-4 (2.22±0.49)	1-4 (2.22±0.53)	1-3 (1.81±0.69)
number of scales between IP and SS		2-5 (2.92±0.68)	2-5 (2.92±0.68)	1-4 (2.48±0.69)
number of scales between SO and SPL		0-3 (1.27±0.78)	0-2 (1.16±0.73)	0-2 (1.52±0.57)
number of SPL to level below center of eye		5-8 (6.53±0.63)	5-8 (6.41±0.69)	6-10 (7.62±0.94)
number of INL to level below center of eye		5-10 (7.27±1.07)	5-8 (6.81±0.79)	6-10 (7.93±1.07)
total number of loreals		26-52 (38.09±6.60)	22-46 (35.10±6.36)	30-49 (39.47±4.62)
number of horizontal loreal scale rows		5-9 (6.78±1.02)	4-8 (6.24±0.95)	5-9 (6.72±1.13)
number of postrostrals		7-10 (7.93±0.81)	6-9 (7.30±0.73)	5-8 (6.28±0.10)
number of postmentals		4-8 (6.18±0.81)	5-8 (6.16±0.55)	4-8 (5.80±1.08)
number of scales between nasals		7-11 (8.26±1.07)	6-10 (8.14±1.08)	6-10 (7.83±0.97)
number of scales between 2nd canthals		v	7-12 (8.84±1.07)	7-10 (8.83±0.80)
number of scales between posterior canthals		8-15 (11.18±1.51)	7-13 (11.71±1.41)	8-13 (10.14±1.06)
Number of medial dorsal scales in one head length		19-29 (23.00±2.36)	17-30 (22.46±3.15)	18-25 (20.76±1.68)
Number of ventral scales in one head length		26-44 (32.20±4.14)	23-52 (32.24±6.65)	20-36 (29.97±3.83)
Number of medial dorsal scales between levels of axilla and groin		26-42 (33.78±3.81)	23-43 (33.73±5.20)	22-36 (28.10±3.90)
Number of ventral scales between levels of axilla and groin		35-56 (44.04±5.13)	32-57 (44.89±5.08)	31-47 (38.07±3.65)

Tab. 1. Selected measurements, proportions and scale characters of *Norops humilis*, *N. quaggulus* and *N. uniformis*. Range is followed by mean value and one standard deviation in parentheses, and then by sample size. Abbreviations: SVL = snout-vent length; HL = head length; HW = head width; SS = supraorbital semicircles; IP = interparietal plate; SO = subocular scales; SPL = supralabial scales, INL = infralabials.

posed of keeled scales; 1-3 rows of scales separating supraorbital semicircles at narrowest point; 1-4 rows of scales separating supraorbital semicircles and interparietal at narrowest point; supraorbitals composed of 6-8 distinctly enlarged, strongly keeled scales; 1-2 enlarged supraorbitals in contact with supraorbital semicircles; supraorbitals decreasing abruptly in size laterally; 2-3 rows of granular scales between enlarged supraoculars and superciliaries at level of mid-orbit; usually 2 elongated superciliaries, the anterior one about two times the length of the following one; interparietal scale not well developed, only slightly enlarged relative to adjacent scales, surrounded by scales of moderate size; canthal ridge distinct, composed of 3-4 large scales; 7-10 scales present between second canthals; 8-13 scales present between posterior canthals; loreal region slightly concave, 30-49 strongly keeled loreal scales in a maximum of 5-9 horizontal rows; keeled subocular scales usually arranged in a single row; subocular series either in contact with supralabials or separated by one complete scale row; 6-10 supralabials to level below centre of eye; mental completely divided medially, bordered posteriorly by 4-8 postmentals; 6-10 infralabials to level below centre of eye; keeled granular scales present on chin and throat; lateral head scales anterior to the ear opening about the same size as those posterior to the ear opening; ear opening usually vertically oval.

Dorsum of body with keeled, subimbricate scales, 18-25 dorsal scales in one head length, 22-36 dorsal scales between levels of axilla and groin; 7-11 median rows of dorsal scales enlarged, dorsals abruptly larger than the smaller, keeled and homogeneous laterals; ventrals at midbody distinctly keeled, mucronate and subimbricate, 20-36 ventral scales in one head length, 31-47 ventral scales between levels of axilla and groin.

Dorsal, lateral and ventral caudal scales strongly keeled, without whorls of enlarged scales, although an indistinct division in segments is discernible; dorsal medial caudal

scales slightly enlarged, not forming a crest; limb scales strongly keeled, imbricate; digital pads dilated, about two times as wide as non-dilated distal portion of toe; distal phalanx narrower than and raised from, dilated pad; 16-23 lamellae under phalanges ii-iv of fourth toe.

The completely everted hemipenis (USNM 496684) is a medium-sized bilobate organ; sulcus spermaticus bifurcates at base of apex and branches continue to tips of lobes; asulcale processus/ridge present; lobes strongly calyculate, truncus with transverse folds.

Acknowledgements

For the loan of or access to specimens we thank L. FORD and D. R. FROST, American Museum of Natural History (AMNH), New York; T. DAESCHLER and N. GILMORE, Academy of Natural Sciences (ANSP), Philadelphia; Carnegie Museum of Natural History (CM), Pittsburgh; N. M. FERRER, J. C. LÓPEZ VIDAL and S. A. MURILLO JIMÉNEZ, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional (ENCB), México D.F.; A. RESETAR, Field Museum of Natural History (FMNH), Chicago; W. E. DUELLMAN and J. E. SIMMONS, University of Kansas, Natural History Museum (KU), Lawrence; J. SEIGEL, Natural History Museum of Los Angeles County (LACM), Los Angeles; A. ROSSMAN, Museum of Natural Science, Louisiana State University (LSUMZ), Baton Rouge; J. HANKEN and J. P. ROSADO, Museum of Comparative Zoology, Harvard University (MCZ), Cambridge; A. DUBOIS, I. INEICH and A. ÖHLER, Museum National d'Histoire Naturelle (MNHN), Paris; F. TIEDEMANN, Naturhistorisches Museum Wien (NMW), Wien; F. BOLAÑOS and G. CHAVES, Museo de Zoología, Escuela de Biología, Universidad de Costa Rica (UCR), San José; K. L. KRYSKO and F. W. KING, Florida Museum of Natural History (UF), Gainesville; R. W. MCDIARMID and W. R. HEYER, National Museum of Natural History (USNM), Washington, D.C.; J. CAMPBELL and C. FRANKLIN, The University of Texas at Arlington (UTA), Arlington; and R. GÜNTHER, Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB), Berlin; J. HALLERMANN, Zoologisches Institut und Zoologisches Museum der Universität Hamburg (ZMH), Hamburg.

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Appendix

Specimens examined

(^H = males with everted hemipenes)

Norops humilis

COSTA RICA: Alajuela: Peñas Blancas: UCR 14942; Río Frio: USNM 19508-13; Cariblanco: NMW 20667 (8); Cinchona: KU 66921, 66922^H, 66923; Cartago: Parque Nacional Tapanti: MD-72^H; Tapanti, Río Grande, Orosi Puente: UCR 811, 2809^H; Tapanti, Río Quirí: UCR 9572; Navarro: ANSP 24466-68; Río Chitarría: LSUMZ 52324; Turrialba: KU 40819, USNM 192585, 339731-33; 1 km SE Tuis: KU 66898; Moravia de Turrialba: KU 66905; 3 km NNE Pavones: KU 66889^H; 3 km S Pavones: KU 103921-23^{all H}; jct. Ríos Tuis and Reventazon: KU 66890-91, 66892^H, 66893; Heredia: "Heredia": AMNH 149606; Parque Na-

cional Braulio Carillo, San Ramón, Distrito La Virgin: UCR 13287; Reserva Biológica Alberto M. Brenes, San Ramón: MD 95; E of Isla Bonita: KU 66910^H, 66911–12; Isla Bonita: KU 103925^H; Limón: N slope Cerro Nimaso, Distrito Bratsi: UCR 8475^H; EB Tierra Media, Matina, Distrito Batán: UCR 12396^H; San Miguel, F. ASACODE, Distrito Sixaola: UCR 12866; Cerro Uatsi, Distrito Bratsi: UCR 13030, 13189; RB Hitoy Cerere: MD-89^H; Approximately 17.0 km WSW Puerto Limón between Río Blanco and Río Toro: UTA R12845-47; Puerto Limón: ANSP 19530-34, ZMH 4594; Estralla Valley, end of Suretka trail: ANSP 21466; Guapiles: ANSP 24470; Rte 32, 6 km E Río Hondo, 2 km N on dirt road: ANSP 32373; La Castilla, lower Río Reventazón: ANSP 23738-47, 24457-58, 34736-38; Los Diamantes: KU 66926^H; Puntarenas: Monteverde, 7 km on road N Santa Elena, 10°21'50"N, 84°48'10.5"W, 1375-1420 m: SMF 85528^H-29; Monteverde, Ecolodge: UCR 17040^H; Fila Cedro, Distrito San Vito: UCR 12784^H; 8 km E Palmar Norte: KU 93969^H; 8 km ENE Palmar Norte: KU 116981^H; San José: Fila Tinamastes, Distrito Barú: UCR 14512^H, 14514^H, 14523^H, 14805^H, 14512; Tinamaste, Distrito Dominical: UCR 15933^H; Alfombra, Distrito Barú: UCR 15968; Km 122 on ruta 2 (N of San Isidro de Perez Zeledon): UTA R12841-44; La Honduras, 4500 ft: ANSP 24471-79, 24482-86, 34739-41; Río Claro, 1 road mi N La Honduras: LSUMZ 30261; 2 mi E Escuadra: LSUMZ 52376; 1 mi N Santa Ana: LSUMZ 52368-69; 15 km SW San Isidro del General: KU 66929^H; 13.4 km N San Isidro del General: KU 66931^H.

PANAMA: "Veragua": ZMB 500, 55223; Bocas del Toro: "Bocas del Toro": AMNH 119729-733; Celentine, road to Chiriquí Grande, 8°47'09"N, 82°11'17"W, 610 m: SMF 85110^H; Cerro Brujo, 9°11'16.4"N, 82°11'25.4"W, 10 m: SMF 85112^H; Río Uyama, 9°08'55"N, 82°19'28"W, 35 m: SMF 85115-16; Quebrada La Gloria, 8°59'08"N, 82°13'56"W, 20 m: SMF 85117; Río Changuinola, near Quebrada El Guabo (16 km airline W Almirante), 100-200 m: AMNH 119033-39; Quebrada Pastores, on coast W of Isla Pastores: USNM 313835; Almirante: USNM 142288, 193449, 339773-75; vicinity of Almirante: ANSP 34055-57, 34066; ca. 5 km W Almirante, 30-40 m: AMNH 107427-31; Laguna de Tierra Oscura, 3.7 km S of Tiger Key: USNM 313816, 313836, 348443-63; Cayo Agua, Punta Norte: USNM 150006, 150010; Cayo Agua, near Punta Limón: USNM 338685; Cayo Nancy: USNM 338532^H, 338532-36, 338537-38^H, 338539-43; Isla Bastimentos, ca. 0.5 mi from

mouth of Alvarez Creek (= Alberry Creek): USNM 297886; Isla Bastimentos, Old Point: USNM 297887; Isla Colon, La Gruta: USNM 338201-08, 338209^H, 338210, 338211^H, 338212-13 Isla Cristobal, Bocatorito camp: USNM 348172-76, 348177^H, 348178-81; Isla Cristobal, Laguna Bocatorito: USNM 313815; Isla Cristobal, NW side of: USNM 348182^H, 348183-84; Isla Escudo de Veraguas, West Point: USNM 347481; Isla Popa, 1 km SE of Deer Island channel: USNM 298111-20; south end of Isla Popa, 1 km E of Sumwood Channel: USNM 319206-09, 347211-27, 347228^H, 347229-42; Chiriquí: Boquete, trail to Palo Alto, 8°48'49"N, 82°23'60"W, 1660 m: SMF 85403; Fortuna: 148885–87^{all H}; Reserva Forestal Fortuna, Laguna, 8°43'N, 82°15'W, 1000 m: SMF 85101^H-02; Reserva Forestal Fortuna, 8°43'35"N, 82°15'41"W, 1050-1150 m: SMF 85103-06^{all H}, 85107-09; Reserva Forestal Fortuna, trail to dam site, 1050-1100 m: SMF 85113^H-14; upper Río Chiriquí, Fortuna Dam Site, 1000-12000 m: AMNH 114273^H, 114274-80, 114281^H, 114280, 114283^H, 114284-85, 114286^H, 114287-303; near the summit Cerro, 1400 m: AMNH 114304; S slope Quebrada de Arena, Río Chiriquí drainage, 1120 m: AMNH 123987-94, 129816-17; continental divide above upper Quebrada de Arena, 1160-1220 m: AMNH 129818-31; Cocle: El Valle de Antón: AMNH 71720-26, 76021-22, 76025, 76032-36, 89879, ANSP 21802-03, 24459-65, 34833; El Valle de Antón, Cerro Gaitál (8°37.31'N; 80°07.54'W), 710–750 m: SMF 80782^H–83^H; continental divide N El Copé (80°36'W), 600-800 m: AMNH 115912-15; Colón: Cerro Bruja [9° 29' N; 79° 35' W]: USNM 54056; Panamá: 8 km NNW Chepo, Gaspar Sabana: UF 124420; Cerro Azul, 457 m, 54179; Cerro Azul, 762 m, 54170; Gatun: ANSP 20855-56; Río Pequeni, head of Madden Lake: ANSP 21697; Cerro Trinidad: UF 135781; Trinidad River: USNM 63985; Cerro Campana: AMNH 106667^H, 106668, 106669^H, 106670, UF 124422-24; km 14.6 on El Llano-Castí road, 370 m: AMNH 110570-71; San Blas: Nusagandi, vicinity of field station, 9°20.50'N, 78°59.64'W, 350–360 m: SMF 80787^H, 80845^H, 80846–47, 80850^H; Nusagandi, Sendero Markis, 270–290 m: SMF 80848–49; Veraguas: 5-6 mi (via road) NW Santa Fe (Pacific drainage): AMNH 119999-120000^{both H}, 120001-02, 147797; Cerro Delgado, 2-4 mi W Santa Fe: AMNH 147798^H.

Norops quagglus

COSTA RICA: Alajuela: Cinchona, 10°13'35"N, 84°10'0.7"W, 1300 m: SMF 85530^H, UCR 1416; between Ciudad Quesada and Aguas Zargas, near

Hotel “El Tucano”, 600 m: SMF 84959-61; Guanacaste: Tilarán: ANSP 24446, 24469; El Silencio: LACM 148892^H-93^H; Volcán Orosí: LACM 148888-91^{all H}; Cerro Cacao: LACM 148894^H-95^H; Heredia: Reserva Biológica La Tirimbina, Sarapiquí, 10°24'N, 84°8'W: MD 83^H; Parque Nacional Braulio Carillo: MD 94^H; Puerto Viejo: UCR 4659-61, 4662^H, ZFMK 48723, 48728, 48734-36, 48738-39; Rara Avis, Catarata, 650 m: SMF 81050^H; La Selva, 1 mi SW Puerto Viejo de Sarapiquí: CM 53943-44, KU 129282^H, 129299^H; Limón: Tortuguero: UCR 5050, 17294; Playa Gandoca, Distrito Sixaola: UCR 12959^H; Boca de Tortuguero: AMNH 85054-56; Caño Palmas, 2-3 mi NW Green Turtle Camp, Tortuguero: AMNH 95088-94; Cerro Tortuguero: AMNH 95085-87; N Tortuguero village, ca. 0.5 mi W Green Turtle Inn: AMNH 102492-94; near Tortuguero, Cano Mora: UF 135782, USNM 244866.

HONDURAS: Gracias A Dios: Bodega de Rio Tapalwas, 14°55'39"N, 84°32'02"W, 190 m: USNM 549361-62; Olancho: 11.5 km NNE La Colonia, Quebrada de Las Marías, 660 m: SMF 78803^H; Yapuwás, 60 m: SMF 79927; Matamoros, 14°40'N, 85°23'W, 150: SMF 80817^H, 80818, USNM 549359-60; Quebrada El Guásimo, 140 m: SMF 80819.

NICARAGUA: “Nicaragua”: AMNH 17233-36, 17238, 17243, USNM 14206, 17902; Atlántico Norte: Parque Nacional Saslaya: SMF 82848; Parque Nacional Saslaya, Estación Biológica Salto Labú, 13°39'51"N, 85°00'55.5"W, 260 m: SMF 82036; Parque Nacional Saslaya, Cerro El Toro, between Camps I and II, 1000 m: SMF 82037; Parque Nacional Saslaya, Cerro El Toro, Campamento I, 720 m: SMF 82038-39; Parque Nacional Saslaya, Cerro El Toro, near Campamento I, 830 m: SMF 83160, 83161-62^{both H}; Parque Nacional Saslaya, Campamento Las Ranas, 920 m: SMF 81938; Parque Nacional Saslaya, Caño El Cedro, 980 m: SMF 81939-40; Parque Nacional Saslaya, Campamento El Carao (13°42.79'N; 84°58.66'W), 400 m: SMF 79638, 82847; Parque Nacional Saslaya, trail from Campamento Las Pavas (13°44.5'N; 85°01.5'W) to Campamento Los Monos (13°45.1'N; 85°02.2'W), 810 m: SMF 79380^H, 79381; Parque Nacional Saslaya, Campamento Los Monos (13°45.1'N; 85°02.2'W), 800 m: SMF 79383^H, 79384, 79593; S slope of Cerro Saslaya, 1100 m: SMF 79385; 1 km E Bonanza, 240 m: KU 101391; Eden Mine: AMNH 17237; Alamikamba (13°30.08'N, 84°13.64'W): SMF 77451-54; Sioux Plantation: AMNH 17259; near Pia Creek: AMNH 17205-14; Musawas, Río Huaspuc: AMNH 75456, 146734, 153427;

Atlántico Sur: Cara de Mono, 50 m: KU 112984, 113013; Río Escondido, 50 mi from Bluefields: USNM 19876, 20695; N side Río Escondido, 10 km below Rama, 20 m: KU 101864; Río Chiquito (11°37.34'N, 84°07.73'W), 42 m: SMF 77455-56, 77557; Kukra: AMNH 17198-204; Kukra, Wholesome Creek: AMNH 17244-50; Kanawá: AMNH 17254-57; Sixicus Creek: AMNH 17258; Cupitna Camp: AMNH 17215-32; Tule Creek: AMNH 17239-42; Camp Santa Ana, Río Huahushan: AMNH 70510-12, 70514, 70518, 70526; Río Pichinga, back of Pearl Lagoon: AMNH 70528-32; Granada: Volcán Mombacho: SMF 78291^H; Matagalpa: 12 km NE Matagalpa, 1100 m: KU 195069-71; Finca Tepeyac, 10.5 km N and 9 km E Matagalpa, 960 m: KU 85642-44; Selva Negra (12°59.96'N, 85°54.55'W): SMF 77342, 77457-64, 77479, 77480-81^{both H}, 77482, 77483-84^{both H}, 77485, 78277-78, 78279-80^{both H}, 78289-90^{both H}, 78516^H, 79821, 79822-23^{both H}; Jinotega: Finca Berlin (13°32.26'N, 85°41.50'W), 1015 m: SMF 79003; Cordillera Isabelia (13°13.55'N, 85°39.21'W): SMF 77449-50; Reserva Biosfera Bosawas, ca. 0.5 km SE Pueblo Wiso (13°59.60'N, 85°19.60'W), 190-200 m: SMF 78517-18^{both H}; Reserva Biosfera Bosawas, ca. 3 km SE Ayapal at Río Curinwas (13°46.62'N, 85°23.17'W), 200 m: SMF 78405; Río San Juan: Río San Juan, Boca de San Carlos (10°47.26'N, 84°11.70'W), 20 m: SMF 79824-26^{all H}; Río Sarnoso, ca. 1 km above confluence with Río San Juan (10°55.35'N, 84°17.40'W), 25 m: SMF 79827^H; Río San Juan, Bartola (10°58.37'N, 84°20.35'W), 30 m: SMF 79828-29, 80944-53; Río San Juan: USNM 24979; Río San Juan, Colorado Junction: USNM 19505; Río San Juan, at junction with Río Sarapiquí, 10°42'50"N, 83°56'05"W, 20 m: SMF 83151-52, 83172-73; Río San Juan, at junction with Río Chimurria, 10°43'31"N, 83°54'29"W, 24 m: SMF 83153, 83154-55^{both H}; Río El Chanco, 5-6 km above junction with Río San Juan, 10°48'60"N, 84°00'59"W, 60 m: SMF 83156, 83158, 83159^H; Río San Francisco, 4 km above junction with Río San Juan, 10°48'43"N, 84°01'35"W, 40 m: SMF 83157^H.

Norops uniformis

BELIZE: Cayo: Blue Hole National Park, ca. 20 km SE Belmopan, 17°08'49"N, 88°41'38"W, 80 m: SMF 83321^H; Caracol, 510 m: SMF 83328; Chiquibul Branch, S Granos de Oro Camp, 89°02'W, 16°35'N: CM 112128; Stann Creek: Cockscomb Basin Wildlife Sanctuary, Ben's Bluff Trail, 80 m: SMF 83322^H, 83323-24, 83329-31^{all H}, 83332-35; Cockscomb Basin Wildlife Sanctu-

ary, Gibnut Trail, 80 m: SMF 83325^H, 83326-27; Cockscomb Basin Wildlife Sanctuary, Pearce Camp, at confluence of Cockscomb Branch and Mexican Branch, 16°46'25"N, 88°31'57"W, 80 m: USNM 496669-81, 497642; Bokowina [= Silk Grass]: FMNH 49132-33; 49137-39; State forest, Stann Creek RR, 4 mi from 12 m: FMNH 4484-85; E slope of Cockscomb Mts., 750-1150 ft: CM 8483, 8486; Toledo: Blue Creek Village vicinity of Slaterry Field Station: UTA R11008-30, 11031^H, 11032-42; Limestone range, 2 km N Blue Creek village, 16°12.4'N, 89°2.9'W, 75 m: UF 87176; Columbia Forest Reserve, 1 mi W Salamanca: CM 105853, 105867-70, 105872; Río Grande, ca. 2 mi SE Big Falls: CM 105893-94; Bladen Nature Reserve, Teakettle Camp on Bladen Branch, 16°31'01"N, 88°49'48"W, 140 m: USNM 496682-83, 496684^H, 496685-92; Champion (camp), Columbia River Forest Reserve, drainage of Río Grande: USNM 326153; Cumbrés (between sinkholes), Columbia River Forest Reserve: USNM 326162-66; vicinity of El Tigre (camp), Columbia River Forest Reserve, drainage of Central River: USNM 326160, 326167, 326157-59; Gloria Camp, Colombia River Forest Reserve, 16°22'N, 89°10'W, 680 m: USNM 319770-72; Maya Mountain Forest Reserve, Snake Creek, 16°28'45"N, 89°01'30"W, 600 m: USNM 498208-09; near San Pedro Columbia, vicinity of Lubaantun Ruins: USNM 326152; Union Camp, Colombia River Forest Reserve, 16°23'05"N, 89°08'36"W, 700 m: USNM 319773;

GUATEMALA: "Guatemala": USNM 24734-50; Alta Verapaz: Coban Parque Nacional: NMW 20667 (1-6), UTA R41886, R41917-19; Finca Rubelpec: UTA R46873; Finca San Juan: UTA R46872^H, R46874^H; N slope Sierra de las Minas, Finca Pueblo Viejo, crest of Río Chiquito/Quebrada Cancoy divide: UTA R26985; N slope Sierra de las Minas, Finca Pueblo Viejo, W slope Río Tinajas/Río Chiquito divide: UTA R26986, R27213-23; Santa Teresa: MCZ 46309; Sepacuite: MCZ 22307; Tucuru: NMW 20667 (7); Huehuetenango: Barillas Finca Chiblac Buena Vista camino a Barillas: UTA R52087-89; Finca Chiblac ca. 22.0 km NNE Barillas: UTA R29569-72, 29573^H, 29574, 29575^H, 29576-82; Sierra de Los Cuchumatanes Finca Chiblac 21.7 road km NNE Barillas: UTA R27224-26, R41921-24; Izabal: betw. Cayo Piedra and San Gil: ANSP 22172-75; Lago de Izabal, 2 mi E El Estor: UF 16312-13; Bananera [=Bananera Morales]: FMNH 35072; Cerro San Gil, Río Frio, 65 m: FMNH 40910; Cerro San Gil, Sector Río Las Escobas, 15°41'N, 88°39'W, 160-240 m: SMF 83952-53^{both H}, 83954-

56, 83957-59^{all H}, 83960; 5.5 km WSW Puerto Santo Tomás near Las Escobas: UTA R15986-92, 15993^H, 15994-16004, R20151-67, R20170-94, R20211-27, R20196-210, R23642-46, R20168, R29537^H, 29538-47, 29548^H, 29549, 29550^H, 29551-60, R29566-68, R33468-69, R33482-83, R41888-93, R41920; E slope Montañas del Mico, 7.2-7.8 km WSW Puerto Santo Tomás: UTA R15983-85; E slope Montañas del Mico, 9.8 km SW Puerto Santo Tomás: UTA R20169; E slope Montañas del Mico, 11.6-13.0 km WSW Puerto Santo Tomás: UTA R15982, R20150, R29534^H, 29535, 29536^H, R29561, 29562-63^{both H}, 29564-65, R29806-35; Montañas del Mico 12.6 km W Puerto Santo Tomás: UTA R41894-95; NW of Puerto Santo Tomas along trail hiking back from Río Tamejar at base of Cerro San Gil: UTA R33505-06; Puerto Barrios Montañas del Mico Cerro del Microondas: UTA R37621-22, R43597; Seshán: UTA R23631-39; Chichipate: UTA R23628-30; El Estor: UTA R23640; Livingston Quebrada El Branchi: UTA R43607; Livingston Siete Altares: UTA R43598-600; Sierra de las Minas, Los Amates Aldea Vista Hermosa: UTA R33507, R37605, R37613-19; Sierra del Espíritu Santo, Municipio de Los Amates, Aldea San Antonio: UTA R29587-89, R29594-96; Sierra del Espíritu Santo, Municipio de Los Amates, Cerro del Nylon: UTA R29586; Sierra del Espíritu Santo, Municipio de Los Amates, S side Cerro del Nylon: UTA R29590-93; Sierra de Caral, Municipio de Morales, Camino Finca La Firmeza a Cerro Pozo de Agua-Cerro Negro Norte: UTA R43577-83, R43593, R43601-02; Sierra de Caral, Municipio de Morales, Camino La Firmeza-Cerro Pozo de Agua: UTA R43595-96; Sierra de Caral, Municipio de Morales, road Quebradas-La Firmeza: UTA R33509-11, R41887; Sierra de Caral, Municipio de Morales, Aldea Mirador: UTA R33484-91; Sierra de Caral, Municipio de Morales, Cerro Bonillistas: UTA R33492-504; Sierra de Caral, Municipio de Morales, Quebradas: UTA R33508; Sierra de Caral, Municipio de Morales, San Miguelito: UTA R37606-12, R37620, R43594; Sierra de Caral, Municipio de Morales, along tributary of Río Bobos: UTA R37604; Sierra de las Minas, Cristina: UTA R20195; Sierra de Santa Cruz Exmibal Forest first crest on road from Finca Semuc just W of El Estor: UTA R52110; Sierra de Santa Cruz Exmibal Forest just W of El Estor: UTA R52109; Sierra de Santa Cruz, near Finca Semuc: UTA R22080-97, R22098-103, R23625-33, R29805, R27246-47; Sierra de Santa Cruz Livingston Aldea La Libertad: UTA R43604-06, R46907-08; Sierra de Santa Cruz S side La Dicha:

UTA R27237; Sierra de Santa Cruz Xiac m: UTA R27238-43; Sierra de Santa Cruz Cerro 1019 east side (next to Aldea La Libertad): UTA R27235-36, R27244-45, R29583-85, R43584-91; Sierra de Santa Cruz Cerro 1019: UTA R27234; Livingston Sierra de Santa Cruz: UTA R43603; Petén: „El Petén“: USNM 71866, 71869, 71892, 71908, 71911, 71915; Altar de los Sacrificios: AMNH 99902-04; ruins of Tikal, Parque Nacional Tikal: AMNH 140242-44, SMF 77182, UF 137535-37; La Libertad Parque Nacional Sierra Lacandón: UTA R46119-20; N of Yaxhá on road to Nakun: UTA R50331; Tikal 1.0 km E of main ruins: UTA R41163; Tikal near Temple 5: UTA R23641; Uaxactum: AMNH 70932; Zacapa: La Unión: CM 57504; Sierra del Merendón Finca San Enrique Sur del Casco: UTA R33470-81;

HONDURAS: Copán: Laguna del Cerro (15°04.74'N, 88°56.39'W), 770 m: SMF 79150-51; trail between Laguna del Cerro and Quebrada Grande, 15°06'N, 88°55'W, 1100 m: USNM 330185; ca. 1 km SSE Tegucigalpa, 15°37.17'N, 88°14.96'W, 40 m: SMF 79130-33, 79148-49, USNM 330186-88; ca. 7 km SSE Tegucigalpa, 370 m: SMF 79134;

MEXICO: Chiapas: Ruinas de Palenque, 140-300 m: ENCB 1477-81, KU 94044-45, LSUMZ 33418, MZFC 488, UIMNH 11323, UTA R3090; vicinity of Cascada Mizda [= Misholha], ca. 19 km from Palenque on road to Ocosingo: AMNH 114818; Solosuchiapa, 440 m: ENCB 15394; Jetja

(Lacandones): AMNH 142451, 142457; Lacandone Forest: AMNH 66437-38; 2 mi W Agua Escondido: KU 41627-28; 13 mi S Palenque: LSUMZ 33416-17; 10-15 mi S Palenque: LSUMZ 33419-20, 33740-41; vicinity Bonampak: MZFC 487; Puente Santa Helena, Río Amparo Agua Tinta, 16°57'08"N, 91°27'36"W, 830-880 m: SMF 81593, 81595; Oaxaca: Sierra Mixes 3.1 mi W Totontepec: UTA R9899; Tabasco: "Tabasco": MNHN 1893.56; Teapa: USNM 46672-74; Veracruz: "Veracruz": AMNH 149655; Río de Las Playas: USNM 118637; 1.8 mi S Juan Díaz Covarrubias: UTA R9793, R9897, R9927, R9934-35, R9956; 11.9 mi N Santiago de Tuxtla: UTA R9896; 7.7 mi (by road) NW Sontecomapan: UTA R2648-50, R9521-603, R9732-49, R9750-79, R9786-92, R9795-807, R9828, R9863-68, R9873-95, R9900-25, R9929-33, R9936-55, R9781-85, R9808-21, R9869-72, R10079-81, R10082-91, R10098-99, R10101-28, R10139, R10141-48, R10151-91, R10200-16, R10221-64; Los Tuxtlas region, 2.1 mi NW (by road) Sontecomapan: UTA R3102, R311726; Los Tuxtlas region, NW edge Lake Catemaco: UTA R3100, R3173; Los Tuxtlas region, 2.5 mi SSW of Sontecomapan: UTA R3005, R3214, R3018-19, R3128; Los Tuxtlas region, Río Yougualtapan ca. 4.5 mi ESE of Sontecomapan: UTA R3161; W slope Volcán Santa Marta: UTA R3210-13; SE slope Volcán San Martín, ca. 1000 m: UMMZ 121373-75; Yucatan: "Yucatan": USNM 24859.

Manuscript received: 4 August 2006

Authors' addresses: GUNTHER KÖHLER, MATTHIAS DEHLING, JAVIER SUNYER, Forschungsinstitut und Naturmuseum Senckenberg, Senckenberganlage 25, D-60325 Frankfurt a.M., Germany, E-Mail: gkoehler@senckenberg.de; SARAH ALT, CHRISTOPH GRÜNFELDER, Universität Trier, Institut für Biogeographie, Gebäude 024, Am Wissenschaftspark 25-27, D-54296 Trier, Germany.