

Morphological variation in anoles related to *Anolis kemptoni* in Panama

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Abstract. We examined the geographical variation in pholidosis, morphometrics, hemipenis morphology, and coloration in anoles of the anoles related to *Anolis kemptoni* in the highlands of western Panama. This cluster includes six nominal species (*Anolis exsul*, *A. fortunensis*, *A. gruuo*, *A. kemptoni*, *A. pandoensis*, and *A. pseudokemptoni*). On the basis of our data, we place *Anolis exsul* in the synonymy of *A. fortunensis* and *A. pandoensis* in the synonymy of *A. kemptoni*. For the four valid species we provide an identification key, colour photographs in life, standardized descriptions, and a distribution map.

Key words. Reptilia, Squamata, Iguanidae, *Anolis exsul*, *A. fortunensis*, *A. gruuo*, *A. kemptoni*, *A. pandoensis*, and *A. pseudokemptoni*, distribution, morphological variation, hemipenis morphology.

Resumen. Examinamos la variación geográfica en pholidosis, morfometría, morfología de los hemipenes y coloración en los anolis del complejo *Anolis kemptoni* de las tierras altas del oeste de Panamá. Este grupo incluye seis especies nominales (*Anolis exsul*, *A. fortunensis*, *A. gruuo*, *A. kemptoni*, *A. pandoensis* y *A. pseudokemptoni*). Basados en nuestros datos, ubicamos a *Anolis exsul* en la sinónimia de *A. fortunensis* y *A. pandoensis* en la sinónimia de *A. kemptoni*. Para las cuatro especies válidas, proveemos una clave de identificación, fotografías en color de las especies en vida, descripciones estandarizadas y un mapa de distribución.

Introduction

Due to its great climatic and topographical diversity, Panama supports one of the most diverse and abundant herpetofaunas of any Central American country (Myers & Duellman 1982, Ibañez et al. 2001). Thirty-four species of anoles (genus *Anolis*) are known to occur in Panama, 14 of which are restricted to the highlands of lower Central America (Köhler 2003, Köhler et al. 2007). However, there remain taxonomic issues to be resolved at the population and species level. This is particularly true for the *A. altae* complex and the species related to *A. pachypus*, *A. pseudopachypus* and *A. tropidolepis*.

Six nominal species related to *Anolis kemptoni* are reported to occur in Panama: *Anolis exsul*, *A. fortunensis*, *A. gruuo*, *A. kemptoni*, *A. pandoensis*, and *A. pseudokemptoni*. Dunn (1940) described *A. kemptoni* on the basis of a series of specimens from “Fin-

ca Lérída, Volcán Chiriquí, 5300 ft, Chiriquí, Panama”. Arosemena & Ibañez (1993, 1994) named two species, *A. fortunensis* and *A. exsul*, respectively, from two nearby localities in the Reserva Forestal de Fortuna, Chiriquí, Panama. Savage & Guyer (1998) described *Anolis pandoensis* from La Changuinolita, 1950 m elevation, Cantón Coto Brus, Puntarenas Province, Costa Rica, close to the border with Panama. However, this species has been placed in the synonymy of *A. kemptoni* by Hulebak & Poe (2006). Most recently, Köhler et al. (2007) described two new species, *A. gruuo* and *A. pseudokemptoni*, from the Serranía del Tabasará that are related to this cluster of species.

Here we report upon the results of our study on the geographic variation in pholidosis, morphometrics, hemipenis morphology and coloration of the anoles related to *A. kemptoni* in the highlands in western Panama.

Materials and methods

A list of the specimens examined is provided in the Appendix. See Fig. 1 for assignment of the OTUs. Abbreviations for museum collections follow those of LEVITON et al. (1985) except for MHCH (Museo Herpetológico de Chiriquí, David, Chiriquí, Panama) and MVUP (Museo de Vertebrados, Universidad de Panamá, Panama City, Panama). Nomenclature of scale characters follows that of KÖHLER (2003). Terminology for hemipenial morphology follows that of MYERS et al. (1993) and SAVAGE (1997). Scale sizes were measured using the ocular micrometer of a stereo microscope (Leica MZ 12) and rounded to the nearest 0.01 mm. All other 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 and ventral scales were counted at midbody along the midline. Tail height and width were measured at the point reached by the heel of the extended hind leg. Subdigital lamellae were counted on phalanges II to IV of the fourth toe. We considered the scale directly anterior to the circumnasal to be a prenasal. Abbreviations used are SVL (snout-vent length), HL (head length), HW (head width), SS (supraorbital semicircles), IP (interparietal plate), SO (subocular scales), SPL (supralabial scales), INL (infralabials), hDT (horizontal diameter of tail), vDT (vertical diameter of tail), DHL (dorsal scales in one head length), VHL (ventral scales in one head length), and OTU (Operational Taxonomic Unit). Abbreviations used for collectors are AB (ABEL BATISTA), GK (GUNTHER KÖHLER), JS (JAVIER SUNYER) and MP (MARCOS PONCE). Abbreviations used for localities PNVB (Parque Nacional Volcán Barú), PILA (Parque Internacional La Amistad). The capitalised colours and colour codes (the latter

in parentheses) are those of SMITHE (1975-1981). Statistical analyses were performed using the computer program Statistica version 6.1. We performed t-tests to assess whether the means of two groups are statistically different ($p < 0.05$). Discriminant Function Analyses were used to test if the taxa in question could be differentiated by a combination of several morphological characters.

Results

The taxonomic status of *Anolis exsul*

In 1994, AROSEMENA & IBAÑEZ described *A. exsul* on the basis of three specimens from Reserva Forestal de Fortuna, along the Río Chiriquí, some 100 m from the mouth of Quebrada Bijau (8°45'11"N, 82°11'07"W), 1050-1075 m elevation, Chiriquí Province, Panama. Thus the type locality of this taxon is in the close vicinity of the type locality of *A. fortunensis*, a taxon that was named by the same authors one year earlier. In March of 2006, MP and AB collected four specimens of an anole related to these two taxa from the general area of the respective type localities of *A. fortunensis* and *A. exsul*. While trying to identify these newly collected specimens we became suspicious of the distinctiveness of these two taxa and finally concluded that none of the supposedly diagnostic characters as proposed in the original description of *A. exsul* (i.e., Table 3 in AROSEMENA & IBAÑEZ 1994) are useful in separating the two nominal species. MP had the privilege of examining the type material of *A. exsul* and *A. fortunensis*. We discuss these characters in turn (data from Table 3 in AROSEMENA & IBAÑEZ 1994 in parentheses).

Number of scales between second canthals (10-12 such scales in *A. exsul* and 15 in *A. fortunensis*): in our series this character varies from 10 to 15. Number of postrostral scales (7-9 in *A. exsul*, 6 in *A. fortunensis*): in our series this character varies from 5 to 8. Bony parietal protuberances (a characteristic stated to be present in *A. exsul*): we failed

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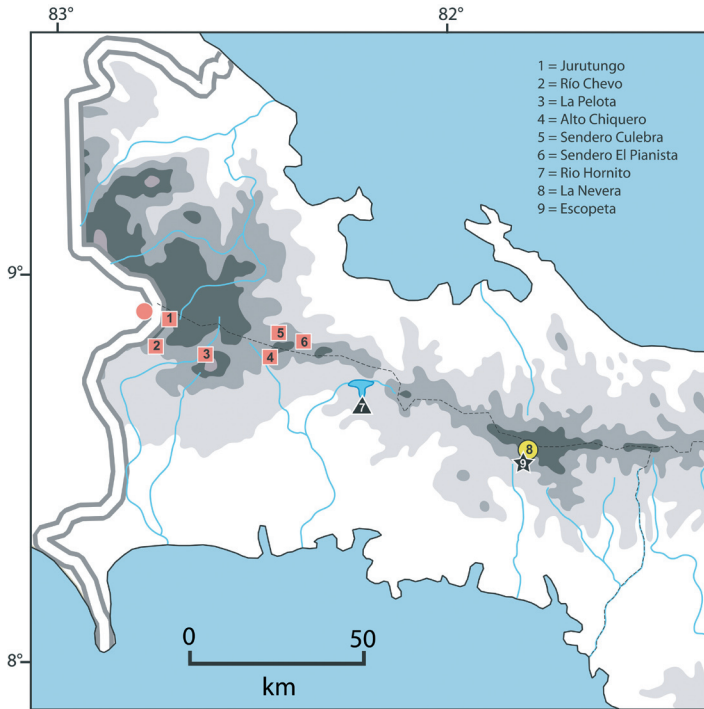
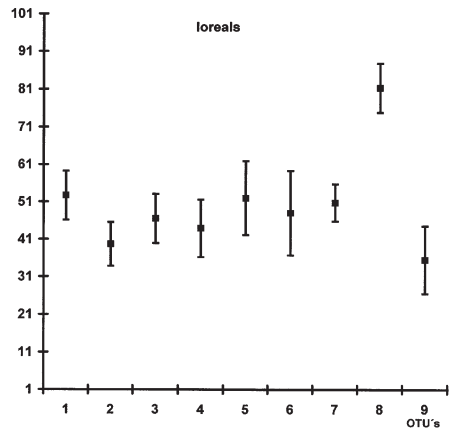
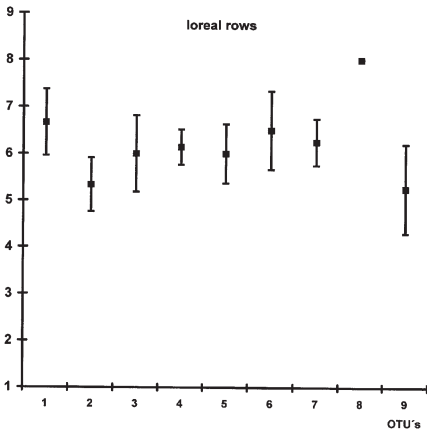
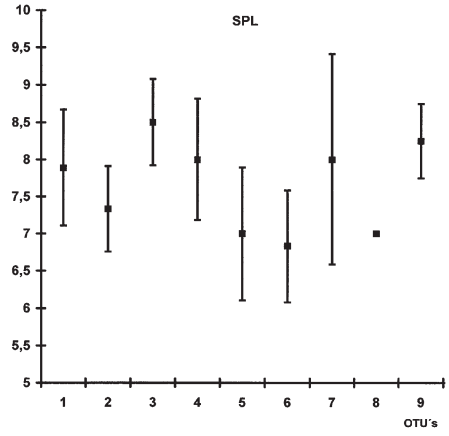
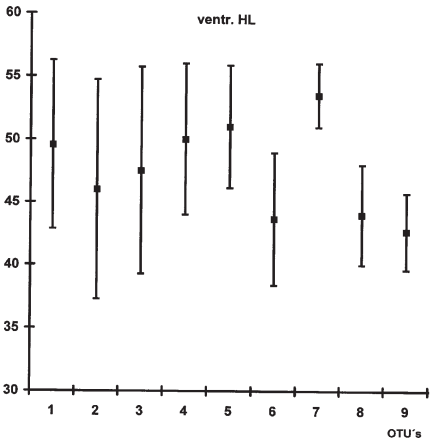
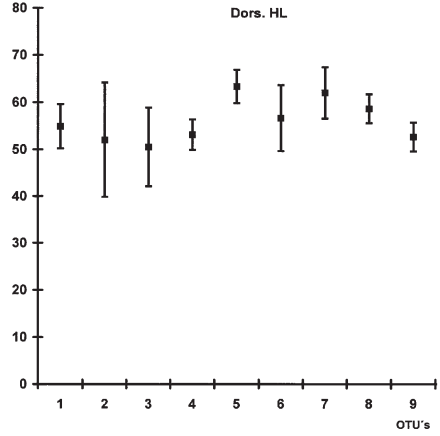
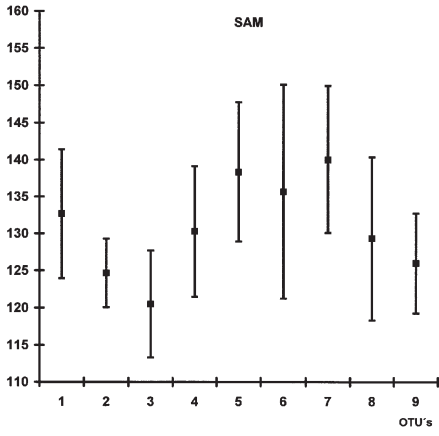


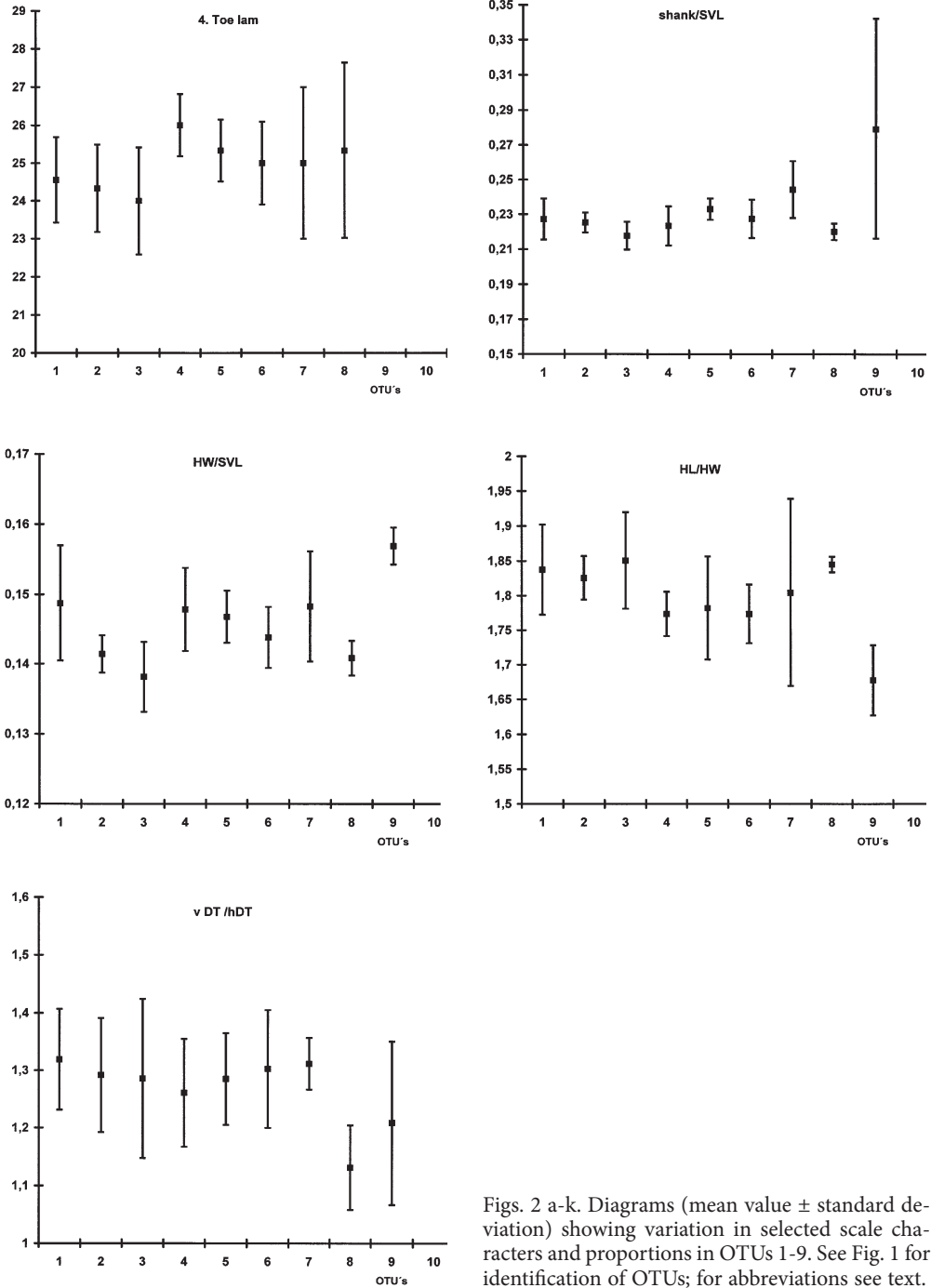
Fig. 1. Distribution of *Anolis fortunensis* (triangle), *A. gruuo* (star), *A. kemptoni* (red squares), and *A. pseudokemptoni* (yellow circle) in western Panama. Red circle indicates La Changuinolita (= type locality of *Anolis pandoensis* SAVAGE & GUYER 1998). Numbers refer to OTUs as used in the analysis. Indicated elevations: pale grey shading 500-1000 m above sea level, medium grey shading 1000-2000 m above sea level, dark grey shading above 2000 m above sea level.

to discern these atop the rear of the head in any of our specimens, and MP was unable to detect this characteristic in the holotype of *A. exsul*. Number of enlarged dorsal scales rows (no enlarged middorsal scales in *A. exsul* and 2 - 4 such scales in *A. fortunensis*): in our specimens the two middorsal scale rows are slightly enlarged relative to the adjacent rows. In other species of this group (e.g., *A. kemptoni*) we found this character to be variable. Thus we do not see any diagnostic value in this character for the two species in question. Posterior insertion of male dewlap (posterior insertion of the dewlap in *A. exsul* at chest level whereas in *A. fortunensis* the dewlap reaches to midventer): in the two males of our series (SMF 86407-08) the posterior insertion of the dewlap is between

the chest and midventer. Hind leg length (the fourth toe of the adpressed hind limb reaches the ear in *A. exsul* and to a point between shoulder and ear in *A. fortunensis*): in two of our specimens (SMF 86406, 86408) the fourth toe reaches the ear, in one specimen (SMF 86405) it reaches to a point between the ear and eye, and in SMF 86407 it reaches to a point between the shoulder and ear. Enlarged postcloacal scales (absent in *A. exsul*, present in *A. fortunensis*): both males in our series have enlarged postcloacal scales. Dewlap colour in males (male dewlap in *A. exsul*: orange base with a cherry-red free margin; *A. fortunensis*: reddish orange base with a red free margin): the dewlap colour in life was recorded for the two males in our series to be Orange Yellow (colour 18 in SMITHE 1975-



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Figs. 2 a-k. Diagrams (mean value \pm standard deviation) showing variation in selected scale characters and proportions in OTUs 1-9. See Fig. 1 for identification of OTUs; for abbreviations see text.

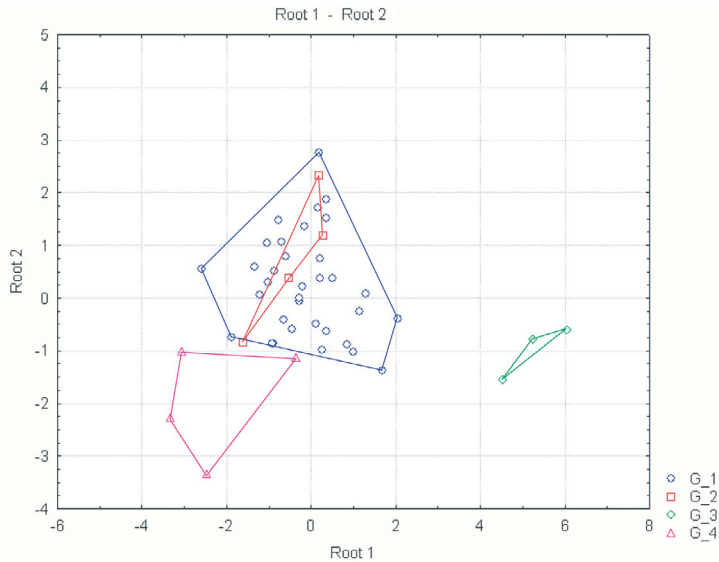


Fig. 3. Discriminant function analysis of species of the *Anolis altae* complex in Panama: 1) *Anolis kemptoni*; 2) = *Anolis fortunensis*; 3) = *Anolis gruuu*; 4) = *Anolis pseudokemptoni*. See text for details.

1981) at the base with the free margin varying from Flame Scarlet (15) to Brick Red (32A).

None of the supposedly diagnostic characters proposed in the original description of *A. exsul* appear to be valid. Furthermore, the comparison of the holotypes of these two nominal species with each other and our series did not yield any characters that distinguish *A. exsul* from *A. fortunensis*. Thus, we conclude that *A. exsul* AROSEMENA & IBAÑEZ is a junior synonym of *A. fortunensis* AROSEMENA & IBAÑEZ.

Geographic and interspecific variation

Morphological variation within and between OTUs is shown in Fig. 2. Although large overlap of ranges is observed for most characters between OTUs, we found statistically distinct differences between some of the OTUs in the following characters. OTU 8 (= *A. pseudokemptoni*) has distinctly more loreal scales and loreal scale rows than any other OTU. In addition the ranges of total loreal scales are al-

most non-overlapping between OTUs 7 (= *A. fortunensis*) and 9 (*A. gruuu*). In relative head length (HL/HW), OTUs 8 and 9 show non-overlapping ranges. Also, the tail of OTU 7 is more compressed than in OTU 8 (non-overlapping ranges of vDT/hDT). Finally, we observe only slightly overlapping ranges in the number of dorsal scales in one head length between OTU 7 and OTUs 8 and 9.

Our OTU 1 is from the close vicinity of the type locality of *A. pandoensis*, whereas our OTU 4 is from the close vicinity of the type locality of *A. kemptoni*. In all characters examined there is large overlap in the ranges between our OTUs 1 and 4, none of the characters appearing to be of diagnostic value. Although we observed some geographical variation between OTUs 1 through 6, none of these OTUs is distinct in any of these characters and we conclude that they should be regarded as representing a single species. Therefore we agree with HULEBAK & POE (2006) that *A. pandoensis* SAVAGE & GUYER is a junior synonym of *A. kemptoni* DUNN. We also reviewed the characters pro-

posed as diagnostic in the original description of *A. pandoensis* and as a result found none of them to be valid.

We conducted a discriminant function analysis (DFA) based on three pholidotic and three morphometric characters (VHL, Loreals, SPL, HL/HW, vDT/hDT, IP/ear) and included four OTUs: OTU 1: = a combined OTU comprising the former OTUs 1-6 (= *A. kemptoni*); OTU 2: = *A. fortunensis*; OTU 3: = *A. gruuo*; OTU 4: = *A. pseudokemptoni*. This DFA yielded a scatter diagram (Fig. 3) that correctly classified 100% of the specimens of OTU's 1 and 3, and 75% of OTU 4. The polygons of OTUs 3 and 4 species do not overlap with those of OTUs 1 and 2, but those of OTUs 1 and 2 largely overlap with each other. The first function is $DS = -0.303275(\text{VHL}) + 0.996622(\text{Loreals}) - 0.509350(\text{SPL}) + 0.343491(\text{HL}/\text{HW}) - 0.160641(\text{vDT}/\text{hDT}) + 0.497529(\text{IP}/\text{ear})$. The second function is $DS = +0.702992(\text{VHL}) - 0.095555(\text{Loreals}) - 0.358664(\text{SPL}) + 0.410196(\text{HL}/\text{HW}) + 0.160641(\text{vDT}/\text{hDT}) + 0.091429(\text{IP}/\text{ear})$.

The data presented above document the distinctness of *A. gruuo* and *A. pseudokemptoni*. None of these characters appear to be useful for the differentiation between *A. kemptoni* and *A. fortunensis*. However, there are several characters aside from those mentioned above that readily separate the two taxa: (1) ventral scales: slightly keeled in *A. kemptoni* (at least on chest and anterior venter), smooth in *A. fortunensis*; (2) dewlap coloration in males: *A. kemptoni*: posterior portion of dewlap Rose Pink (colour 108D in Smith 1975-1981) to Deep Vinaceous (4), anterior portion Burnt Orange (116), with or without a basal Buff (124) blotch; *A. fortunensis*: posterior portion Orange Yellow (18) with a greenish cast, anterior portion varying from Flame Scarlet (153) to Brick Red (132A); (3) maximum SVL: in *A. kemptoni* 54 mm (males) and 57 mm (females); in *A. fortunensis* 47 mm (males) and 49 mm (females).

On the basis of our results we recognize four species of this complex in Panama (Fig. 1): *Anolis fortunensis*, *A. gruuo*, *A. kemptoni*,

and *A. pseudokemptoni*. Morphological variation between these four species is summarized in Table 1. Coloration of male dewlaps in life of the four species is shown in Fig. 4, those of female *A. kemptoni* and *A. pseudokemptoni* in Fig. 5. We provide standard descriptions of these species as well as an identification key (appendix 2).

Species accounts

Anolis fortunensis AROSEMENA & IBAÑEZ, 1993

1993 *Anolis fortunensis* AROSEMENA & IBAÑEZ, *Revista de Biología Tropical* 41: 267; type locality: Reserva Forestal de Fortuna, along the Río Chiriquí, in front of the Estación Hidrometeorológica del Instituto de Recursos Hidráulicos y Electrificación (IRHE) in Bijau, 1050-1075 m elevation, Chiriquí Province, Panama. Holotype: MVUP 756.

1994 *Anolis exsul* AROSEMENA & IBAÑEZ, *Caribbean Journal of Science* 30:222; type locality: Reserva Forestal de Fortuna, along the Río Chiriquí, some 100 m from the mouth of Quebrada Bijau (8°45'11"N, 82°11'07"W), 1050-1075 m elevation, Chiriquí Province, Panama. Holotype: MVUP 901.

Geographic distribution: known only from three localities, all in the close vicinity of Bijau, Reserva Forestal Fortuna, Chiriquí, Panama (Fig. 1).

Diagnosis: *Anolis fortunensis* (Fig. 6) is a medium-sized species (SVL to 47 mm in males, 49 mm in females) of the genus *Anolis* (sensu POE, 2004) which is most similar in external morphology to a cluster of Central American species that are short-legged (longest toe of adpressed hind leg reaches only to tympanum), usually have a single elongated prenasal scale, smooth to slightly keeled ventral scales, a slender habitus, and are often delicate (*A. altae*, *A. carpenteri*, *A. fortunensis*, *A. fuscoauratus*, *A. gruuo*, *A. kemptoni*, *A. pseudokemptoni*). *Anolis fortunensis* differs from the species in this cluster by the following characteristics (conditions for *A. fortun-*

Tab. 1. Selected measurements, proportions and scale characters of *Anolis fortunensis*, *A. gruuu*, *A. kemptoni*, and *A. pseudokemptoni*. Range is followed by mean value and one standard deviation in parentheses. Abbreviations see text.

	Sex	<i>A. fortunensis</i>	<i>A. gruuu</i>	<i>A. kemptoni</i>	<i>A. pseudokemptoni</i>
Sex (n)		m (2), f (2)	m (3), f (1)	m (16), f (19)	m (2), f (1)
Maximum SVL	m	43.0	47.0	54.0	54.5
	f	49.0	42.0	57.0	55.0
Tail length/SVL	m	1.79-1.81 (1.80±0.01)	1.74	1.87- 2.25 (2.00±0.12)	1.79
	f	1.81	1.73	1.87-2.00 (2.00±0.10)	1.72
Tail diameter vertical/ horizontal	m	1.26-1.36 (1.31±0.06)	1.15-1.40 (1.25±0.13)	1.12-1.47 (1.31±0.08)	1.08-1.20 (1.15±0.10)
	f	1.27-1.32 (1.29±0.01)	1.09	1.09-1.41 (1.27±0.09)	1.1
HL/SVL	m	0.25-0.27 (0.26±0.01)	0.26	0.25-0.29 (0.27±0.01)	0.26
	f	0.25-0.28 (0.26±0.02)	0.26	0.24-0.28 (0.26±0.01)	0.25
HL/HW	m	1.85-1.88 (1.86±0.02)	1.65-1.73 (1.68±0.047)	1.68-1.98 (1.82±0.08)	1.82-1.85 (1.84±0.01)
	f	1.59-1.89 (1.75±0.20)	1.63	1.71-1.87 (1.79±0.04)	1.86
IP/ear	m	1.99-2.52 (2.24±0.38)	1.62-2.91 (2.30±0.65)	0.91-3.43 (2.08±0.81)	3.39-3.57 (3.48±0.13)
	f	1.41-2.96 (2.18±1.07)	1.17	1.16-4.20 (2.60±0.81)	2.68
Shank length/SVL	m	0.21-0.25 (0.23±0.01)	0.23-0.36 (0.29±0.07)	0.22-0.24 (0.23±0.01)	0.20-0.22 (0.21±0.01)
	f	0.22-0.27 (0.25±0.02)	0.24	0.21-0.23 (0.22±0.08)	0.21
Axilla-groin distance/SVL	m	0.44-0.46 (0.45±0.01)	0.43-0.44 (0.43±0.01)	0.37-0.49 (0.44±0.01)	0.44-0.46 (0.45±0.00)
	f	0.46-0.47 (0.46±0.01)	0.47	0.43-0.48 (0.46±0.02)	0.47
Subdigital lamellae of 4th toe	m & f	24-28 (25±2.00)	23-26 (24.5±1.28)	23-27 (24.91±1.16)	24-28 (25.32±2.31)
Number of scales between SS	m & f	1-2 (1.5±0.50)	0-1 (0.75±0.50)	0-2 (1.27±0.62)	1
Number of scales between IP and SS	m & f	2-3 (2.75±0.50)	2-3 (2.75±0.50)	1-4 (2.38±0.71)	2-3 (2.25±0.50)
Number of scales between SO and SPL	m & f	0	0	0	0
Number of SPL to level below centre of eye	m & f	6-9 (7.5±1.40)	8-9 (8.25±0.50)	6-9 (7.66±0.89)	6-9 (7.5±1.40)
Number of INL to level below centre of eye	m & f	7-9 (8.50±1.00)	8-9 (8.25±0.50)	6-9 (7.66±0.89)	7-9 (8.32±1.14)

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	Sex	<i>A. fortunensis</i>	<i>A. gruuo</i>	<i>A. kemptoni</i>	<i>A. pseudokemptoni</i>
Total number of loreals	m & f	47-58 (50.75±5.00)	28-48 (35.50±9.00)	33-66 (47.75±8.40)	75-88 (81.32±6.51)
Number of horizontal loreal scale rows	m & f	6-7 (6.25±0.50)	4-6 (5.25±0.96)	5-8 (6.16±0.68)	8
Number of postrostrals	m & f	5-8 (6.75±1.26)	6-8 (7.25±0.96)	5-8 (6.19±0.68)	7-8 (7.32±0.58)
Number of postmentals	m & f	5-6 (5.75±0.50)	6	4-8 (6.19±0.68)	4-6 (5.32±1.14)
Number of scales between nasals	m & f	7-9 (8±0.82)	7-8 (7.25±0.50)	6-9 (7.41±0.70)	7-9 (8.00±1.00)
Number of scales between 2nd canthals	m & f	8-12 (10.5±1.72)	8-9 (8.50±0.58)	6-10 (8.02±1.08)	9-10 (9.67±0.58)
Number of scales between posterior canthals	m & f	10-15 (12±2.15)	9-12 (10.5±1.28)	7-12 (9.19±1.34)	10-11 (10.32±0.58)
Number of medial dorsal scales in one head length	m & f	50-56- (53.5±2.52)	38-46 (41.5±3.42)	36-58 (48.88±6.35)	40-48 (44±4.00)
Number of ventral scales in one head length	m & f	58-70 (62±5.42)	50-58 (54±3.64)	42-68 (55.75±7.00)	56-62 (58.67±3.06)

ensis in parentheses): *Anolis altae*: male dewlap more or less uniformly reddish orange (posterior portion greenish beige, anterior portion reddish orange); hemipenis bilobate (unilobate); number of scales between posterior canthals 7-9 (10-15). *Anolis carpenteri*: body greenish in life (reddish brown); male dewlap uniform orange (posterior portion greenish beige, anterior portion reddish orange). *Anolis fuscoauratus*: male dewlap uniform pinkish brown to red (posterior portion greenish beige, anterior portion reddish orange). *Anolis gruuo*: male dewlap extending to level of axilla (between chest and midventer); male dewlap more or less uniform dull orange (posterior portion greenish beige, anterior portion reddish orange); hemipenis bilobate (unilobate); shank length/SVL 0.23-0.36 (0.21-0.25). *Anolis kemptoni*: posterior portion of male dewlap rose pink, anterior portion burnt orange, small cream colored basal blotch in some populations (posterior portion greenish beige, anterior portion reddish orange, basal blotch always absent); maximum SVL 57 mm (49 mm); tail length/SVL 1.87-2.25 (1.79-1.81); number of scales between posterior canthals 7-12 (10-15). *Anolis*

pseudokemptoni: posterior portion of male dewlap vinaceous, anterior portion orange, anterodorsal corner cream colour (posterior portion greenish beige, anterior portion reddish orange, including anterodorsal corner); total number of loreal scales 75-88 (47-58); maximum SVL 55 mm (49 mm); hemipenis bilobate (unilobate).

Description: Maximum SVL 47.0 mm in males, 49.0 mm in females; tail length/SVL 1.79-1.81; HL/SVL 0.25-0.27 in males, 0.25-0.28 in females; HL/HW 1.85-1.88 in males, 1.71-1.87 in females; shank length/SVL 0.21-0.25 in males 0.22-0.27 in females; longest toe of adpressed hind leg usually reaching to ear; tail slightly to distinctly laterally compressed in cross section, tail vDT/hDT 1.26-1.36 in males, 1.27-1.32 in females.

Scales on snout keeled; 5-8 postrostrals; 7-9 scales between nasals; usually a single large prenasal, prenasal occasionally divided, in contact with supralabial and rostral; distinct frontal depression with smooth and flattened or slightly granular scales; supraorbital semicircles well developed, composed of keeled scales; 0-2 rows of scales separating supraorbital semicircles at narrowest point; 2-3 rows



Fig. 4. Dewlaps of males in life of a) *Anolis fortunensis* (SMF 86407); b) *A. gruuo* (SMF 85416); c) *A. kemptoni*; d) *A. pseudokemptoni* (SMF 85420).

of scales separating supraorbital semicircles and interparietal at narrowest point; supraorbitals composed of 5-7 distinctly enlarged, keeled scales; 4-5 rows of granular scales between enlarged supraoculars and superciliaries at level of mid-orbit; usually 1 elongate superciliary; interparietal scale well developed relative to adjacent scales, surrounded by scales of moderate size; canthal ridge distinct, composed of 4-5 large scales; 8-12 scales present between second canthals; 10-15 scales present between posterior canthals; loreal region slightly convex, 47-58 smooth loreal scales in a maximum of 6-7 horizontal rows; subocular scales in contact with supralabials; 6-9 supralabials to level below centre of eye; mental partial divided medially, bordered posteriorly by 5-6 postmentals; 7-9 infralabials to level below centre of eye; keeled scales present on chin and granular scales present

on throat; lateral head scales anterior to the ear opening about same size as those posterior to the ear opening; ear opening usually vertically oval.

Dorsum of body with granular scales, 36-58 dorsal scales in one head length; 0-4 median rows of dorsal scales slightly enlarged; ventral scales smooth; 58-70 ventral scales in one head length; all caudal scales strongly keeled except at base of tail; caudal middorsal scales slightly enlarged, without whorls of enlarged scales, although an indistinct division in segments is discernible; ventral medial caudal scales larger than dorsal scales; limb scales keeled, imbricate; digital pads dilated, about three times as wide as non-dilated distal portion of toe; distal phalanx narrower than and raised from, dilated pad; 24-28 lamellae under phalanges II-IV of fourth toe.

The completely everted hemipenis (SMF

86408) is a small unilobate organ; the truncus and the lobes are not calyculate; several transverse folds present on asulcate surface of apex; sulcus spermaticus bifurcates at the base of the apex and the branches continue obliquely to the tip.

Colour in life of a specimen from near Río Hornito, Reserva Forestal Fortuna (SMF 86408): dorsal ground color of body and head Raw Umber (223); ventral surface of body dirty white, with small Walnut Brown (221B) punctations; posterior portion of male dewlap Orange Yellow (18) with a greenish cast, anterior portion varying from Flame Scarlet (153) to Brick Red (132A).

Natural history notes: our specimens were collected at night at the edge of the forest while they were sleeping on vegetation about 1.5 m above the ground.

Anolis gruuo KÖHLER, PONCE, SUNYER & BATISTA, 2007

2007 *Anolis gruuo* KÖHLER, PONCE, SUNYER & BATISTA, *Herpetologica* 63: 376; type locality: near the headwaters of Río San Félix, ca. 2 km N Escopeta Camp, Serranía del Tabasará, 900 m elevation, Comarca Ngöbe Buglé, Distrito de Nole Düima, Corregimiento de Jadeberi, Panama. Holotype: SMF 85416.

Geographic distribution: known only from the type locality.

Diagnosis: *Anolis gruuo* is a medium-sized species (SVL to 47 mm in males, 42 mm in females) of the genus *Anolis* (sensu POE, 2004) that is most similar in external morphology to a cluster of Central American species that are short-legged (longest toe of adpressed hind leg reaches only to tympanum), usually have a single elongated prenasal scale, smooth to slightly keeled ventral scales, a slender habitus, and are often delicate (i.e., *A. altae*, *A. carpenteri*, *A. fortunensis*, *A. fuscoauratus*, *A. gruuo*, *A. kemptoni*, *A. pseudokemptoni*). *Anolis gruuo* differs from the species in this cluster by the following characteristics (conditions for *A. gruuo*

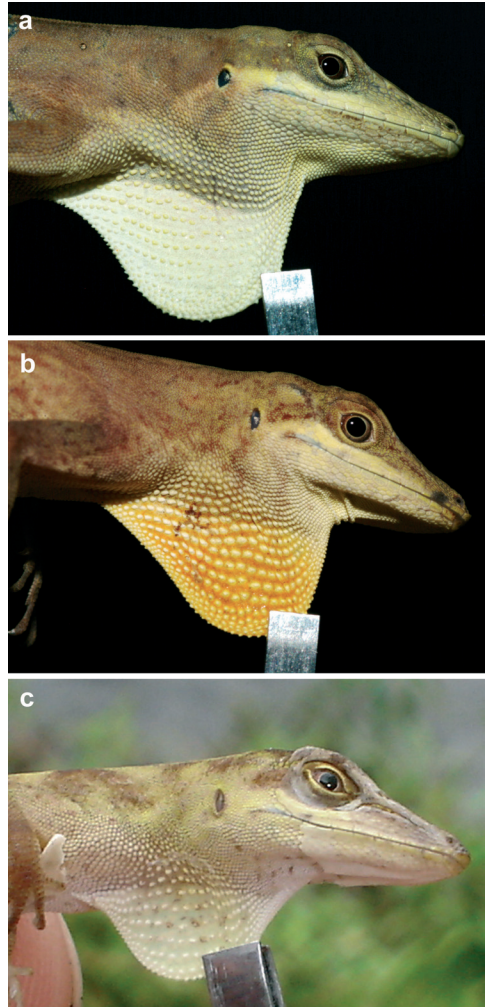


Fig. 5. Dewlaps of females in life of a) *Anolis kemptoni*; b) *A. pseudokemptoni* (SMF 85421); c) *A. fortunensis* (SMF 86406).

in parentheses): *Anolis altae*: male dewlap more or less uniformly reddish orange (more or less uniformly dull orange) in females (a small orange dewlap in females); tail not conspicuously contrastingly dark and pale banded (contrasting banding present). *Anolis carpenteri*: tail not conspicuously contrastingly dark and pale banded (contrasting

banding present); dorsal coloration with a greenish cast in life (no greenish cast in life); no dewlap in females (a small orange dewlap in females). *Anolis fortunensis*: male dewlap extending to a point between chest and mid-venter (to level of axilla); posterior portion of male dewlap greenish beige, anterior portion reddish orange (more or less uniformly dull orange); tail length/SVL 1.79-1.81 (1.74); number of scales between posterior canthals 10-15 (9-12). *Anolis fuscoauratus*: male dewlap uniform pinkish brown to red (more or less uniformly dull orange); hemipenis unilobate (bilobate). *Anolis kemptoni*: posterior portion of male dewlap rose pink, anterior portion orange, a small cream colored basal blotch in some populations (more or less uniformly dull orange); hemipenis unilobate (bilobate); maximum SVL 57 mm (47) in females; shank length/SVL 0.22-0.24 (0.23-0.36). *Anolis pseudokemptoni*: posterior portion of male dewlap vinaceous, anterior portion orange, anterodorsal corner cream color (more or less uniformly dull orange); total number of loreal scales 75-88 (28-48); shank length/SVL 0.20-0.22 (0.23-0.36).

Description: maximum SVL 47.0 mm in males, 42.0 mm in females; tail length/SVL 1.74 in males 1.73 in females; HL/SVL 0.26 in both males and females; HL/HW 1.65-1.73 in males, 1.63 in females; shank length/SVL 0.23-0.36 in males 0.24 in females; longest toe of adpressed hind leg reaching to point between tympanum and eye; tail slightly to distinctly laterally compressed in cross section, tail vDT/hDT 1.15-1.40 in males 1.09 in females.

Scales on snout keeled; 6-8 postrostrals; 7-8 scales between nasals; usually a single large prenasal, prenasal occasionally divided, in contact with supralabial and rostral; scales in distinct prefrontal depression slightly tuberculate; supraorbital semicircles well developed, composed of keeled scales; 0-1 rows of scales separating supraorbital semicircles at narrowest point; 2-3 rows of scales separating supraorbital semicircles and interparietal at narrowest point; supraorbitals composed

of 10-12 distinctly enlarged, keeled scales; 3-4 rows of small keeled scales extending between enlarged supraorbitals and superciliaries at level of mid-orbit; usually 1 elongate superciliary; interparietal scale well developed relative to adjacent scales, surrounded by scales of moderate size; canthal ridge distinct, composed of 3-6 large scales; 8-9 scales present between second canthals; 9-12 scales present between posterior canthals; loreal region slightly convex, 28-48 smooth loreal scales in a maximum of 4-6 horizontal rows; subocular scales in contact with supralabials; 8-9 supralabials to level below centre of eye; mental partial divided medially, bordered posteriorly by 6 postmentals; 8-9 infralabials to level below centre of eye; keeled scales present on chin and granular scales present on throat; lateral head scales anterior to ear opening about same size as those posterior to ear opening; ear opening usually vertically oval.

Dorsum of body with granular scales, 38-46 dorsal scales in one head length; 2-3 median rows of dorsal scales slightly enlarged; ventrals scales smooth; 50-58 ventral scales in one head length; all caudal scales strongly keeled except at base of tail; caudal middorsal scales slightly enlarged, without whorls of enlarged scales, although an indistinct division in segments is discernible; a pair of enlarged postanal scales present (width 0.61-0.95 mm); limb scales keeled, imbricate; digital pads dilated, about three times as wide as non-dilated distal portion of toe; distal phalanx narrower than, and raised from dilated pad; 23-26 lamellae under phalanges II-IV of fourth toe.

The completely everted hemipenis (SMF 85416) is a medium-sized bilobate organ; sulcus spermaticus bordered by well developed sulcal lips and bifurcating at base of apex; branches of sulcus spermaticus continue to tips of lobes, bordered by well-developed sulcal lips; surface of apex and distal truncus strongly calyculate, base of truncus with transverse folds; no asulcate processes present.

Colour in life of the holotype (SMF 85416): Dorsal ground colour Light Drab (119C) suffused with Hair Brown (119A); dorsal surface of head Light Drab; chin white with Warm Sepia (221A) flecks; venter dirty white with Dark Drab (119B) mottling, mottling more intensive towards sides; tail Drab grey (119D) with contrasting transverse Fuscous (21) bands; iris Robin Rufous (340); dewlap Spectrum Orange (17) grading to Chrome Orange (16) anteriorly, gorgetals greyish Brown (20).

Natural history notes: All specimens were active during the day in a shaded coffee plantation. One of the adults was on a tree (Lauraceae) about 5-6 m above the ground, whereas most of the others were collected on a citrus tree about 5 m above the ground. One juvenile was in a coffee tree 1 m above the ground.

Anolis kemptoni DUNN, 1940

1940 *Anolis kemptoni* DUNN, Proc. Acad. nat. Sci. Philad. 92: 111; type locality: Finca Lérica, Volcán Chiriquí, 5300 ft, Chiriquí, Panama. Holotype: ANSP 21708 (examined by GK: this info not included in other accounts).

1998 *Norops pandoensis* SAVAGE & GUYER, Rev. Biol. Trop. 46 (3): 805; type locality: La Changuinolita, 1950 m elevation, Cantón Coto Brus, Puntarenas Province, Costa Rica. Holotype: CRE 5290 (not examined by authors: this info not included in other accounts).

Geographic distribution: eastern portion of the Cordillera de Talamanca in western Panama and adjacent Costa Rica (Fig. 3).

Diagnosis: *Anolis kemptoni* is a medium-sized species (SVL to 54 mm in males, 57 mm in females) of the genus *Anolis* (sensu POE, 2004) that is most similar in external morphology to a cluster of Central American species that are short-legged (longest toe of adpressed hind leg reaches only to tympanum), usually have a single elongated prenasal scale, smooth to slightly keeled ventral scales, a slender habitus, and are often delicate

(*Anolis altae*, *A. carpenteri*, *A. fortunensis*, *A. fuscoauratus*, *A. gruuo*, *A. kemptoni*, *A. pseudokemptoni*). *Anolis kemptoni* differs from the species in this cluster by the following characteristics (conditions for *A. kemptoni* in parentheses): *Anolis altae*: maximum SVL 50 mm (57 mm); dewlap more or less uniformly reddish orange (posterior portion rose pink, anterior portion burnt orange, small cream colored basal blotch present in some populations); hemipenis bilobate (unilobate). *Anolis carpenteri*: body greenish in life (greyish brown), yellow with numerous small dark punctations in preservative, resulting in a fine speckled appearance (uniform without dark punctations); male dewlap uniform orange (posterior portion rose pink, anterior portion burnt orange, small cream colored basal blotch present in some populations); maximum SVL 45 mm (57 mm). *Anolis fortunensis*: posterior portion of male dewlap greenish beige, anterior portion reddish orange (posterior portion rose pink, anterior portion burnt orange, small cream colored basal blotch present in some populations); maximum SVL 49 mm (57 mm); tail length / SVL 1.79-1.81 (1.87-2.25); number of scales between posterior canthals 10-15 (7-12); ventral scales smooth (slightly keeled). *Anolis fuscoauratus*: male dewlap uniform pinkish brown to red (posterior portion rose pink, anterior portion burnt orange, small cream colored basal blotch present in some populations); maximum SVL 50 mm (57 mm); no dewlap in females (a small dewlap present). *Anolis gruuo*: male dewlap more or less uniformly dull orange (posterior portion rose pink, anterior portion burnt orange, small cream colored basal blotch present in some populations); hemipenis bilobate (unilobate); maximum SVL 47 mm (57 mm); shank length / SVL 0.23-0.36 (0.22-0.24); ventral scales smooth (slightly keeled). *Anolis pseudokemptoni*: hemipenis bilobate (unilobate); total number of loreal scales 75-88 (33-66); ventral scales smooth (slightly keeled); female dewlap orange (white).

Description: maximum SVL 54.0 mm in



Fig. 6. Adult male of *Anolis fortunensis* (SMF 86408; SVL 44 mm) from near Río Hornito, Reserva Forestal Fortuna, Chiriquí, Panama.



Fig. 7. Adult male of *Anolis gruuo* (SMF 85416; SVL 47 mm) from near Campamento Escopeta, Comarca Ngöbe Buglé, Panama.



Fig. 8. Adult male of *Anolis kemptoni* from Alto Chiquero, Chiriquí, Panama.



Fig. 9. Adult male of *Anolis pseudokemptoni* (SMF 85420; SVL 54mm) from La Nevera, Comarca Ngöbe Buglé, Panama.

males, 57.0 mm in females; tail length/SVL 1.87-2.25; HL/SVL 0.25-0.29 in males, 0.24-0.28 in females; HL/HW 1.68-1.98 in males, 1.71-1.87 in females; shank length/SVL 0.22-0.24 in males 0.21-0.23 in females; longest toe of adpressed hind leg usually reaching to ear; tail slightly to distinctly laterally compressed in cross section, tail vDT/hDT 1.12-1.47.

Scales on snout keeled; 5-8 postrostrals; 6-9 scales between nasals; usually a single large prenasal present, prenasal occasionally divided, in contact with supralabial and rostral; scales in distinct frontal depression keeled; supraorbital semicircles well developed, composed of keeled scales; 0-2 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 5-10 distinctly enlarged, keeled scales; 2-4 rows of granular scales between enlarged supraoculars and superciliaries at level of mid-orbit; usually 1 elongate superciliary, interparietal scale well developed relative to adjacent scales, surrounded by scales of moderate size; canthal ridge distinct, composed of 3-6 large scales; 6-10 scales present between second canthals; 7-12 scales present between posterior canthals; loreal region slightly convex, 33-66 smooth loreal scales in a maximum of 5-8 horizontal rows; subocular scales in contact with supralabials; 6-9 supralabials to level below centre of eye; mental partial divided medially, bordered posteriorly by 4-8 postmentals; 6-9 infralabials to level below cen-

tre of eye; keeled scales present on chin and granular scales present on throat; lateral head scales anterior to the ear opening about same size as those posterior to ear opening; ear opening usually vertically oval; weak nuchal ridge present in males

Dorsum of body with granular scales, except some scales in vertebral row keeled and subimbricate, 36-58 dorsal scales in one head length; 0-4 median rows of dorsal scales slightly enlarged; ventrals at midbody slightly keeled, 42-68 ventral scales in one head length; all caudal scales strongly keeled except at base of tail; caudal middorsal scales slightly enlarged, without whorls of enlarged scales, although indistinct division in segments discernible; limb scales keeled, imbricate; digital pads dilated, about three times as wide as non-dilated distal portion of toe; distal phalanx narrower than, and raised from, dilated pad; 23-27 lamellae under phalanges II-IV of fourth toe.

The completely everted hemipenis (SMF 85406) is a small unilobate organ; the truncus has a few transverse folds and the apex is strongly calyculate; on the asulcate surface a processus is present at the base of the apex; sulcus spermaticus opens in two concave areas at the base of the apex.

Colour in life of a specimen from near the type locality (MHCH 700): dorsal ground colour of body and head Cinnamon (123A); head with a Hair Brown (119A) interorbital bar; ventral surface of body Cream Color (54); chin dirty white; iris Raw Sienna (136); posterior portion of male dewlap Rose Pink (108D), anterior portion Burnt Orange (116). Colour in life of a specimen from Jurutungo (MHCH 701) agrees with that description, except in the following details: Ground colour of head and body Light Drab (119C), iris Verona Brown (223B); the posterior portion of the male dewlap Deep Vinaceous (4), anterior portion Burnt Orange (116) with a Buff (124) basal blotch. Females have a small dirty white dewlap.

Natural history notes: The majority of the specimens were collected at night while

the animals were sleeping on low vegetation (0.3-0.6 m above the ground). One adult male was sitting upside-down on a fence post exposed to direct sunlight. Other individuals were encountered on low vegetation during the daytime.

Anolis pseudokemptoni KÖHLER, PONCE, SUNYER & BATISTA, 2007

2007 *Anolis pseudokemptoni* KÖHLER, PONCE, SUNYER, BATISTA, *Herpetologica* 63: 380; type locality: Cerro La Nevera, 8°29'45"N, 81°46'35"W, 1600 m elevation, Serranía del Tabasará, Comarca Ngöbe Buglé, Distrito de Nole Düüma, Corregimiento de Jadeberi, Panama. Holotype: SMF 85420.

Geographic distribution: known only from the type locality.

Diagnosis: *Anolis pseudokemptoni* is a medium-sized species (SVL to 54 mm in males, 55 mm in females) of the genus *Anolis* (sensu POE, 2004) that is most similar in external morphology to a cluster of Central American species that are short-legged (longest toe of adpressed hind leg reaches only to tympanum), usually have a single elongated prenasal scale, smooth to slightly keeled ventral scales, a slender habitus, and are often delicate (*A. altae*, *A. carpenteri*, *A. fortunensis*, *A. fuscoauratus*, *A. gruuu*, *A. kemptoni*, *A. pseudokemptoni*). *Anolis pseudokemptoni* differs from the species in this cluster by the following characteristics (conditions for *A. pseudokemptoni* in parentheses): *Anolis altae*: male dewlap more or less uniformly reddish orange (male dewlap tricolored: posterior portion vinaceous, anterior portion orange, anterodorsal corner chamois); no dewlap in females (a small orange dewlap in females); total number loreal scales 32-56 (75-88). *Anolis carpenteri*: body greenish in life (greyish brown), yellow with numerous small dark punctations in preservative, resulting in a fine speckled appearance (uniform greyish brown without dark punctations); male dewlap orange (male dewlap tricolored: posterior

portion vinaceous, anterior portion orange, anterodorsal corner chamois); no dewlap in females (a small orange dewlap in females); maximum SVL 45 mm (55 mm); total number loreal scales 46-56 (75-88). *Anolis fortunensis*: posterior portion of male dewlap greenish beige, anterior portion reddish orange (male dewlap tricolored: posterior portion vinaceous, anterior portion orange, anterodorsal corner chamois); maximum SVL 49 mm (55 mm); total number of loreal scales 47-58 (75-88); number of scales between posterior canthals 10-15 (10-11). *Anolis fuscoauratus*: male dewlap uniform pinkish brown to red (male dewlap tricolored: posterior portion vinaceous, anterior portion orange, anterodorsal corner chamois); maximum SVL 50 mm (55 mm). *Anolis gruuo*: male dewlap uniformly dull orange (male dewlap tricolored: posterior portion vinaceous, anterior portion orange, anterodorsal corner chamois); maximum SVL 47 mm (55 mm); shank length/SVL 0.23-0.36 (0.20-0.22). *Anolis kemptoni*: hemipenis unilobate (bilobate); total number of loreal scales 33-66 (75-88); ventral scales slightly keeled (smooth).

Description: maximum SVL 54.0 mm in males, 55.0 mm in females; tail length/SVL 1.72-1.79; HL/SVL 0.26 in males, 0.25 in females; HL/HW 1.82-1.85 in males, 1.86 in females; shank length/SVL 0.20-0.22 in males 0.21 in females; longest toe of adpressed hind leg reaching to ear; tail slightly compressed in cross section, tail vDT/hDT 1.08-1.20 in males 1.1 in females.

Scales on snout keeled; 4-6 postrostrals; 7-9 scales between nasals; usually a single large prenasal present, prenasal occasionally divided, in contact with supralabial and rostral; distinct frontal depression with smooth scales; supraorbital semicircles well developed, composed of keeled scales; 1 row of scales separating supraorbital semicircles at narrowest point; 2-3 rows of scales separating supraorbital semicircles and interparietal at narrowest point; supraorbitals composed of 6-10 distinctly enlarged, keeled scales; 3-4 rows of granular scales between enlarged su-

praoculars and superciliaries at level of mid-orbit; usually a single elongated superciliary; interparietal scale well developed relative to adjacent scales, surrounded by scales of moderate size; canthal ridge distinct, composed of 4-6 large scales; 9-10 scales present between second canthals; 10-11 scales present between posterior canthals; loreal region slightly convex, 75-88 smooth loreal scales in a maximum of 8-9 horizontal rows; subocular scales in contact with supralabials; 6-9 supralabials to level below centre of eye; mental partial divided medially, bordered posteriorly by 4-6 postmentals; 7-9 infralabials to level below centre of eye; keeled scales present on chin and granular scales on throat; lateral head scales anterior to the ear opening about same size as those posterior to ear opening; ear opening usually vertically oval.

Dorsum of body with granular scales, 40-48 dorsal scales in one head length; 0-4 median rows of dorsal scales slightly enlarged; ventral scales smooth, 56-62 ventral scales in one head length; all caudal scales strongly keeled except at base of tail; caudal middorsal scales slightly enlarged, without whorls of enlarged scales, although indistinct division in segments discernible; limb scales keeled, imbricate; digital pads dilated, about three times as wide as non-dilated distal portion of toe; distal phalanx narrower than, and raised from dilated pad; 24-28 lamellae under phalanges II-IV of fourth toe.

The completely everted hemipenis (SMF 85420) is a medium-sized bilobate organ with a short and stout truncus; sulcus spermaticus bordered by well developed sulcal lips and bifurcating at base of apex; branches of sulcus spermaticus continue to tips of lobes, bordered by well-developed sulcal lips, tip of lobe of each branch opens into a broad concave area; surface of apex and sulcate side of truncus strongly calyculate, asulcate side of truncus with folds; a large asulcate process present.

Colour in life of the holotype (SMF 85420): ground colour of dorsal surfaces of body, limbs and tail Citrine (51), suffused

with Dark Drab (119B) in vertebral area and with indistinct Cinnamon (123A) transverse bands in flank region; a Prout's Brown (121A) interorbital bar present; tail with Hair Brown (119A) bands, edged with Sepia (119); venter dirty white with Army Brown (219B) flecks; cloacal region and ventral surface of base of tail Olive Yellow (52); iris Cinnamon; posterior portion of dewlap Vinaceous (3) with Deep Vinaceous (4) tint, anterior portion Burnt Orange (116), anterodorsal corner Chamois (123).

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References

- AROSEMENA, F.A. & R. IBAÑEZ D. (1993): Una nueva especie de *Anolis* (Squamata: Iguanidae) del grupo *fuscoauratus* de Fortuna, Panamá. – *Revista de Biología Tropical*, **41**(2): 267-272.
- AROSEMENA, F.A. & R. IBAÑEZ D. (1994): Una Saurio nuevo del Género *Anolis* (Reptilia Polychrotidae), grupo *fuscoauratus*, de las tierras altas de Chiriquí, Panamá. – *Caribbean Journal of Science*, **30**(3-4): 222-227.
- DUNN, E.R. (1940): New and noteworthy herpetological material from Panama. – *Proceedings of the Academy of Natural Sciences of Philadelphia*, **92**: 105-122.
- GUYER, C. & J.M. SAVAGE (1987): Cladistic relationships among anoles (Sauria: Iguanidae). – *Systematic Zoology*, **35**: 509-531. "1986".
- GUYER, C. & J.M. SAVAGE (1992). Anole systematics revisited. – *Systematic Biology*, **41**: 89-110.
- HULEBAK, E. & S. POE (2006): *Anolis* (*Norops*) *pandoensis* SAVAGE and GUYER 1998 is a junior synonym of *Anolis kemptoni* DUNN 1940. – *Caribbean Journal of Science* **42**(2): 265-267.
- IBÁÑEZ D.R., F.A. SOLÍS, C.A. JARAMILLO & A.S. RAND (2001): An overview of the herpetology of Panama. In: JOHNSON, J.D., R.G. WEBB & O.A. FLORES-VILLELA (eds.): *Mesoamerican herpetology: Systematics, zoogeography, and conservation*. – El Paso (The University of Texas El Paso): 159-170.
- KÖHLER, G. (2003): *Reptiles of Central America*. – Offenbach (Herpeton): 367 pp.
- KÖHLER, G., M. PONCE, J. SUNYER & A. BATISTA (2007): Four new species of anoles (genus *Anolis*) from the Serranía de Tabasará, west-central Panama (Squamata: Polychrotidae). – *Herpetologica*, **63**(3): 375-391.
- LEVITON, A.E., R.H. GIBBS jr., E. HEAL & C.E. DAWSON (1985): Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. – *Copeia*, **1985**: 802-832.
- MYERS, C.W. & W.E. DUELLMAN (1982): A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographic notes from western Panama. – *American Museum Novitates*, **2752**: 1-32.

- MYERS, C., E.E. WILLIAMS & R.W. MCDIARMID (1993): A new anoline lizard (*Phenacosaurus*) from the highland of Cerro de la Neblina, southern Venezuela. – *American Museum Novitates*, **3070**: 1-15.
- POE, S. (2004): Phylogeny of anoles. – *Herpetological Monographs*, **18**: 37-89.
- SAVAGE, J.M. (1997): On terminology for the description of the hemipenes of squamate reptiles. – *Herpetological Journal*, **7**: 23-25.
- SAVAGE, J.M. & C. GUYER (1998): A new species of anole lizard, genus *Norops* (Squamata: Polychrotidae), from the Cordillera de Talamanca, Costa Rica. – *Revista de Biología Tropical*, **46**(3): 805-809.
- SMITHE, F.B. (1975-1981): Naturalist's color guide. Part I. Color guide. 182 color swatches. New York (American Museum of Natural History).
- Appendix 1**
Specimens examined
- Anolis altae*
COSTA RICA: Alajuela: Cinchona, 1600 m: KU 103953-66; between La Cinchona and Angel Falls, 1370 m: LACM 151319; Heredia: San Rafael de Vara Blanca, 10°10'55"N, 84°09'10"W, 1675 m: SMF 85555; Paso Llano, S slope Volcan Barba, 2230 m: KU 66933; 2.5 km N Vara Blanca, 1900 m: KU 66934; Vara Blanca: KU 129336-37; San José: Alto La Palma: LACM 114187; 2 km N La Palma on road La Palma-La Hondura, 1500 m: LACM 151309; 0.5 mi S Alto La Palma, 1500 m: LACM 151310; 1.4 mi S Alto La Palma, 1500 m: LACM 151311.
- Anolis carpenteri*
COSTA RICA: Cartago: Turrialba, IICA Experimental Cacao Grove: MCZ 146765; Heredia: OTS Finca La Selva: MCZ 174169; Finca La Suerte: SMF 81823; Limón: Finca La Lola: MCZ 128509-10; Tortuguero, next to Caribbean Conservation Commission Camp: USNM 244860; San José: Caspirola: LSUMZ 52385. NICARAGUA: Matagalpa: 12 km NE Matagalpa, 1100 m: KU 195056; Finca Tepeyac, 10.5 km N and 9 km E Matagalpa, 960 m: KU 85722; Río San Juan: by Isla de Diamante on Río San Juan: OMNH 36370; Bartola, 10°58.37'N, 84°20.35'W, 30 m: SMF 80958, 81821-22. PANAMA: Bocas del Toro: southern end of Isla Popa, 1 km E of Sumwood Channel: USNM 347200-04; Rambala: ZFMK 52204; Laguna de Tierra Oscu-
ra, 3.7 km S of Tiger Key: USNM 348442; Colón: "Colón": USNM 266152; Río Frijoles and Pipeline Road: USNM 266153.
- Norops fortunensis*
PANAMA: Chiriquí, Gualaca, Reserva Forestal Fortuna, 8° 43'04.7"N, 82°13'42.1"W, 1074 m: SMF 86405-08; Reserva Forestal de Fortuna, along the Río Chiriquí, some 100 m from the mouth of Quebrada Bijau (8°45'11"N, 82°11'07"W), 1050-1075 m: MVUP 901 (holotype of *Anolis exsul*); Reserva Forestal de Fortuna, along the Río Chiriquí, in front of the Estacion Hidrometeorológica del Instituto de Recursos Hidráulicos y Electrificación (IRHE) in Bijau, 1050-1075 m: MVUP 756 (holotype of *Anolis fortunensis*).
- Anolis fuscoauratus*
BOLIVIA: Bení: Tributary of upper Río Bení: SMF 10967. ECUADOR: Tena, 518 m: SMF 77252; near Mera: SMF 77253; near Misahualli, 420 m: SMF 77254; Arutam, 1°47.28'S, 77°48.31'S, 760 m: SMF 78699. PANAMA: Darién: Río Chíco, near Avolinos: AMNH 57703. VENEZUELA: Iguapo, upper Orinoco: SMF 10971.
- Anolis gruuu*
PANAMA: Comarca Ngöbe Buglé: Nole Düüma, Jadeberi, Serranía de Tabasará, from near the headwaters of Río San Félix, ca. 2 km N Escopeta Camp ca. 8°32'N, 81°50'W, 900 m: SMF 85416-19.
- Anolis kemptoni*
PANAMA: Chiriquí: Boquete, PNVB, 8°50'56"N, 82°29'11"W, 1610 m: SMF 85404-10; Bugaba, Bambito, Cerro La Pelota: SMF 85411-12, 85414-15; Parque Nacional La Amistad, 08°54'02.9"N, 82°36'38"W, 1890 m: SMF 85423-31; Parque Nacional La Amistad, 8°52'33.5"N, 82°28'10.5"W, 1700 m: MHCH 475-476, 497-502; headwaters of Río Chevo, 08°52'27.6"N, 82° 44'31.7"W, 1615 m: SMF 85448-50.
- Anolis pseudokemptoni*
PANAMA: Comarca Ngöbe Buglé: Nole Düüma, Jadeberi, Serranía de Tabasará, La Nevera, 8°29'45"N, 81°46'35"W, 1600 m: SMF 85420-22.

Morphological variation in anoles

Appendix 2

Key to the species related to *Anolis kemptoni* in Panama

- 1a** Usually a single elongated prenasal scale; short-legged (longest toe of adpressed hind leg reaches only to tympanum); ventral scales smooth to slightly keeled; dorsal ground colour greyish-brown; habitus slender, often delicate. **2**
- 1b** Combination of characters not as above. **all other Panamanian species of *Anolis***
- 2a** Total number of loreal scales from 75 to 88; hemipenis bilobate. ***Anolis pseudokemptoni***
- 2b** Total number of loreal scales from 33 to 66; hemipenis unilobate or bilobate **3**
- 3a** Ventral scales slightly keeled; SVL to 54 mm in males, to 57 mm in females; hemipenis unilobate; posterior portion of dewlap rose pink, anterior portion burnt orange, small cream colored basal blotch in some populations. ***Anolis kemptoni***
- 3b** Ventral scales smooth; SVL to 47 mm in males, to 49 mm in females; hemipenis unilobate or bilobate; male dewlap colour not as above. **4**
- 4a** Hemipenis unilobate; posterior insertion of male dewlap between chest and midventer; posterior portion of male dewlap greenish beige, anterior portion reddish orange; tail without conspicuous dark and pale vertical banding. ***Anolis fortunensis***
- 4b** Hemipenis bilobate; posterior insertion of male dewlap at level of axilla; male dewlap more or less uniform dull orange; tail with conspicuous dark and pale vertical banding. ***Anolis gruuo***

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