



Cryptic species and hybridization in the *Anolis polylepis* complex, with the description of a new species from the Osa Peninsula, Costa Rica (Squamata: Polychrotidae)

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Abstract

Based on differences in hemipenial morphology we recognize two species of anoles related to *Anolis polylepis*: *Anolis polylepis* (Pacific versant of central and southern Costa Rica and western Panama, excluding the Osa Peninsula) and a species described herein which is restricted to the Osa Peninsula. The two species differ in hemipenial morphology (hemipenis bilobed in *A. polylepis* versus unilobed in the species from the Osa Peninsula) but show no discernable differences in external morphology (i.e., morphometrics, scalation, coloration, male dewlap). We therefore consider them to be cryptic species. At the neck of the Osa Peninsula where the ranges of the two species meet we detected a narrow (about 1 km wide) hybridization zone in which only individuals with an intermediate hemipenial morphology occur.

Key words: *Anolis*; Central America; Cryptic Species; Hybridization; New species; Polychrotidae; Reptilia; Squamata

Resumen

Basados en diferencias en la morfología del hemipene reconocemos dos especies de anolis relacionados con *Anolis polylepis*: *A. polylepis* (vertiente Pacífica del centro y sur de Costa Rica y oeste de Panamá, excluyendo la Península de Osa) y la especie aquí descrita la cual está restringida a la Península de Osa. Las dos especies difieren entre sí en la morfología del hemipene (hemipene bilobulado en *A. polylepis* y unilobulado en la especie de la Península de Osa) pero no muestran diferencias discernibles en su morfología externa (morfometría, foliosis, coloración, abanico gular del macho), por lo que las consideramos especies crípticas. En el cuello de la Península de Osa las áreas de distribución de ambas especies sobrelapan en la vecindad del pueblo de Rincón de Osa y se detectó una estrecha zona de hibridación (de aproximadamente 1 Km. de ancho) donde solamente se encontró individuos con una morfología intermedia del hemipene.

Introduction

Cryptic species are two or more distinct species that were included in a single species due to their similarity in external morphology (for a review of cryptic species see Pfenninger & Schwenk 2007). Examples of such cryptic species are known for several species pairs and complexes in Central American anoles (e.g. Köhler *et al.* 2007, Köhler & Sunyer 2008, Köhler 2009).

Recent field research in Costa Rica and western Panama has revealed the presence of yet another pair of cryptic species of anoles. We studied the geographic variation of hemipenial and external morphology in lizards currently referred to as *Anolis* (or *Norops*) *polylepis*. This species is distributed along the Pacific versant of central and southern Costa Rica and western Panama, including the Osa Peninsula. In 1873, Peters described the new species *Anolis polylepis* based on a series of twelve syntypes that originated from “Chiriqui”. Barbour and Loveridge (1929) and Barbour (1934) indicate that the Museum of Comparative Zoology (MCZ) had received two of the original syntypes in exchange (now MCZ 21962-63). However, we received on loan from Museum für Naturkunde der Humboldt–Universität zu Berlin (ZMB), Berlin, Germany, eleven specimens supposedly the

remaining syntype series at ZMB (now ZMB 7825–26, 7830, 58002–09). Together with the MCZ specimens these would add up to thirteen specimens, not twelve as stated in Peters (1873). We are not able to provide an explanation for this discrepancy. Since the original description, *A. polylepis* has been considered valid and no synonyms have been described (Peters & Donoso-Barros 1970, Savage 2002, Köhler 2008).

Here we report upon the results of our study of the variation in hemipenial and scalation morphology as well as morphometrics of the anoles commonly referred to as *Anolis* (or *Norops*) *polylepis*.

Material and methods

In evaluating whether multiple species exist within the *Anolis polylepis* complex, we follow the Evolutionary Species Concept (Simpson 1961, Wiley 1978), and operationalize this concept by identifying species based on consistent differences between populations, assuming these differences are result of different evolutionary histories (Frost & Kluge 1994). Along Costa Rican Highway 34 (Dominical to Palmar Sur), Highway 2 (Palmar Sur to Ciudad Neily) and Road 245 (Chacarita to the tip of the Peninsula de Osa), we systematically collected adult males of *Anolis polylepis* (2–5 specimens about every 5 km along the road) in order to map different hemipenial morphs of this species. Furthermore, we compared morphometrics and pholidosis of museum specimens (complete list in appendix I). Abbreviations for museum collections follow those of Leviton *et al.* (1985) except for MHCH (Museo Herpetológico de Chiriquí, David, Chiriquí, Panama). For the synonymy lists, we included only those works that cite actual specimens. Nomenclature of scale characters follows that of Köhler (2008). Terminology for dewlap morphology follows that of Fitch and Hillis (1984). Terminology for hemipenial morphology follows that of Myers *et al.* (1993) and Savage (1997). Our designations of nasal scalation and dorsal color pattern types are shown in Figures 1 and 2, respectively. Scale sizes were measured using the ocular micrometer of a stereo microscope (Leica MZ 12) to the nearest 0.01 mm. All other measurements were made using precision calipers to the nearest 0.1 mm. Values are given as minimum–maximum (mean \pm standard deviation). Head length (HL) 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 (HW) 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 4th toe. We considered the scale directly anterior to the circumnasal to be a prenasal. Relative hind leg length was examined in the field by folding the hind leg of the specimen in life towards its head and determining the point reached by the tip of the longest toe. The capitalized colors and color codes (the latter in parentheses) are those of Smithe (1975–1981). Additional abbreviations used are 4FDL (lamellae under distal phalanx of fourth finger), 4FL (lamellae under phalanges II–IV of fourth finger), 4TDL (lamellae under distal phalanx of fourth toe), 4TL (lamellae under phalanges II–IV of fourth toe), AGD (axilla–groin distance), CanthsLarge (number of enlarged canthal scales), CanthsTotal (total number of canthal scales), DHL (number of medial dorsal scales in one head length), EH (ear height), EL (ear length), IN (transverse scale count in a straight line between circumnasals), INL (infralabials), IO (minimum number of scales between SS), IP (interparietal plate), IPIO (number of scales between IP and SS), LR (number of loreal rows), PM (number of postmental scales), PostCanth (transverse scale count in a straight line between posterior canthals), PR (number of postrostral scales), SAM (number of scales around midbody), ScaxgrD (number of dorsal scales between levels of axilla and groin), ScaxgrV (number of ventral scales between levels of axilla and groin), SecondCanths (transverse scale count in a straight line between second canthals), SL (snout length), SO (subocular scales), SOSPL (number of scale rows between SO and SPL), SPL (supralabial scales), SS (supraorbital semicircles), SVL (snout–vent length), TNLS (total number of loreal scales on one side), VHL (number of medial ventral scales in one head length). For statistical comparisons, we divided all specimens into two groups depending on type of hemipenial morphology (see below). Analyses were performed separately for males and females; juveniles (SLV <35 mm) were excluded. We compared the two hemipenial groups using principal component analyses (PCA). For PCA we standardized all variables using z-transformations. All statistical computations were performed with the software R, Version 2.7.1 (R Development Core Team 2008).

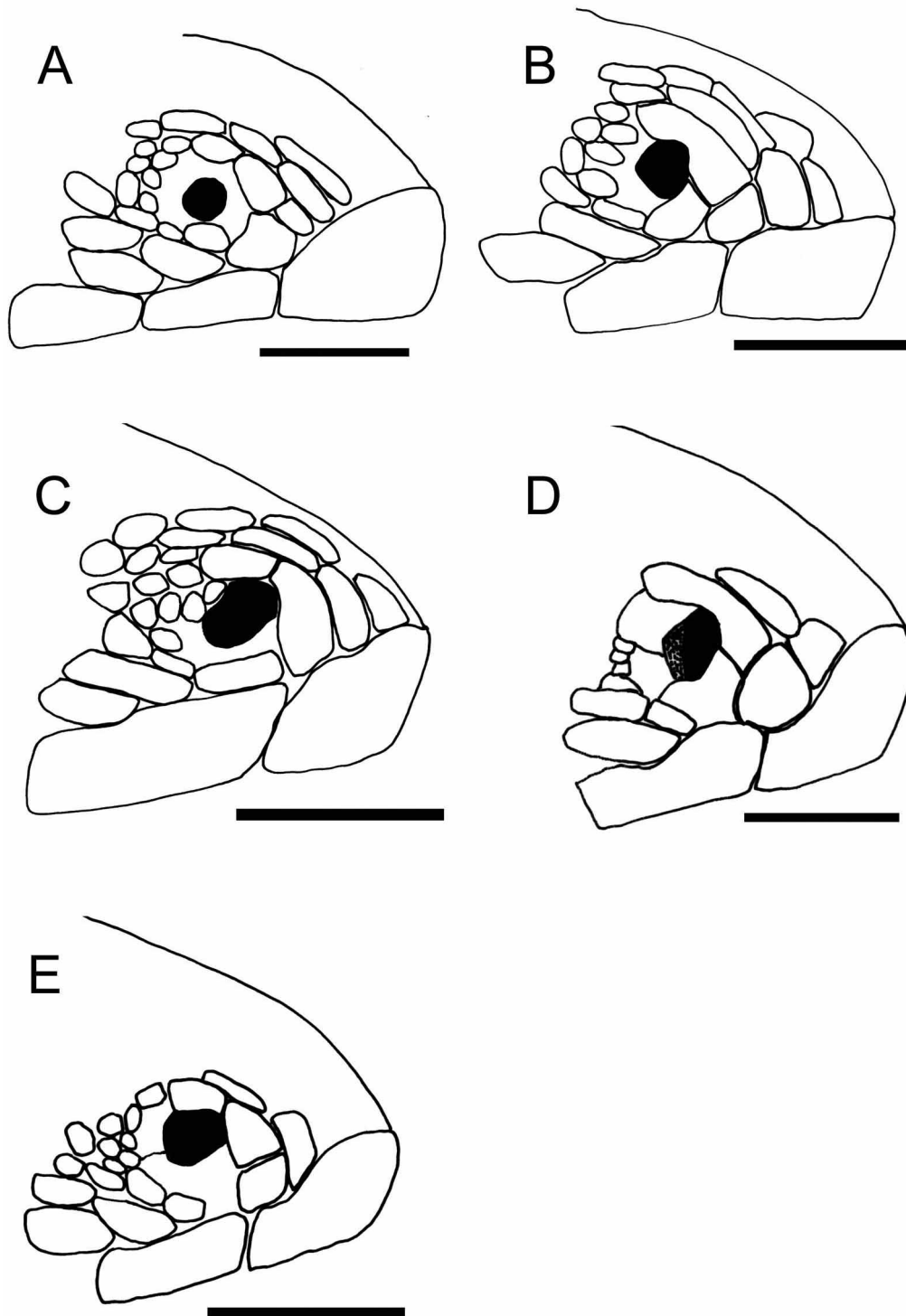


FIGURE 1. Designation of nasal scalation types. (a) Type A (UCR 20713); (b) Type B (SMF 89430); (c) Type C (SMF 89210); (d) Type D (UCR 14257); (e) Type E (UCR 20732). Scale bar = 1.0 mm. See Text for details.

Results

Two distinctly different hemipenial morphotypes are evident in the specimens we examined. In type A (Fig. 3; $N = 61$ adult males with everted hemipenes), the hemipenis is a medium-sized bilobed organ (length of lobes equal length of truncus); the sulcus spermaticus bifurcates at the base of the apex and the branches open into concave areas, one on each lobe; asulcate side of apex strongly calyculate, truncus with transverse folds. In type B (Fig. 4; N

= 47 adult males with everted hemipenes), the hemipenis is unilobed and slightly smaller relative to body size as compared to the type A hemipenis; the sulcus spermaticus opens at base of apex into a broad concave area that covers the complete sulcate side of the apex; asulcate side of apex with fine calyces, truncus with transverse folds. The distribution of the two hemipenial morphs is highly correlated geographically (Fig. 6). Mapping of the morphs revealed that the distributions of both groups are parapatric with a narrow contact zone in the vicinity of the village of Rincón de Osa. In this area of about 1 km width we collected individuals of this anole that have an intermediate hemipenial morphology (Fig. 5, $N = 25$ adult males with everted hemipenes). We assume that these individuals represent hybrids between the two distinct hemipenial morphs. Moreover, the integrity of the two distinct hemipenial morphs is maintained over large geographic areas (in the case of the bilobed morph across a distance of some 300 km).

TABLE 1. PCA variable loadings for the first and second principal components. For abbreviations see text.

	PC1	PC2
SVL	0.265	0.250
Shank length	0.242	0.267
AGD	0.253	0.095
EH	0.053	0.064
EL	0.102	-0.070
IP length	-0.087	0.238
IP width	-0.063	0.237
SL	0.139	0.327
HW	0.160	0.276
HL	0.228	0.286
VHL	0.169	0.094
DHL	0.083	-0.204
4TL	0.211	-0.063
4TDL	0.199	-0.003
4FL	0.129	0.114
4FDL	0.211	-0.037
LR	0.132	-0.091
TNLS	0.190	-0.104
SOSPL	0.024	0.222
SPL	0.135	-0.121
SBL	0.130	-0.110
IPIO	0.209	-0.120
IO	0.148	-0.139
CanthsLarge	0.133	-0.001
CanthsTotal	0.169	-0.122
PostCanth	0.190	-0.137
SecondCanths	0.173	-0.112
PM	0.027	-0.048
PR	0.084	-0.099
IN	0.191	0.053
SAM	0.082	-0.232
ScaxgrD	0.112	-0.242
ScaxgrV	0.235	-0.089

In external morphology as well as in male dewlap coloration, however, the two hemipenial morphs are extremely similar. We detected no differences between the two groups in the PCA (Fig. 7, Table 1).

None of the males in the syntype series of *Anolis polylepis* has everted hemipenes. However, its type locality data, although not precise, allow for a reliable allocation to the bilobed hemipenial morph. Thus, on geographic reasons *Anolis polylepis* is clearly referable to our Type A. There is no available scientific name for our Type B. We therefore describe it as a new species below.

Anolis polylepis Peters

Anolis polylepis Peters, 1873:738; syntypes (ZMB 7825-26, 7830, 58002-09) from “Chiriqui”. Barbour (1934), Dunn (1930), Slevin (1942), Taylor (1956), Etheridge (1959), Poe (2004; in part.), Köhler *et al.* (2008).

Diagnosis. A medium-sized species (SVL in largest specimen 59.4 mm) of the genus *Anolis* (sensu Poe 2004) that differs from all other Lower Central American beta anoles (sensu Etheridge 1967) except *Anolis apletophallus*, *A. cryptolimifrons*, and *A. limifrons* in that it is long-legged (longest toe of adpressed hind leg reaches to at least center of eye), has smooth ventral scales, and a slender habitus, often delicate. *Anolis polylepis* differs from the species in the cluster listed above by having two elongate, overlapping superciliaries (one such scale in *A. apletophallus*, *A. cryptolimifrons*, and *A. limifrons*), usually two anterior prenasal scales (versus one elongate prenasal scale) and dewlap coloration (usually orange with a darker orange basal portion in *A. polylepis* versus dirty white with a basal orange-yellow blotch in *A. cryptolimifrons* and *A. limifrons*, almost uniformly orange-yellow in *A. apletophallus*). Additionally, *A. polylepis* differs from *A. limifrons*, the only species of this cluster with which it occurs sympatrically, by having a bilobed hemipenis (unilobed in *A. limifrons*). For a comparison with the somewhat similar species *A. tropidogaster* and *A. cupreus* see Diagnosis section of *A. osa*. For variation in selected morphometric and scalation characters of *A. polylepis* see Table 3.

Description. *Norops polylepis* is a medium sized anole (maximum recorded SVL 59.4 mm in males, 53.5 mm in females); dorsal head scales in internasal region keeled (Fig. 8), in prefrontal, parietal, and frontal areas rugose to tuberculate; deep frontal depression present, parietal depression absent; 7–11 (7.90 ± 0.87) postrostrals; anterior nasal divided in most individuals, usually in contact with rostral and first supralabial, for variation in nasal region see also Table 2 and Figure 1; 7–11 (8.52 ± 1.19) internasals; canthal ridge sharply defined; scales comprising supraorbital semicircles weakly keeled, largest scale in semicircles about same size as largest supraocular scale; supraorbital semicircles well defined; 1–5 (2.69 ± 0.83) scales separating supraorbital semicircles at narrowest point; 2–7 (3.80 ± 1.03) scales separating supraorbital semicircles and interparietal at narrowest point; interparietal well defined, greatly enlarged relative to adjacent scales, surrounded by scales of moderate size, longer than wide, usually larger than ear opening; 5–22 enlarged, keeled supraocular scales on each side, in 2–4 rows; enlarged supraoculars not in contact with supraorbital semicircles; 2 elongate supraciliaries, posterior one much shorter than anterior one; 3–6 enlarged canthals; 7–16 (1.46 ± 1.66) scales between second canthals; 12–18 (14.4 ± 1.9) scales present between posterior canthals; loreal region slightly concave, 37–92 (57.69 ± 11.38) mostly keeled (some smooth or rugose) loreal scales in a maximum of 6–10 (8.06 ± 1.05) horizontal rows; 6–9 (7.17 ± 0.65) supralabials to level below center of eye; suboculars keeled, suboculars usually in broad contact with supralabials; ear opening vertically oval; scales anterior to ear opening granular, similar in size to those posterior to ear opening; 6–9 (6.82 ± 0.96) postmentals, outer pair usually largest; keeled granular scales present on chin and throat; male dewlap large, extending onto chest; 6–8 horizontal gorgetal-sternal rows with 26–38 scales per row, rows somewhat irregular, some of them with pairs or triplets of scales, apical portion of dewlap between marginal pairs and last gorgetal-sternal row free of scales; modal number of marginal pairs 4–5; female dewlap absent; no nuchal crest or dorsal ridge; 2 middorsal scale rows slightly enlarged, weakly keeled, dorsal scales lateral to middorsal series gradually larger than granular lateral scales; no enlarged scales scattered among granular laterals; 62–118 (87.3 ± 13.18) dorsal scales along vertebral midline between levels of axillae and groin in males, 66–111 (95.1 ± 11.2) in females; 35–68 (51.7 ± 6.9) dorsal scales along vertebral midline contained in one head length in males, 39–76 (55.8 ± 7.99) in females; ventral scales on midsection about the same size as largest dorsal scales; ventral body scales smooth, subimbricate; 56–85 (69.9 ± 8.3) ventral scales along midventral line between levels of axilla and groin in males, 57–76 (66.92 ± 5.30) in females; 36–62 (48.9 ± 5.72) ventral scales contained in one head length in males, 36–56 (44.0 ± 5.12) in females; 134–212 (164.6 ± 14.5) scales around midbody in males, 140–212

(178.5±17.2) in females; tubelike axillary pocket absent; preanal scales not keeled; postcloacal scales usually not enlarged; tail laterally compressed in cross section, tail height/tail width 1.20–1.85 (1.43±0.13); basal subcaudal scales smooth; lateral caudal scales keeled, homogeneous; dorsal medial caudal scale row slightly enlarged, keeled, not forming a crest; most scales on lateral surface of antebrachium weakly keeled, unicarinate; 21–29 (24.66±1.52) subdigital lamellae on Phalanges II–IV of Toe IV of hind limbs; 7–12 (9.4±1.0) subdigital scales on Phalanx I of Toe IV of hind limbs; SVL 42.2–59.4 (51.3±3.76) mm in males, 39.6–53.5 (47.3±3.52) mm in females; HL 10.8–14.4 (12.8±0.88) mm in males, 10.1–13.7 (11.9±0.78) mm in females; TAL 80.1–117.0 (102.1±10.28) mm in males, 70.0–101.5 (86.3±8.29) mm in females; SHL 11.6–16.0 (13.9±1.12) mm in males, 10.5–14.0 (12.4±0.98) mm in females; TAL/SVL 1.53–2.22 (2.01±0.23) in males, 1.39–2.50 (1.92±0.3) in females; HL/SVL 0.24–0.27 (0.26±0.01) in males, 0.24–0.29 (0.26±0.0) in females; SHL/SVL 0.25–0.32 (0.29±0.02) in males, 0.25–0.34 (0.25±0.0) in females; SHL/HL 0.98–1.22 (1.14±0.08) in males, 0.97–1.17 (1.06±0.1) in females; longest toe of adpressed hind limb usually reaching to a point between anterior border of eye and tip of snout. Of 45 specimens examined, the longest toe of the adpressed hind leg reached to mid-eye in 3 individuals (6.7%), to anterior margin of eye in 29 individuals (64.4%), and to a point between eye and snout in 13 individuals (28.9%).

Coloration in life of an adult male specimen (SMF 89509) of *Anolis polylepis* from Hacienda Café de Eleta, 8.87157°N, 82.77099°W, 1380 m elevation, Chiriquí, Panama, was recorded as follows: Dorsal ground color Citrine (51) suffused with Dark Brownish Olive (129); a narrow Dark Brownish Olive (129) interorbital bar present; lateral longitudinal stripe Cream Color (54); venter Cream Color (54) with a suggestion of Lime Green (59); ventral surfaces of limbs Dark Drab (119B); dewlap Spectrum Orange (17) with the apical portion more yellowish; gorgetals Raw Umber (23); iris Raw Sienna (136). Coloration in life of the dewlap of an adult male specimen (SMF 89606) of *Anolis polylepis* from near Uvita, Province Puntarenas, Costa Rica, was recorded as follows: Orange Yellow (18) except for dirty white basal portion and a Raw Umber (23) central area; iris Raw Umber (23). For variation in dorsal pattern see also Table 2 and Figure 2.

Geographic distribution. *Anolis polylepis* is distributed along the Pacific versant of central Costa Rica to western Panama, exclusive of the Peninsula de Osa, from near sea level to 1615 m elevation.

TABLE 2. Frequency distribution of nasal region and dorsal pattern types in *Anolis osa* and *A. polylepis*.

	<i>Anolis osa</i>	<i>A. polylepis</i>
	<i>N</i> = 37	<i>N</i> = 56
Nasal region Type 1	33 (80.5%)	51 (71.8%)
Nasal region Type 2	0 (0%)	9 (12.7%)
Nasal region Type 3	1 (2.4%)	0 (0%)
Nasal region Type 4	2 (4.9%)	8 (11.3%)
Nasal region Type 5	5 (12.2%)	2 (2.8%)
Dorsal pattern Type 1	8 (19.5%)	10 (14.1%)
Dorsal pattern Type 2	10 (24.4%)	2 (2.8%)
Dorsal pattern Type 3	3 (7.3%)	8 (11.3%)
Dorsal pattern Type 4	6 (14.6%)	5 (7.0%)
Dorsal pattern Type 5	10 (24.4%)	16 (22.5%)
Dorsal pattern Type 6	0 (0%)	15 (21.1%)

***Anolis osa* sp. nov.**

Figs. 9–11

Anolis polylepis: Poe (2004, in part.).

Holotype. SMF 80645, an adult male from about 6.3 km WSW Rincón de Osa, 8°40'36.7"N, 83°32'7.9"W, about 150 m elevation, Puntarenas Province, Costa Rica, collected 22 February 2008 by Gunther Köhler and Johannes Köhler. Field tag number GK 2092.

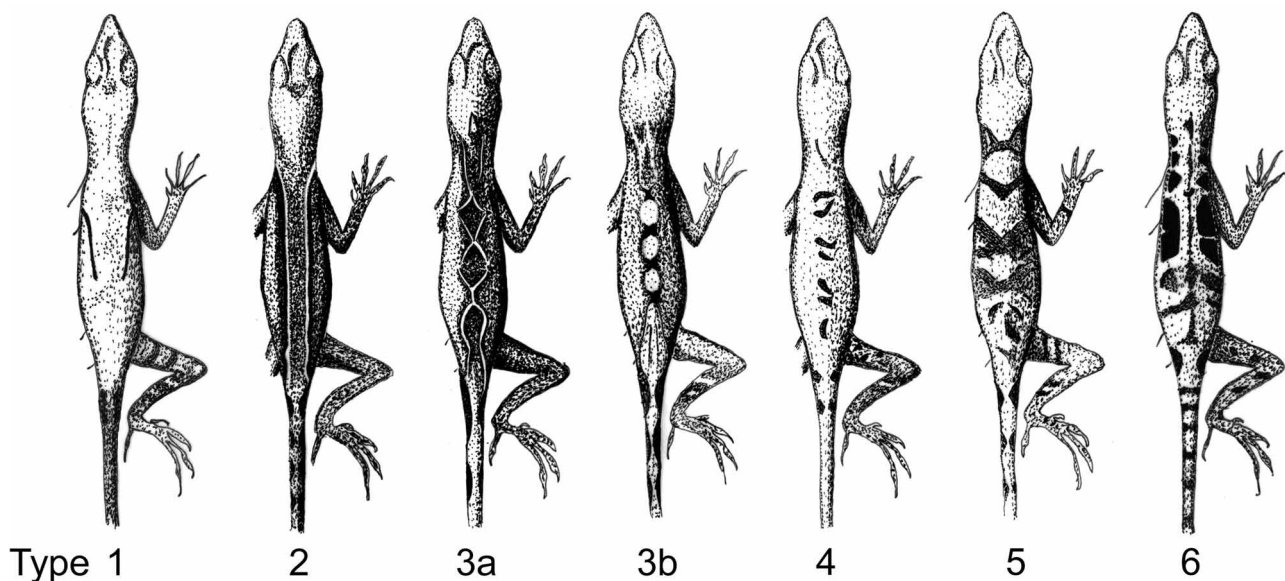


FIGURE 2. Designation of dorsal color pattern types.

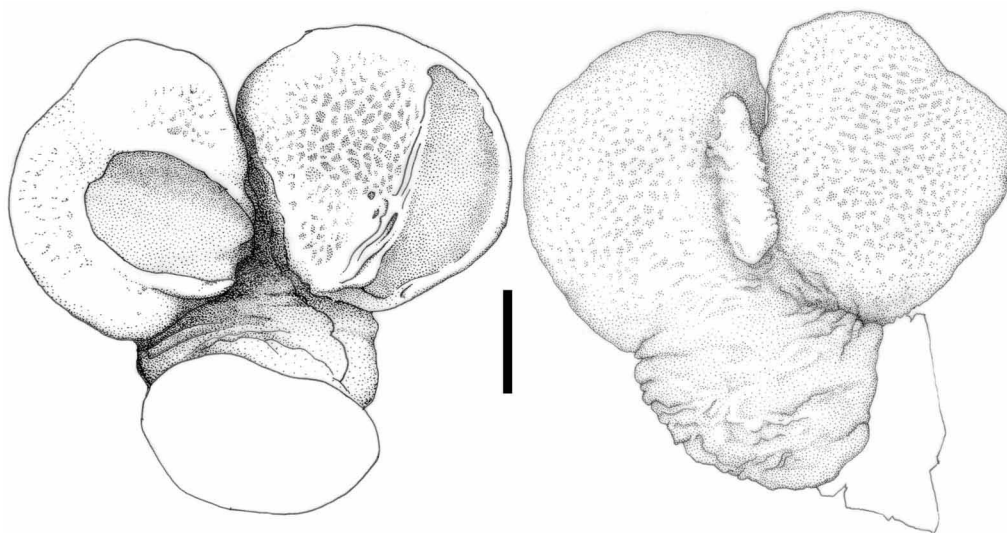


FIGURE 3. Hemipenis of *Anolis polylepis* (MHCH 1024). Scale bar = 1.0 mm.

Paratypes. SMF 89227–32, same collecting data as holotype. SMF 89215–21, UCR 20733–35, 2 km W Rincón de Osa, about 10 m elevation, Puntarenas Province, Costa Rica, collected 22 February 2008 by Gunther Köhler and Johannes Köhler. SMF 89260–61, 89427–29, Parque Nacional Corcovado, Estación Sirena, 8.48°N, 83.58°W, Puntarenas Province, Costa Rica, collected 10–11 August 2005 by Matthias Dehling. SMF 89227–29, SMF 89260–61, 89427–29, UCR 20733–35 are adult males with everted hemipenes. SMF 89230–32 are adult females.

Referred Specimen: See Appendix I.

Diagnosis. A medium-sized species (SVL in largest specimen 57 mm) of the genus *Anolis* (sensu Poe 2004) that differs from all other Lower Central American beta anoles (sensu Etheridge 1967) except *Anolis apletophallus*, *A. cryptolimifrons*, and *A. limifrons* in that it is long-legged (longest toe of adpressed hind leg reaches to at least center of eye), has smooth ventral scales, and a slender habitus, often delicate. *Anolis osa* differs from the species in the cluster listed above, except *A. polylepis*, by having two elongate, overlapping superciliaries (one such scale in *A. apletophallus*, *A. cryptolimifrons*, and *A. limifrons*), usually two anterior prenasal scales (versus one elongate prenasal scale) and dewlap coloration (usually orange with a darker orange basal portion in *A. osa* versus dirty

white with a basal orange-yellow blotch in *A. cryptolimifrons* and *A. limifrons*, almost uniformly orange-yellow in *A. apletophallus*). *Anolis osa* differs from *A. polylepis* by having a unilobed hemipenis (bilobed in *A. polylepis*). Other anole species from Lower Central America that are somewhat similar in appearance to both *A. osa* and *A. polylepis* are *A. tropidogaster* and *A. cupreus*, the latter of which occurs syntopically at some localities with *A. polylepis*. However, both *A. tropidogaster* and *A. cupreus* have strongly keeled ventral scales (smooth in *A. osa* and *A. polylepis*). Also, the majority of males in *A. tropidogaster* have a pair of greatly enlarged postcloacal scales (these scales usually not enlarged in *A. osa* and *A. polylepis*). In the field, most individuals of *A. osa* and *A. polylepis* have a pale longitudinal lateral stripe (absent in Costa Rican populations of *A. cupreus*). For variation in selected morphometric and scalation characters of *A. osa* see Table 3.

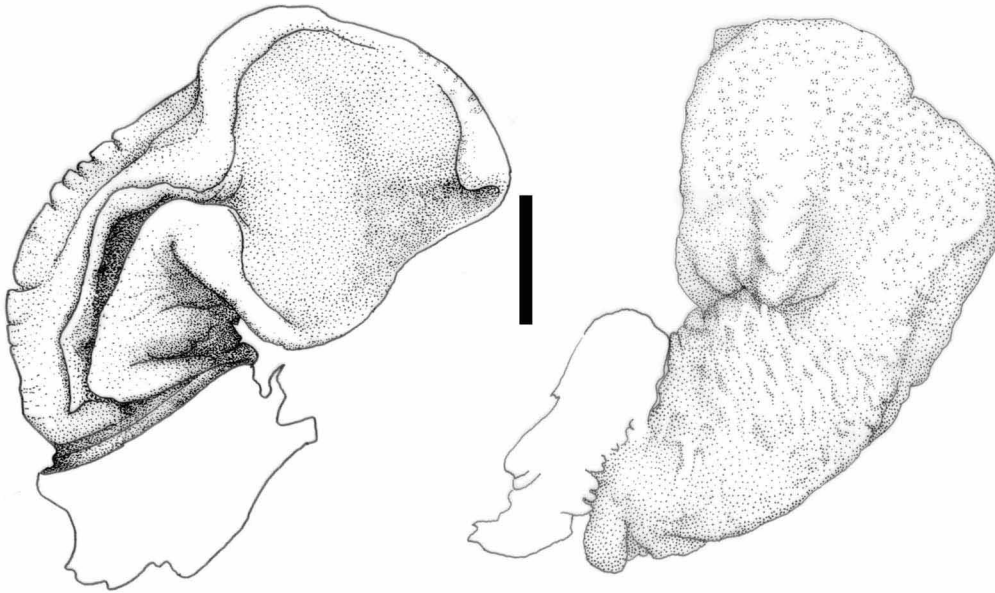


FIGURE 4. Hemipenis of *Anolis osa* (SMF 89260). Scale bar = 1.0 mm.



FIGURE 5. Hemipenis of a suspected hybrid (SMF 89181) between *Anolis polylepis* and *A. osa*. Scale bar = 1.0 mm.

Description of the holotype. Adult male as indicated by everted hemipenes and presence of large dewlap; SVL 50.5 mm; tail length 106 mm, tail complete; tail compressed in cross section, tail height 2.0 mm, tail width 1.4 mm; axilla to groin distance 20.8 mm; head length 13.3 mm, head length/SVL ratio 0.26; snout length 6.6 mm; head width 8.2 mm; longest toe of adpressed hind limb reaching to a point between eye and snout; shank length 14.6 mm, shank length/head length ratio 1.1; longest finger of extended forelimb reaching tip of snout; longest finger of adpressed forelimb reaches to anterior insertion of hind limbs. Scales on snout keeled (Fig. 10); 9 postrostrals; 10 scales between nasals; scales in distinct prefrontal depression slightly wrinkled; supraorbital semicircles well developed, separated by a minimum of 2 scales; supraorbital disc composed of 6 distinctly enlarged keeled scales; two elongated, strongly overlapping superciliaries, the anterior one much larger than the posterior scale; about 3–4 rows of small keeled scales extending between enlarged supraorbitals and superciliaries; interparietal scale well developed, 1.8 x 1.0 mm (length x width), surrounded by scales of moderate size; 2 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 3 large (posterior two largest) and 6 small anterior canthal scales; 11 scales present between second canthals; 12 scales present between posterior canthals; 70 (right)–63 (left) mostly keeled loreal scales in a maximum of 8 (right)–9 (left) horizontal rows, with the scales of lower rows mostly keeled, and those of upper rows mostly tuberculated; subocular scales keeled, narrowly in contact with supralabials; 8 supralabials to level below center of eye; ear opening 0.7 x 1.4 mm (length x height); mental distinctly wider than long, almost completely divided medially, bordered posteriorly by 8 postmentals (outer larger than inner); 7 infralabials to level below center of eye; sublabials undifferentiated; slightly keeled granular scales present on chin and throat; dewlap extending well onto chest, anterior insertion at level of posterior canthals, posterior insertion about 6.0 mm beyond level of axilla; dorsum of body with keeled granular scales, 2 medial rows of slightly enlarged scales, largest dorsal scales about 0.28 x 0.22 mm (length x width); about 54 medial dorsal scales in one head length; about 85 medial dorsal scales between axilla and groin; lateral scales keeled, granular and homogeneous, average size 0.15 mm in diameter; ventrals at midbody smooth, bulging, subimbricate, about 0.23 x 0.23 mm (length x width); about 54 ventral scales in one head length; about 94 ventral scales between axilla and groin; about 176 scales around midbody; caudal scales strongly keeled; caudal middorsal scales slightly enlarged, without whorls of enlarged scales; precloacal scales pointed and granular; postcloacal scales not enlarged; no tube-like axillary pocket present; scales on dorsal surface of forelimb slightly keeled, imbricate, about 0.25 x 0.27 mm (length x width); digital pads dilated, dilated pad about 2 times width of non-dilated scales on distal phalanx; distal phalanx narrower than and raised from dilated pad; 25 (right)–25 (left) lamellae under phalanges II–IV of fourth toe; 9 scales under distal phalanx of fourth toe.

The completely everted hemipenis is a small unilobed organ; sulcus spermaticus bordered by well developed sulcal lips and opens at base of apex into a concave field without ornamentation; a small asulcate process present; asulcal side of apex covered with fine calyces, truncus with transverse folds.

The extended dewlap in life has 6–7 horizontal gorgetal-sternal rows with 26–42 scales per row, rows somewhat irregular, some of them with pairs or triplets of scales, apical portion of dewlap between marginal pairs and last gorgetal-sternal row free of scales; modal number of anterior marginal pairs 4–5.

Coloration in life was recorded as follows: Dorsal ground color Dark Drab (119B) with a Pale Horn Color (92) broken longitudinal lateral stripe, edged diffusely by Mars Brown (223A) pigment; a Sepie (119) shoulder spot, edged posteriorly by a Yellow Ocher (123C) blotch; dorsum of head Dark Drab (119B) with a Hair Brown (119A) interorbital bar; dorsal surfaces of limbs Army Brown (219B) with indistinct Tawny Olive (223D) markings; tail Brick Red (132A) with indistinct Tawny Olive (223D) banding; tip of tail Tawny Olive (223D); ventral surfaces Glaucus (79); dewlap Orange Yellow (18), basal portion suffused with Raw Umber (23), gorgetals dirty white; iris Mars Brown (219A). Coloration after one year preservation in 70% ethanol agrees well with this description.

Variation. The paratypes agree well with the holotype in general appearance, morphometrics and scalation (see Table 1). We documented variation in relative hind leg length in this species. Of 66 specimens examined, the longest toe of the adpressed hind leg reached to mid-eye in 5 individuals (7.6%), to anterior margin of eye in 33 individuals (50.0%), and to a point between eye and snout in 28 individuals (42.4%). For variation in nasal region see Table 2 and Figure 1. For variation in dorsal pattern see Table 2 and Figure 2.

Etymology. The name *osa* is used as a noun in apposition and in reference to the Peninsula de Osa where the type series of the species was collected and where it is probably restricted.

TABLE 3. Selected measurements, proportions and scale characters of *Anolis polylepis* and *A. osa*. Range is followed by mean value and standard deviation in parentheses. For abbreviations see text.

		<i>A. polylepis</i>	<i>A. osa</i>
		♂ 47	♂ 22
		♀ 24	♀ 19
SVL	♂	42.2–59.4 (51.3 ± 3.76)	49.9–55.4 (50.2 ± 2.28)
	♀	39.6–53.5 (47.3 ± 3.52)	41.9–50.7 (46.4 ± 2.60)
Tail length	♂	80.1–117.0 (102.1 ± 10.28)	84.9–107.2 (97.3 ± 6.88)
	♀	70.0–101.5 (86.3 ± 8.29)	73.1–93.0 (82.0 ± 4.59)
HL	♂	10.8–14.4 (12.8 ± 0.88)	11.3–13.9 (12.4 ± 0.62)
	♀	10.1–13.7 (11.9 ± 0.78)	10.4–12.8 (11.5 ± 0.60)
HW	♂	6.7–8.5 (7.7 ± 0.48)	7.0–8.2 (7.5 ± 0.35)
	♀	6.3–8.5 (7.3 ± 0.56)	6.7–7.9 (7.1 ± 0.36)
Shank length	♂	11.6–16.0 (13.9 ± 1.12)	12.2–15.0 (13.6 ± 0.66)
	♀	10.5–14.0 (12.4 ± 0.98)	11.0–13.2 (12.3 ± 0.65)
Axilla–groin distance	♂	16.3–26.1 (21.2 ± 2.16)	18.5–24.4 (21.3 ± 1.32)
	♀	15.5–24.1 (19.87 ± 2.14)	17.8–29.4 (20.7 ± 2.60)
Tail length / SVL	♂	1.80–2.16 (2.00 ± 0.09)	1.74–2.06 (1.94 ± 0.10)
	♀	1.69–1.91 (1.82 ± 0.06)	1.68–1.87 (1.78 ± 0.06)
Tail diameter vertical / horizontal	♂	1.20–1.85 (1.46 ± 0.14)	1.26–1.69 (1.47 ± 0.16)
	♀	1.23–1.55 (1.36 ± 0.10)	1.20–1.46 (1.33 ± 0.08)
HL / SVL	♂	0.24–0.27 (0.25 ± 0.01)	0.23–0.26 (0.25 ± 0.01)
	♀	0.24–0.27 (0.25 ± 0.01)	0.24–0.26 (0.25 ± 0.01)
HL / HW	♂	1.55–1.80 (1.66 ± 0.06)	1.53–1.76 (1.65 ± 0.06)
	♀	1.52–1.77 (1.63 ± 0.06)	1.52–1.68 (1.61 ± 0.04)
Shank length / SVL	♂	0.25–0.30 (0.27 ± 0.01)	0.25–0.30 (0.27 ± 0.01)
	♀	0.23–0.28 (0.26 ± 0.01)	0.25–0.28 (0.26 ± 0.01)
Axilla–groin distance / SVL	♂	0.37–0.46 (0.41 ± 0.02)	0.38–0.46 (0.42 ± 0.02)
	♀	0.39–0.46 (0.42 ± 0.02)	0.40–0.60 (0.45 ± 0.04)
Subdigital lamellae of 4th toe		21–29 (24.66 ± 1.52)	22–28 (25.34 ± 1.71)
Number of scales between SS		1–5 (2.69 ± 0.83)	1–4 (2.85 ± 0.73)
Number of scales between IP and SS		2–7 (3.80 ± 1.03)	1–5 (3.98 ± 0.94)
Number of scales between SO and SPL		0–1 (0.75 ± 0.44)	0–1 (0.41 ± 0.50)
Number of SPL to level below center of eye		6–9 (7.17 ± 0.65)	7–9 (7.56 ± 0.59)
Number of INL to level below center of eye		5–9 (7.34 ± 0.81)	6–10 (7.66 ± 0.85)
Total number of loreals		37–92 (57.69 ± 11.38)	41–83 (56.78 ± 8.91)
Number of horizontal loreal scale rows		6–10 (8.06 ± 1.05)	6–10 (8.02 ± 0.88)
Number of postrostrals		7–11 (7.90 ± 0.87)	7–11 (8.12 ± 0.93)
Number of postmentals		6–9 (6.82 ± 0.96)	6–10 (7.00 ± 1.02)
Number of scales between nasals		7–11 (8.52 ± 1.19)	7–11 (8.59 ± 1.22)
Number of scales between 2nd canthals		7–16 (10.49 ± 1.66)	9–13 (10.63 ± 1.18)
Number of scales between posterior canthals		8–18 (12.20 ± 1.92)	9–16 (12.41 ± 1.43)
Number of medial dorsal scales in one head length		35–76 (53.10 ± 7.48)	44–68 (56.29 ± 6.67)
Number of medial ventral scales in one head length		36–62 (47.23 ± 5.97)	38–58 (46.83 ± 4.71)

Natural history notes. *Anolis osa* is an extremely common anole that reaches high population densities. At most sites on the Peninsula de Osa it was the most abundant species of anole. During daytime, most individuals were observed perching head down on the lower parts (30–120 cm above the ground) of trunks of small trees and other plants such as heliconias (Heliconiaceae) and banana plants (Musaceae). Males of *A. osa* are very territorial and will show aggressive display behavior whenever another adult male is placed in reaching distance (less than about 150 cm). The species was studied in detail by Andrews (1971, 1983), and Savage (2002) summarized much of the information provided by her.

Geographic distribution. As currently known, *Anolis osa* is restricted to the Peninsula de Osa, Costa Rica. It occurs both in protected areas (Corcovado National Park) and in disturbed areas such as at the type locality. The documented vertical range of the species is from sea level to about 550 m elevation.

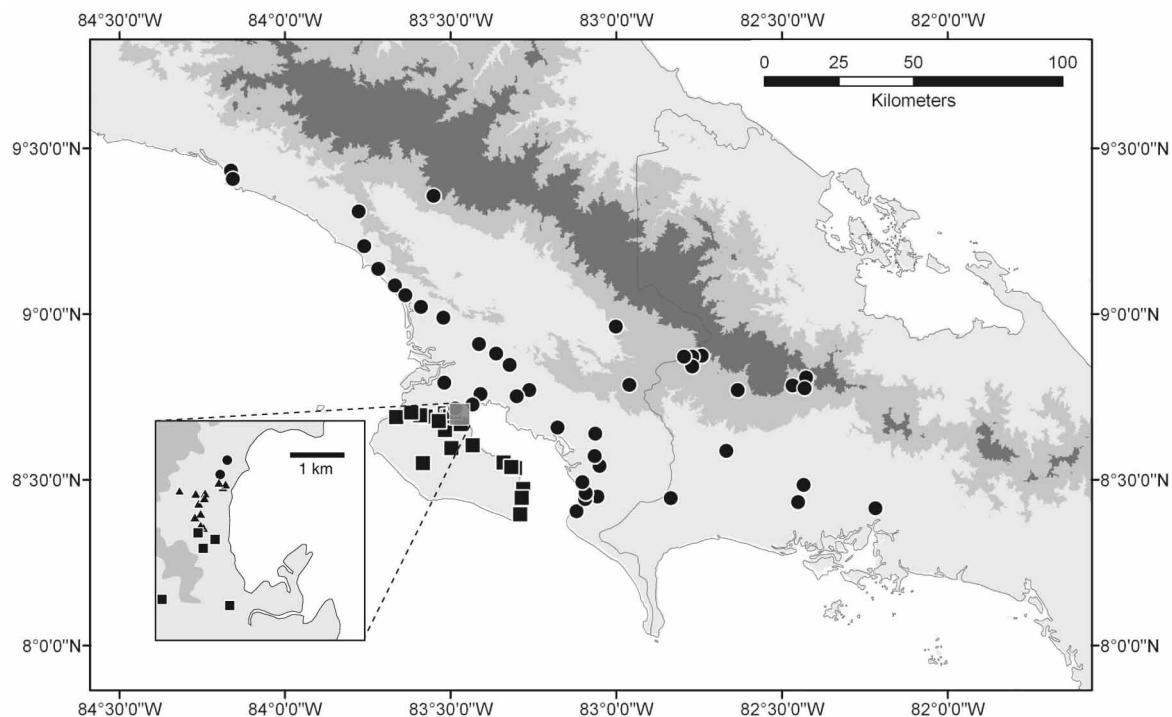


FIGURE 6. Map indicating known collecting sites mentioned in text of Central American anoles formerly referred to as *Anolis polylepis*. Each symbol can represent one or more nearby localities. Areas above 500 and 1000 m are shaded gray. Circles: Hemipenis Type A; squares: Hemipenis Type B. Insert: Map indicating the suspected hybrid zone. See text for details. Circles: Hemipenis Type A; squares: Hemipenis Type B; triangles: specimens with intermediate hemipenial morphology. Areas above 200 m are shaded gray.

Discussion

The distinctness of the differences in hemipenial morphology, the strict geographical correlation, the abrupt shift of this feature as well as its uniformity within the range of each morph, strongly support the assumption that the two forms represent different phylogenetic lineages, with different evolutionary histories. We therefore consider our proposed taxonomic consequences justified, not least to ensure future research work on these anoles takes these findings into account. The narrowness of the assumed hybridzone (Fig. 6 insert) indicates that gene flow between the two forms is reduced to some degree if present at all. However, in external morphology the two species are extremely similar and there is no morphometric or scalation character to differentiate between the two species. Our data indicate that even the male dewlap coloration and size are identical in the two species. Therefore, we assume a very recent split of these two species. We consider an allopatric speciation scenario to be the most plausible explanation in this case because of the geological history of the region. Climatic fluctuations during the Pleistocene resulted in sea level oscillations of at least 100 m in the Golfo Dulce region (Malzer 2001). As most of the neck of the Peninsula de Osa has a current elevation of less than 50 m above sea level and because it is assumed that this

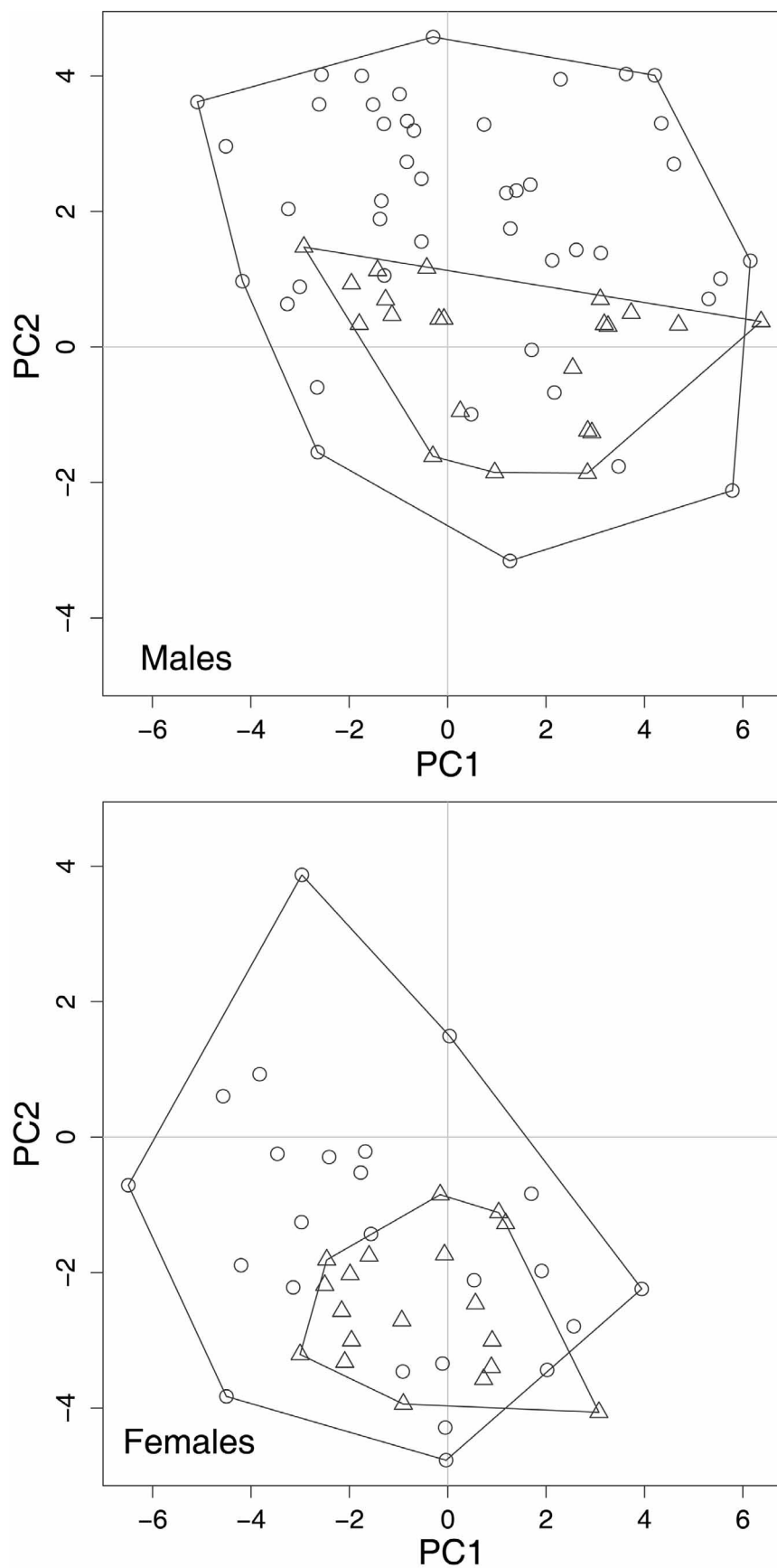


FIGURE 7. Principal component scatterplots (axes one and two) for males and females of the two hemipenial types of Central American anoles formerly referred to as *Anolis polylepis*. Open circles = Type A; open triangles = Type B. See text for details.

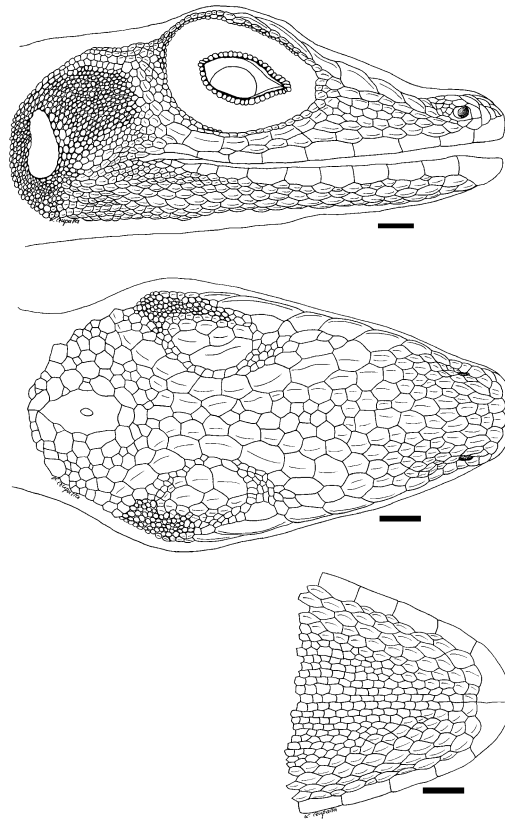


FIGURE 8. Head of *Anolis polylepis* (SMF 85206). Scale bars = 1.0 mm.

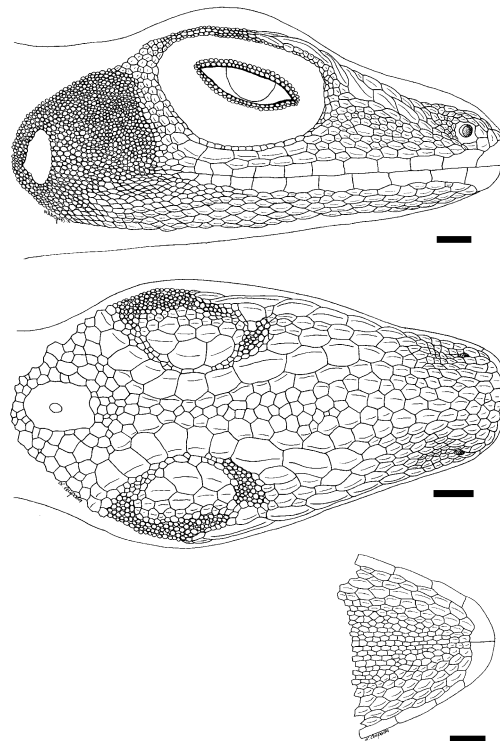


FIGURE 9. Head of *Anolis osa* (SMF 80645). Scale bars = 1.0 mm.



FIGURE 10. Adult male of *Anolis osa* (not collected) at Puerto Escondido in life with extended dewlap.



FIGURE 11. Adult female of *Anolis osa* (not collected) at Puerto Escondido in life.

peninsula has experienced elevational fluctuations of several hundred meters (Malzer 2001), it is likely that the Osa has been a real island or group of islands several times during the recent geological history. We therefore postulate that the ancestors of *A. osa* were *polylepis*-like populations in the Golfo Dulce region that became isolated from the mainland populations and, in the isolation of the Osa as an island, evolved independently from the *polylepis*-like populations on the mainland. This speciation process is evidenced by the obvious differences in hemipenial morphology. Preliminary molecular data provide evidence for a monophyletic Osa clade and therefore support this assumption (Köhler *et al.* submitted).

Acknowledgments

Collecting and exportation permits were provided by J. Guevara Sequeira, SINAC Central, Ministerio del Ambiente y Energía (MINAE), San José, Costa Rica; and by A. Salazar, Y. Hidalgo and J. García, Autoridad Nacional del Ambiente (ANAM), Panama City, Panama. We thank L. Czupalla for providing drawings used in this paper. We thank S. Lotzkot for sharing his original data with us. For the loan of or access to specimens we thank S. P. Rogers, Carnegie Museum of Natural History (CM), Pittsburgh; D. Rossman, Museum of Natural Science, Louisiana State University (LSUMZ), Baton Rouge; F. Bolaños, G. Chaves and A. García R., Museo de Zoología Universidad de Costa Rica (UCR), San José; R. W. McDiarmid and W. R. Heyer, National Museum of Natural History (USNM), Washington, D.C.; W. Böhme, Zoologisches Forschungsinstitut und Museum A. Koenig (ZFMK), Bonn; R. Günther, Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB), Berlin; and F. Glaw and D. Fuchs, Zoologische Staatssammlung München (ZSM), Munich.

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