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A new species of semiaquatic *Anolis*
(Squamata: Dactyloidae) from Oaxaca and Veracruz, Mexico

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We describe a new species of semiaquatic *Anolis* (*A. purpuronectes*) from the Chimalapas region of eastern Oaxaca and adjacent Veracruz, Mexico, and investigate its phylogenetic relationships with the closely related species *A. barkeri* to which the populations under investigation have previously been assigned to. *Anolis barkeri* and the new species appear to be allopatric, and differ primarily in male dewlap colour (red and orange in *A. barkeri*, pale purple in *A. purpuronectes*). A partitioned Bayesian analysis of the mitochondrial genes encoding ND1 (part), ND2, and the intervening tRNAs revealed that *A. barkeri* and *A. purpuronectes* are genetically distinct (uncorrected genetic distance between them=11.5%), nested within the *A. schiedii* group as sister species, and most closely related to a clade composed of *A. cymbops*, *A. milleri*, and *A. parvicirculatus*.

Key words: Anole, *Anolis barkeri*, *Anolis schiedii* group, Chimalapas, Mexico, new species, semiaquatic lizard

INTRODUCTION

The anoline fauna of Mexico is highly diverse. Recent descriptions largely from southern Mexico have increased the number of species to over 50 (including more than 30 endemics), despite several described species also having recently been shown to be junior synonyms (Köhler, 2012; Nieto-Montes de Oca et al., 2013; Köhler et al., 2014; Poe, 2014). Mexico thus harbours the world's third richest anoline fauna after Colombia (approximately 71 species) and Cuba (approximately 63 species). However, Mexico includes varied topography and diverse climatic regions (Ramamoorthy et al., 1998), suggesting that the anoline fauna is still underestimated and the number of species is likely to increase in the near future.

The semiaquatic *Anolis barkeri* is perhaps the most distinctive species of Mexican *Anolis*, and is found along clear, fast-moving streams and rivers in Veracruz, Oaxaca, Tabasco, and Chiapas; its ecology is fairly well studied (Brandon et al., 1966; Meyer, 1968; Birt et al., 2001). Like other semiaquatic anoles, *A. barkeri* escapes pursuers by diving and swimming (Robinson, 1962; Brandon et al., 1966; Meyer, 1968; Birt et al., 2001). This unusual ecology is paralleled by morphological traits such as nearly nonexistent toepads, a long narrow body, and a strongly compressed tail with two middorsal rows of scales.

The geographic distribution of *A. barkeri* is fragmented. The species was described from "Cascajal, upper Uzpanapa river, Vera Cruz, Mexico," although the holotype was "probably taken about 3 km from Cascajal in the Las Cuevas hills, which rise to about 150 m" (Meyer, 1968). Specimens referable to *A. barkeri* are known from isolated populations in the Los Tuxtlas region, southern Veracruz, and several scattered localities in southeastern Veracruz, western Tabasco, northwestern Chiapas, and the Chimalapas region in eastern Oaxaca (Meyer, 1968; Powell & Birt, 2001). The dewlap of male *A. barkeri* was described as large, with wide red areas crossed by 6–8 rows of small, orange scales (Meyer, 1968; Powell & Birt, 2001). No variation in this colouration or pattern has been reported. Herein, we present morphological (dewlap colouration) and molecular evidence to describe a new species from the Chimalapas region of Oaxaca and adjacent Veracruz. We adopt the evolutionary species concept (Simpson, 1961; Wiley, 1978) by identifying species based on consistent differences between populations. That is, we hypothesise that populations that are diagnosable by major differences in the frequencies of traits are distinct evolutionary lineages or species (see Wiens & Servedio, 2000).

METHODS

We compared a sample of the putative new species from the Chimalapas region of Oaxaca and adjacent Veracruz (*n*=12; populations with a purple dewlap) with samples of *A. barkeri* from approximately 7 km south of its type-locality in Veracruz, north-northwest Chiapas, and Los Tuxtlas, Veracruz (*n*=6, 5, and 1, respectively; populations with a red-orange dewlap). Measurements were made with digital calipers on preserved specimens and are given in millimeters (mm) to the nearest 0.1 mm. Snout-

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vent length (SVL) was measured from the tip of the snout to the anterior margin of the cloaca. Head length was measured from the tip of the snout to the anterior margin of the ear opening. Head width was measured at the broadest part of the head, between the posterolateral corners of the orbits. Femoral length was measured from the midline of the venter to the knee, with the limb bent at a 90-degree angle. Shank length was measured from the knee to the heel. When the condition of a given character in the holotype was not identical on both sides, the conditions on the left and right sides are given, in that order, separated by a slash (/). Scale terminology and characters follow Williams et al. (1995). Institutional abbreviations for museums and collections follow Sabaj-Pérez (2013). UOGV and POE are abbreviations for field numbers of uncatalogued specimens deposited in the MZFC.

Anolis barkeri was included in a phylogenetic analysis of the Mexican species groups of *Anolis* based on partial sequences of the mitochondrial gene encoding the first unit of the NADH dehydrogenase (ND1) and complete sequences of the gene encoding the second unit of the NADH dehydrogenase (ND2) and genes encoding the tRNAs that flank it (approximately 2541 base pairs in total; A. Nieto-Montes de Oca, unpublished data). This analysis included nearly all species of *Anolis* in Mexico and representatives of most of the series and species groups of *Norops* clade anoles in Savage & Guyer's (1989) infrageneric classification of the anoles. Preliminary analyses revealed that the new species is most similar to *A. barkeri*, which is most closely related to Mexican species of the *A. schiedii* species group. Thus, to investigate the phylogenetic relationships of the putative new species, we performed a phylogenetic analysis of the *schiedii* group based on the same mitochondrial fragment. We included one individual of the putative new species (from the Chimalapas region) and two individuals of *A. barkeri* (one from Las Choapas, Veracruz, and one from western Tabasco). A total of 14 species from Mexico and Guatemala and three from Honduras have been placed in the *Anolis schiedii* group by different authors: *Anolis alvarezdeltoroi*, *A. breedlovei* (=*A. cuprinus*), *A. campbelli*, *A. cobanensis*, *A. cymbops*, *A. duellmani*, *A. hobartsmithi*, *A. johnmeyeri*, *A. matudai*, *A. milleri*, *A. naufragus*, *A. parvicirculatus*, *A. pijolense*, *A. polyrhachis* (=*A. rubiginosus*), *A. pygmaeus*, *A. purpurgularis*, and *A. schiedii* (Lieb, 1981; Savage & Guyer, 1989; Lieb, 2001; Nieto-Montes de Oca, 2001; Nicholson, 2002; Köhler & Smith, 2008). However, because the preliminary analysis showed that the Honduran species (*A. johnmeyeri*, *A. pijolense* and *A. purpurgularis*) are distantly related to other species in the group, we excluded them from the current analysis. We used representatives of several other species groups (*A. crassulus*, *A. gadovii*, *A. laeviventris*, *A. lemurinus* and *A. uniformis*) as outgroups, and *A. sagrei* to root the tree. Locality data for the vouchers and GenBank accession numbers for the sequences are given in Online Appendix 1. We verified the identity of all of the vouchers.

We extracted genomic DNA from liver or muscle tissue with the use of the standard phenol-chloroform method (Hillis et al., 1996) and utilised polymerase chain reaction (PCR) to amplify the aforementioned fragment with the primers from Macey et al. (1999). PCR cycle parameters were an initial denaturation cycle at 94° C for 5 min followed by 38 cycles of denaturation at 94° C for 30 s, primer annealing at 45–50° C for 30 s, and extension at 72° C for 1 min, and a final extension cycle at 72° C for 5 min. We purified PCR products with polyethylene glycol precipitation (Lis, 1980). Purified DNA templates were sequenced with the BigDye Terminator v.3.1 cycle sequencing kit (Applied Biosystems, Inc.) and an automated DNA sequencer (ABI 3100 Genetic Analyzer Sequencer, Applied Biosystems, Inc.)

We aligned the sequences visually in Mesquite v.3.01 (Maddison & Maddison, 2014) and generated a mtDNA phylogeny using MrBayes v.3.2 (Ronquist et al., 2012). We used jModeltest v.2.1.4. (Darriba et al., 2014) to obtain the best fitting evolutionary models for four partitions of the data set (one for each codon position and one for the combined tRNAs) using the Bayesian information criterion. The best fitting models for the first, second, and third codon position partitions were HKY+Γ+I, TIM1+Γ+I, and GTR+Γ+I, respectively; the best fitting model for the combined tRNAs partition was TPM1uf+Γ. Analyses in MrBayes consisted of two runs (nruns=2) conducted with the default settings and sampling every 5000 generations for 50,000,000 generations. We used TRACER v.1.6 (Rambaut et al. 2014) to ascertain convergence and stationarity. We conservatively discarded the trees from the first 25% of generations from both runs as burn-in. A 50% majority-rule consensus tree was computed from the sampled trees of the estimated posterior distribution and edited in TreeGraph v.2.0 (Stöver & Müller, 2010). We considered clades with posterior probabilities (Pp) > 0.95 as significantly supported (Alfaro et al., 2003; Huelsenbeck & Rannala, 2004; but see the caveat in Brandley et al. 2005). In addition, we performed a maximum likelihood analysis with RAxML v.8.1 (Stamatakis, 2014) under the GTRGAMMA model. To evaluate nodal support, we conducted a nonparametric bootstrap with 1000 replicates. We considered clades with bootstrap values ≥ 70 as significantly supported (Hillis & Bull, 1993). We performed the Bayesian and maximum likelihood analyses through the CIPRES Science Gateway v.3.1 (Miller et al., 2010).

RESULTS

There were no evident differences among the compared samples of the putative new species and *A. barkeri* in the compared morphometric and scalation characters. However, the sample from the Chimalapas region had on average more scale rows between the supraocular semicircles than the other samples (1–4, x=2.5, n=12; versus 0–2, x=1.2, n=12 in *A. barkeri*; Table 1). Meyer (1968) found a similar trend. Also, the dewlap in male *A. barkeri* from the Chimalapas region was clearly different in colouration and pattern from the dewlap in males from the other populations (Fig. 3).

In the Bayesian consensus tree (Fig. 1), the *A. schiedii* group (exclusive of *A. johnmeyeri*, *A. pijolense*, and *A.*

purpurgularis, see above) was monophyletic, and *A. cobanensis* was the sister taxon to all of the other species in the group. However, relationships among the latter species were not fully resolved; instead, *A. alvarezdeltoroi*, *A. campbelli*, *A. hobartsmithi*, and two small groups of species formed a pentatomy. In one of these groups, the clade (*A. cuprinus* + *A. matudai*) was sister to the clade ((*A. rubiginosus*) + (*A. naufragus* + *A. schiedii*)). In the other group, the haplotype of *A. barkeri* from the Chimalapas region was sister to the other haplotypes of *A. barkeri*; the clade with these three haplotypes was sister to the clade ((*A. cymbops* + (*A. milleri* + *A. parvicirculatus*)), and the clade (*A. duellmani* + *A. pygmaeus*) was sister to the former two clades. All of these groupings were significantly supported, except for the group composed of the clades (*A. cuprinus* + *A. matudai*) and ((*A. rubiginosus*) + (*A. naufragus* + *A. schiedii*)). The maximum likelihood tree (not shown) was essentially similar to the Bayesian tree except in some poorly supported nodes. The uncorrected genetic distance (*p*) between the haplotype of *A. barkeri* from the Chimalapas region and the haplotypes from other localities was moderately

Table 1. Variation in selected characters in *Anolis barkeri* and *A. purpuronectes*. For each character, the range in parentheses follows the average. Morphometric characters were recorded only in specimens with SVL>65.0 mm. [1]Sample size unless noted otherwise.

Character / Species	Anolis barkeri	Anolis purpuronectes
Scalation	$n=12^1$ (8 m, 4 f)	$n=12^1$ (6 m, 6 f)
No. of postrostrals	7.2 (6–8)	7.7 (6–9), $n=10$
No. of scales between nostril and rostral	2.2 (2–3)	2.0 (2–2)
No. of scales across snout between 2nd canthals	8.6 (7–11)	9.8 (9–12)
No. of scale rows between supraorbital semicircles	1.2 (0–2): 0, 1; 1, 8; 2, 3	2.5 (1–4): 1, 1; 2, 5; 3, 5; 4, 1
No. of scales between interparietal and supraorbital semicircle	3.5 (2–5)	4.1 (3–5)
No. of loreal rows	7.0 (6–8)	8.1 (7–9)
Supralabial-suborbital rows contact	Usually separated by one scale row (2+ supralabials contacting suboculars in 4 specimens)	Usually separated by one scale row (2 supralabials contacting suborbitals in 2 specimens)
No. of supralabials	9.7 (8.5–11.0)	9.5 (9–10); $n=11$
No. of postmentals	5.6 (4–6)	4.8 (4–6)
No. of middorsal scales between levels of axilla and groin	85.9 (75–96)	84.6 (73–96)
No. of middorsal scales in 5% SVL	8.8 (8–10.5)	9.4 (8–11)
No. of midventral scales in 5% SVL	8.8 (7–11)	9.2 (7–13)
No. of gorgetal-sternal scale rows	7.9 (7–9), $n=7$	9.8 (7–14), $n=5$
No. of subdigital lamellae on phalanges II and III of 4th toe	15.6 (14–19)	16.5 (15–18)
Morphometric (SVL > 69 mm)	$n=9$ (7 m, 2 f)	$n=10$ (6 m, 4 f)
SVL	70.8–93.5 mm	69.5–91.7 mm
Axilla-groin / SVL	0.46 (0.44–0.50)	0.43 (0.39–0.47)
Head length / SVL	0.23 (0.22–0.24)	0.24 (0.23–0.25)
Interparietal length / head length	0.10 (0.08–0.12)	0.07 (0.05–0.12)
Ear height / head length	0.13 (0.11–0.16)	0.12 (0.10–0.15)
Interparietal length / ear height	0.77 (0.61–1.06)	0.60 (0.41–0.84)
Femoral length / SVL	0.29 (0.27–0.31)	0.30 (0.29–0.32)
Shank length / Head length	1.01 (0.96–1.05)	0.96 (0.84–1.04)
Shank length / SVL	0.23 (0.23–0.24)	0.23 (0.21–0.25)
Fourth toe length / SVL	0.17 (0.14–0.19)	0.17 (0.16–0.19)

Fig. 1. Bayesian phylogenetic hypothesis of the relationships of *Anolis barkeri* and *A. purpuronectes*. Numbers above the branches are posterior probability values. Numbers below the branches are bootstrap values from the RAxML analysis.

high (11.5%), with higher distances between the former haplotype and the haplotypes of *A. cymbops*, *A. milleri*, and *A. parvicirculatus* (17.6–17.8%). On the basis of its distinctive dewlap and genetic divergence, we consider the population previously assigned to *A. barkeri* from the Chimalapas region to actually represent an undescribed species distinct from *A. barkeri*, and describe it below.

Systematic Account
Anolis purpuronectes new species
(Figs. 2, 3, 4; Table 1)
Anolis barkeri. Meyer, 1968 (in part); Powell & Birt, 2001 (in part).

Holotype.—MZFC 28961 (field number POE 4362), a male from approximately 1.6 km N of Chalchijapa, municipality of Santa María Chimalapa, Oaxaca, Mexico, 17.04377° N, 94.66586° W, 268 m in elevation, collected on 18 November 2012 by Steven Poe, Donald Mahler, and Julián Velasco.

Paratypes.—Eleven specimens, all from Mexico: nine from Oaxaca, municipality of Santa María Chimalapa: four from the same locality as the holotype (MSB 94840, 94844, 94848, 94851); one from Campamento piloto Chalchijapa, 17.07694° N, 94.59917° W, 575 m (MZFC 18811), three from 1–2 km S Campamento piloto Chalchijapa, 304–335 m (MZFC 18807, 18814–15), one from 3 km SW Chalchijapa, 17.05417° N, 94.65389° W, 280 m (MZFC 18809); and two from municipality of Uxpanapa, Veracruz: one from Ejido Pancho Villa, 17.21872° N, 94.55581° W, 163 m (MZFC 28962), and one from approximately 9 km SE Ejido La Laguna, 17.17981° N, 94.58217° W, 165 m (MZFC 28963).

Referred specimens.—Thirteen, all from Oaxaca, municipality of Santa María Chimalapa: four from 2–3 km S Campamento Piloto Chalchijapa (see above), 457–670 m (MZFC 18800–18802, 18813); two from 1–2 km S Campamento Piloto Chalchijapa, 335 m (MZFC 18815–18816); four from Chalchijapa, 17.05417° N, 94.65389°
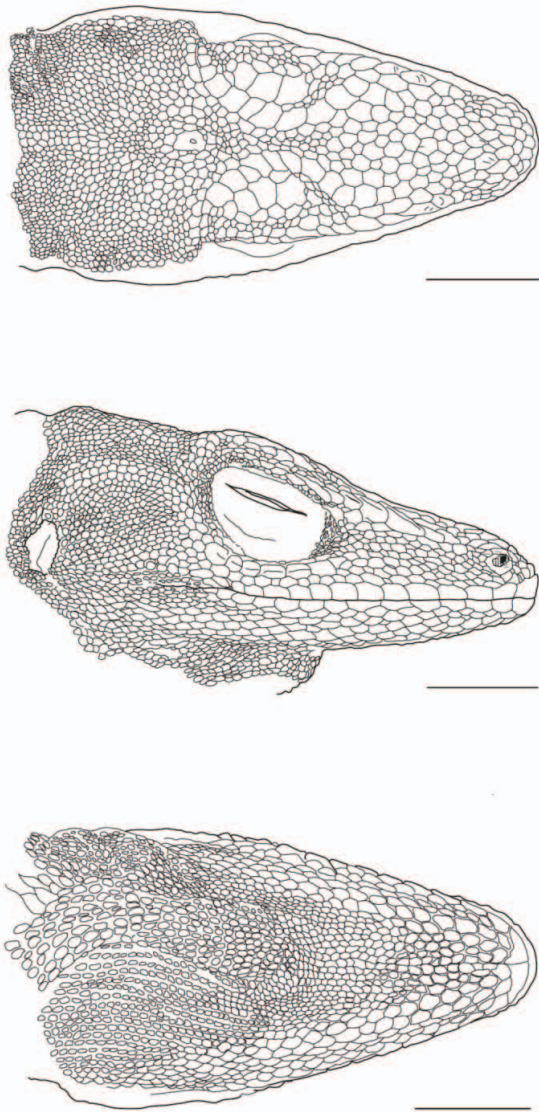
Fig. 2. Head scales of *Anolis purpuronectes* in (top) dorsal view; (middle) lateral view; and (bottom) ventral view. Scale bars represent 5 mm.

W, 304–396 m (MZFC 18803–18806); one from 3 km NE Chalchijapa, 219 m (MZFC 18799), and two from 2–3 km SW Chalchijapa, 235–280 m (MZFC 18808, 18810). In addition, four specimens also are tentatively referred to *Anolis purpuronectes*: one from 2 km SW San Isidro La Gringa, 17.09397° N, 94.12375° W, 185 m (MZFC 18817), two from 1–3 km S San Isidro La Gringa, 17.09583° N, 94.12° W, 182 m (MZFC 18798, 18812), and one from Cerro Azul, La Gloria, municipality of Loma Bonita, Oaxaca, 16.8372° N, 94.6887° W (MCZ 58221).

Diagnosis.— *Anolis purpuronectes* and *A. barkeri* are the only Mexican *Anolis* with semiaquatic ecology. They also are the only species in Mexico with two middorsal rows of caudal scales and narrow, indistinct toepads. *Anolis purpuronectes* overlaps *A. barkeri* in most scale characters (Table 1), but displays a starkly different male dewlap colour (purple versus a complex red, orange, and white dewlap in *A. barkeri*; Fig. 3). Meyer (1968) found that *A. barkeri* from La Gloria, Oaxaca (=*A. purpuronectes*) and Los Tuxtlas region, Veracruz, lacked a light lateral stripe

70%–79% of the time, whereas samples of *A. barkeri* from Mal Paso and Pichucalco, Chiapas, had at least a faint or incomplete stripe in all instances.

Comparisons.— *Anolis purpuronectes* is unlikely to be confused with any other species besides *A. barkeri* because of its semiaquatic ecology, large body size (maximum SVL 90 mm) and distinctive scalation (Table 1). It differs from other large (> 85 mm maximum SVL) Mexican species in its two middorsal caudal scale rows, purple dewlap, and narrow, indistinct toepads. In addition, among large Mexican species, *A. biporcatus* is usually solid green dorsally (lacking the patterning and light lateral stripe of *A. purpuronectes*) and has a shorter, stockier body than *A. purpuronectes*; *A. capito* has an extremely short head and similar-sized dewlaps in males and females (long head and large male, very small female dewlap in *A. purpuronectes*); *A. macrinii* is usually solid green or olive brown dorsally (lacking the patterning and light lateral stripe of *A. purpuronectes*) with a moderate dewlap in females (very small or absent dewlap in females of *A. purpuronectes*); *A. petersi* is stockier and has a much smaller male dewlap (barely extending past the axillae) than *A. purpuronectes* (male dewlap extends to mid-chest; Fig. 3), and a moderate female dewlap (very small or absent dewlap in females of *A. purpuronectes*); and *A. serranoi* has a shorter body and longer limbs (toe of adpressed hindlimb usually extends past eye in *A. serranoi;* usually between ear and eye in *A. purpuronectes*), and displays fewer supralabials from the rostral to the center of the eye (6–8 in *A. serranoi*; 9–11 in *A. purpuronectes*).

Description of holotype.— (Paratype variation listed in Table 1)**.**—Medium-sized adult male (SVL 89.6 mm) with moderately large, elongate head (head length 24.9% of SVL), long trunk (axilla-groin length 43.9% of SVL), moderately long limbs and tail (shank nearly as long as head, 23.9% of SVL; femoral length 31.9% of SVL; tail length 1.75 times SVL), and large dewlap (posterior limit at posterior end of chest).

Head length 22.3 mm, head width 12.6 mm, snout length 9.8 mm; scales on dorsal surface of head flat, except scales of supraorbital semicircles anterior to level of mid-orbit barely elevated; dorsal head scales mostly smooth, except scales on internasal region and sides of snout with short, blunt, weak keels and most enlarged scales on supraocular region weakly striate; eight postrostrals between first supralabials; nasal separated by two small scales from rostral on left side (scales apparently fused into single large scale on right side), separated from supralabials by one small scale row on each side; nine scales between nasals and 10 scales across snout between second canthals; shallow frontal depression; supraorbital semicircles well developed, separated from each other at level of mid-orbit by three rows of small scales (rows combined width slightly less than that of semicircle scales), broadly in contact with enlarged supraoculars (single row of small circumorbitals anterior to level of mid-orbit on left side; absent on right side); supraocular disk composed of one medial longitudinal
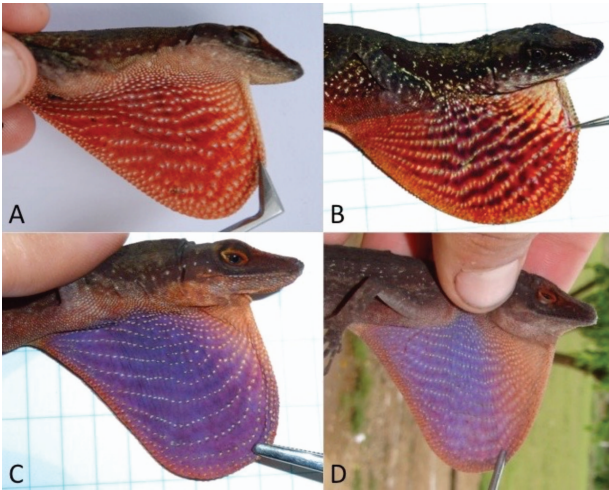
Fig. 3. Dewlaps of adult males. (A) *Anolis barkeri* from Ejido Piedritas, municipality of Las Choapas, Veracruz (~ 7 km S type-locality). (B) *A. barkeri* from near Ixhuatán, Chiapas (POE 4214). (C) *A. purpuronectes* (holotype) from near Chalchijapa, Oaxaca (MZFC 28961). (D) *A. purpuronectes* from ~ 9 km SE Ejido La Laguna, municipality of Uxpanapa, Veracruz (UOGV 1927).

row of 3/4 conspicuously enlarged supraoculars and one adjacent lateral row of 3/4 mid-sized scales on each side, with scales in lateral row separated from superciliaries by 2–3 granular scale rows at level of mid-orbit; 6/7 small superciliary scales extending posteriorly to about three-fourths length of orbit, followed by granular scales to posterior of orbit; first four superciliaries slightly imbricate, not elongate except for third one, with remaining scales in row juxtaposed; parietal area slightly depressed; interparietal small, maximum width 1.0 mm, maximum length 1.5 mm, about 2–3 times as long as adjacent parietals, distinctly shorter than ear height (=2.5 mm); pineal eye small; minimum count of 5/4 scale rows between interparietal and supraorbital semicircles; parietals barely larger than upper temporals and nape scales, abruptly merging with them before reaching parietal crests.

Canthus rostralis sharp, straight, moderately inclined, composed of 5/4 enlarged, imbricate canthals, with anteriormost one separated from nasal by 3/4 small scales; nasal large, squarish; scales in front of nasal small, undifferentiated (anterior nasal not differentiated); 7/7 rows of smooth loreals from second canthal to supralabials; 7/7 enlarged, keeled scales in preocular/subocular series abruptly differentiated from much smaller, smooth scales bordering orbit anteriorly and posteriorly; subocular and supralabial scale rows separated by one row of small, bluntly keeled lorilabials; 10/10 supralabials from rostral to centre of eye; external ear opening vertically oval, small (height 3.0/2.5 mm, about 11.0% of head length).

Mental about twice as wide as long, partially divided medially; 11/11 infralabials from mental to level of mid-eye; four postmentals; no enlarged sublabial series; about four rows of lateral gulars slightly larger than central gulars.

Dewlap large (posterior limit located at about end of chest); 10 scale rows of single scales across anterior margin of dewlap; about 10 gorgetal-sternal rows; about 26 scales (average) in middle gorgetal-sternal rows; about 101 transverse scale rows along dewlap margin.

Axilla to groin length 39.4 mm; dorsals small, those in about four medial rows slightly enlarged (approximately 90 scales along midline between levels of axilla and groin; nine in 5% SVL), keeled, slightly imbricate, gradually decreasing in size laterally, becoming juxtaposed, bluntly keeled on sides of dorsum and smooth, granular on flanks; lateral scales homogeneous in size; ventral scales small (approximately 80 slightly oblique scale rows between levels of axilla and groin; about 9 in 5% SVL), flat, bluntly keeled, imbricate; no enlarged postcloacal scales.

Axillary pocket present, but shallow; tail long (157.0 mm), markedly compressed vertically in cross section (width 4.1 mm, height 8.0 mm at distance equal to one head length from cloaca); caudal scales keeled, imbricate; those along midline in double middorsal row, slightly larger than scales on sides, otherwise undifferentiated; whorls of enlarged caudal scales absent; suprabrachials, pre- and supra-antebrachials, pre- and suprafemorals, and supratibials small, flat, slightly imbricate, unicarinate; shank and femoral length 21.4 mm and 28.6 mm, respectively; shank as long as distance from tip of snout to point 0.7 mm before ear; length of fourth toe 15.3 mm; subdigital scales under phalanges II–III (to distal end of toe pad) and II–IV (from base of digit to distal end of toe pad) 16 and 23, respectively; 15 non-dilated scales under terminal phalanx of fourth toe; maximum width of toe pad of fourth toe more than twice that of non-dilated scales of distal phalanx (width 1.8 mm and 0.8 mm, respectively).

Colouration in life. — Background colour usually brown to purplish brown, sometimes speckled with small white or bluish markings on flanks. Sometimes a pale stripe is present, running along the flanks from near the ear opening to the hindlimb. Males often more brightly coloured than females (Fig. 4), with a red-orange tint, especially on the ventral portion of the flanks. Females are more drab, lacking the bright red-orange highlighting and with scattered pale markings over a generally brown

Fig. 4. Holotype of *Anolis purpuronectes* (MZFC 28961). Photograph by Donald Mahler.

background. The male dewlap is purple, with the darkest colouration at the base, becoming paler toward the margins (Fig. 3). The anterior base of the dewlap tends to be a cream or peach colour.

Distribution.— Because *Anolis barkeri* and *A. purpuronectes* differ externally from each other only in male dewlap colour and pattern and these attributes are lost in preserved specimens, the assignment of preserved specimens to one of these species or the other is difficult. *Anolis purpuronectes* is definitively found in the western portion of the Chimalapas region in extreme northeastern Oaxaca and adjacent southeastern Veracruz (Fig. 5). However, the distributional boundaries of the new species are unclear, as much of the Chimalapas region has not been intensely surveyed for herpetofauna. Nonetheless, because all of the known localities for *A. barkeri* are located north and east of the Chimalapas region in Veracruz, Tabasco, and Chiapas, we consider that Meyer's (1968) records of *A. barkeri* from Oaxaca actually represent *A. purpuronectes*, given that they lie south of the holotype locality in the Chimalapas region. Meyer's (1968) records correspond to specimens collected by Thomas MacDougall along two streams: Río Grande, a tributary of Río Chicapa (the only specimens known from the Pacific versant), and Río Negro, a stream west of Santa María Chimalapa. Similarly, we tentatively consider specimens from the San Isidro La Gringa area in the northeastern end of the Chimalapas region to represent *A. purpuronectes*. The Chimalapas share some

biogeographical affinities with the El Ocote region of northwestern Chiapas (pers. obs.), but semiaquatic anoles from near El Ocote appear to be the more widespread *A. barkeri*. Currently, the closest record of *A. barkeri* to our northernmost locality for *A. purpuronectes* (Ejido Pancho Villa, municipality of Uxpanapa, Veracruz; 17.21872° N, 94.55581° W) is that of Ejido Piedritas, municipality of Las Choapas, Veracruz; 17.55059° N, 94.13995° W (about 7 km south from the type-locality of *A. barkeri*), which lies about 57.4 km (airline) to the northeast.

Etymology.— The specific epithet *purpuronectes*, a noun in apposition, is a combination of the Latin adjective *purpureus* (purple) and the Greek noun *nektes* (a swimmer).

Ecology and habitat.— All of the specimens of *A. purpuronectes* at the type locality were collected sleeping on low vegetation (up to 0.8 metres) within one metre of a stream. In the vicinity of Chalchijapa, 17 specimens were collected in or near streams in tropical rainforest (15) or secondary vegetation/crops (2) at 185–670 m elevation between 1015 and 1600 hours; eight were collected on boulders or logs in or along streams, and seven were collected on boulders, logs, or wet leaf litter or within boulder crevices near small waterfalls.

The type locality is a corridor of closed-canopy forest surrounded by highly disturbed areas. A clear stream approximately two to five metres wide traverses the area. This stream includes small waterfalls and is
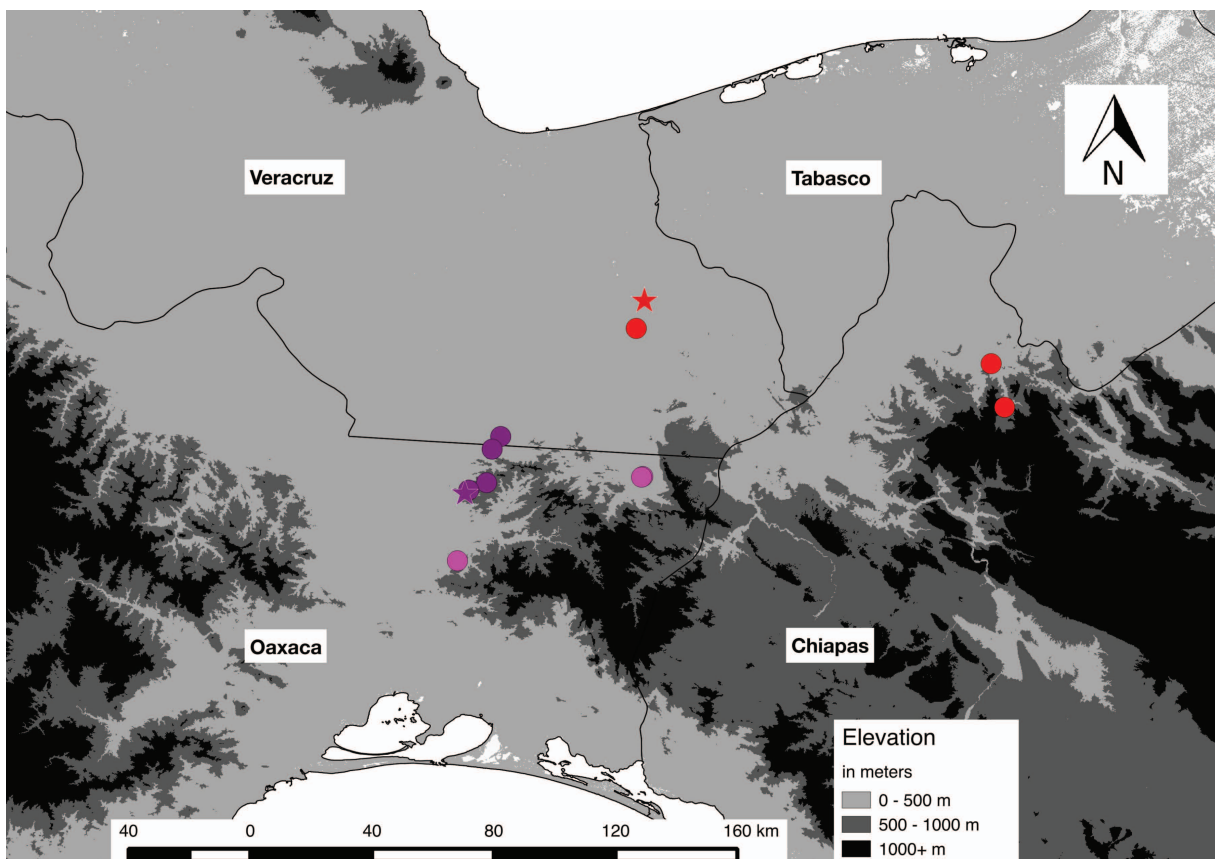

Fig. 5. Sampled localities of *Anolis purpuronectes* and *A. barkeri*. Purple circles represent *A. purpuronectes*, pink circles represent presumed *A. purpuronectes*, and red circles represent *A. barkeri*. Stars represent type localities.

interrupted by some boulders and tree fall. Meyer (1968: 90) stated that MacDougall collected his specimens in Oaxaca at elevations of 400–500 m in "high rainforest," and that the lizards were taken as they moved about on boulders in the streams, and also that MacDougall saw *A. purpuronectes* at a ranch at about 350 m on the Río Chicapa, where the vegetation was "sub-deciduous, with dry country evergreen oaks and pine."

Little is known of the ecology of *A. purpuronectes*, although we assume similarities with *A. barkeri* based on collection of the new form only along streams. Although considered semiaquatic, *A. barkeri* does not appear to spend a large portion of its time swimming (Birt et al., 2001). Individuals are almost always found within a metre of a flowing stream (Robinson, 1962). Prey items for *A. barkeri* include a variety of terrestrial insects the lizards encounter on their perches (Robinson, 1962; Brandon et al., 1966). Near Ixhuatán, Chiapas, we found *A. barkeri* sleeping primarily on boulders, though overhanging vegetation was also used. Individuals in populations where rocks are uncommon were recorded to be sleeping on "low vegetation at the water's edge" (Meyer, 1968).

DISCUSSION

Although *A. purpuronectes* and *A. barkeri* are similar in most aspects of external morphology and ecology, they exhibit clearly different male dewlaps (Fig. 3) that are relatively invariant within populations. In addition, *A. purpuronectes* and *A. barkeri* appear to be allopatric and are considerably divergent genetically from each other (Fig. 1). Thus, recognition of *A. purpuronectes* as an evolutionary species distinct from *A. barkeri* is warranted.

Meyer (1968) placed *Anolis barkeri* in the beta section (=*Norops* clade) and *fuscoauratus* species series of *Anolis*. Later, Savage & Guyer (1986) and Nicholson (2002) listed *A. barkeri* as a *Norops* of uncertain status, and Poe (2004) found *A. barkeri* to group with *A. aquaticus* and *A. loveridgei* based on morphological data. Most recently, Nicholson et al. (2012) placed *A. barkeri* in the *N. auratus* species group. According to Nicholson et al. (2012), *A. barkeri* is placed in a polytomy along with beta anoles from several different species groups. Herein, we present the first molecular data for *A. barkeri* and show that both *A. barkeri* and *A. purpuronectes* are nested within the *A. schiedii* group, and are most closely related to a subgroup composed of *A. cymbops*, *A. milleri*, and *A. parvicirculatus*. These three species occur on low to intermediate elevations on the slopes of the mountain ranges along the Atlantic versant of Mexico west and east of the Isthmus of Tehuantepec (from central Veracruz to western Chiapas). Notably, most species in the *A. schiedii* group have a dewlap that is some shade of purple.

Anolis barkeri is listed as an endemic species subject to special protection in the NORMA Oficial Mexicana NOM-059-SEMARNAT-2010 (SEMARNAT, 2010). *Anolis purpuronectes* also is endemic of Mexico and has a more restricted distribution than *A. barkeri*. However, like *A. barkeri*, it appears highly abundant in suitable habitat along streams. Therefore, we stress the importance of maintaining streamside habitat for the conservation of these species.

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APPENDIX

Material Examined.

Anolis barkeri: MEXICO: <u>Chiapas</u>: Municipality of Ixhuatán, river approximately 2 km N of Ixhuatán, 17.30852° N, 93.00987° W (MSB 94834, 94835, 94838, 94843, 94847, POE 4214, 4219–4222); Municipality of Rayón, Rayón-Teapa Rd, 17.44233° N, 93.05101° W (POE 4229–31); Municipality of Solusuchiapa, 32 mi. S Solusuchiapa (MCZ 85008); <u>Veracruz</u>: Municipality of Las Choapas, Ejido Piedritas, 17.55059° N, 94.13995° W, 70 m (UOGV 2649–58; 2660–61); Municipality of Catemaco, Los Tuxtlas, 2.5 mi NW Sontecomapan (MCZ 92103), Los Tuxtlas, Santa Martha (MZFC 4680).