

Atheris subocularis (Serpentes: Viperidae) Revisited: Molecular and Morphological Evidence for the Resurrection of an Enigmatic Taxon

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Recent reptile collections from southwestern Cameroon contain four specimens referable to *Atheris subocularis* Fischer, currently considered a synonym of *Atheris squamigera* (Hallowell), and previously known only from the holotype collected prior to 1888. Phylogenetic analysis of a 647 bp DNA fragment of the mitochondrial cytochrome *b* gene indicates that *A. subocularis* forms a monophyletic group. Based on this analysis and a suite of morphological characters that readily differentiate *A. subocularis* from its congeners, we resurrect *A. subocularis* Fischer from the synonymy of *A. squamigera* (Hallowell). Female *A. subocularis* remain unknown, and the distribution of this taxon lies completely within that of its closest relative, *A. squamigera*. We provide taxonomic accounts for *A. subocularis* and *A. squamigera* in the area of sympatry and discuss evolutionary hypotheses for the presence of *A. subocularis*.

AMONG his descriptions of new taxa, Fischer (1888) erected *Atheris subocularis* based on a single specimen from an unspecified locality in Cameroon. After examining the type in the British Museum, Boulenger (1896) included *A. subocularis* in his synonymy of *Atheris squamigera* (Hallowell, 1856) without comment. A recent review of the genus by Broadley (1998) and a new checklist (McDiarmid et al., 1999) perpetuate Boulenger's arrangement. Fischer based the description of *A. subocularis* on a number of scale count and arrangement characters, most notably that of the fourth supralabial entering the orbit. Supralabial-orbit contact does not obtain in any other members of the genus with the exception of a single, apparently aberrant specimen of *A. squamigera* from the Ituri (Boulenger, 1919; Broadley, 1998). Known only from the type specimen, *A. subocularis* received little or no attention in the 103 intervening years between Boulenger and Broadley.

Recent collections from southwestern Cameroon near the presumed type locality of *A. subocularis* (see Discussion) contain four specimens agreeing with Fischer's description of *A. subocularis* in having one or more supralabials entering the orbit. Like the holotype of *A. subocularis*, the new specimens are all males. In addition to the supralabial arrangement, specimens referable to *A. subocularis* differ markedly from sympatric male and female *A. squamigera* in characters of scalation, morphology, and color pattern. Boulenger's Ituri specimen of *A. squamigera* in which the supralabial entered the orbit apparently differs from other *A. squamigera* only in supralabial-orbit contact (vide Broadley, 1998). Based on this new, readily diagnosable

material and tissue samples from sympatric Cameroon *A. squamigera*, five other *Atheris* taxa, and *Proatheris* and *Bitis* outgroups, we reexamine the taxonomic validity and biology of *A. subocularis*.

MATERIALS AND METHODS

Morphological characters follow recent treatments of the genus by Broadley (1998), Lawson (1999), and Lawson and Ustach (2000). Features of scalation were examined under a dissecting microscope. Scale terminology generally follows Klauber (1956). Suprarostrals and interorbitals are used in keeping with Broadley (1998). Interrictal counts refer to scales across the back of the head between the posterior supralabials. Anterior dorsal scale rows were counted approximately one head-length posterior to the head. Posterior dorsal scale rows were counted approximately one head-length anterior to the vent. Color descriptions in preservative and life are based on a published standard (Smithe, 1975). Snout-vent length (SVL) and tail length (TL) were measured to the nearest millimeter using a meter stick. Other standard measurements were taken to the nearest 0.1 mm using a dial caliper held under a dissecting microscope. Measurements are abbreviated head length, HL; head width, HW. Sex of specimens was determined by direct observation of hemepenes and by probing or dissection.

We extracted DNA from frozen tissues (liver) or shed skins of two specimens referable to *A. subocularis*, seven species of *Atheris* including five specimens referable to *A. squamigera* taken with the *A. subocularis* material, and the outgroup

taxa *Proatheris superciliaris*, *Bitis gabonica*, and *B. nasicornis*. We used the proteinase K digestion, phenol-chloroform/chloroform extraction, and ethanol-NaCl precipitation methods described by Hillis et al. (1996). An approximately 647-base pair fragment at the 5' end of the mitochondrial cytochrome *b* gene was amplified by polymerase chain reaction (PCR) using the primers Gludg (5' TGA CTT GAA RAA CCA YCG TTG 3'; Palumbi, 1996), and ATRCB3 (5' TAG AAG TTT TCY GGG TCR TT 3'; P. Chipindale, pers. comm.). Temperature cycling profiles were 1 × 94 C 2 min 30 sec/45 C 1 min/68 C 3 min, 39 × 94 C 30 sec/50 C 45 sec/72 C 30 sec, and 1 × 72 C 5 min. Reactions contained 20–30 ng of template, and 0.5 units of Taq polymerase in a total volume of 12.5 µl. Reaction mixtures also contained 1.6% DMSO, 0.3 µl of each primer at 10.0 µM, 1.0 µl dNTPs, each dNTP at 2.0 mM, Fisher 10× reaction buffer, and MgCl₂ to a final concentration of 2.5 mM. PCR products were treated with shrimp alkaline phosphatase and Exonuclease I (Amersham/USB) to remove primers and unincorporated nucleotides. DNA was sequenced using the Sequitherm Excel© kit from Epicenter and dye-labeled primers. Reactant volumes were reduced to one quarter of those recommended. Temperature cycling profiles were 1 × 95 C 2 min, 29 × 95 C 30 sec/56 C 30 sec/70 C 1 min. Sequence products were separated on a 66 cm, 3.75% Long Ranger acrylamide gel using a LICOR 4200 sequencer with current and voltage restricted to 35 mA and 3000 V, respectively. Sequences were aligned using the clustal algorithm of MegAlign in DNASTar for Macintosh. Alignment was unambiguous with no gaps introduced.

Mitochondrial sequence data were subjected to phylogenetic analysis using PAUP (vers. 4.061, prerelease versions provided by D. L. Swofford) with the branch-and-bound search option under the criterion of maximum parsimony. To compensate for differential transition/transversion and codon position bias, characters were differentially weighted based on empirical observations of change made using MacClade (vers. 3.0, W. P. Maddison and D. R. Maddison, Sinauer, Sunderland, MA, 1992, unpubl.). One thousand nonparametric bootstrap pseudoreplicates (Felsenstein, 1985; Hillis and Bull, 1993) were performed under the criterion of maximum parsimony to determine support for proposed relationships. In addition, maximum-likelihood analysis was used with MODELTEST (vers. 2.1, Posada and Crandall, 1998) to determine the optimal combination of topology, model of DNA substitution, and other pa-

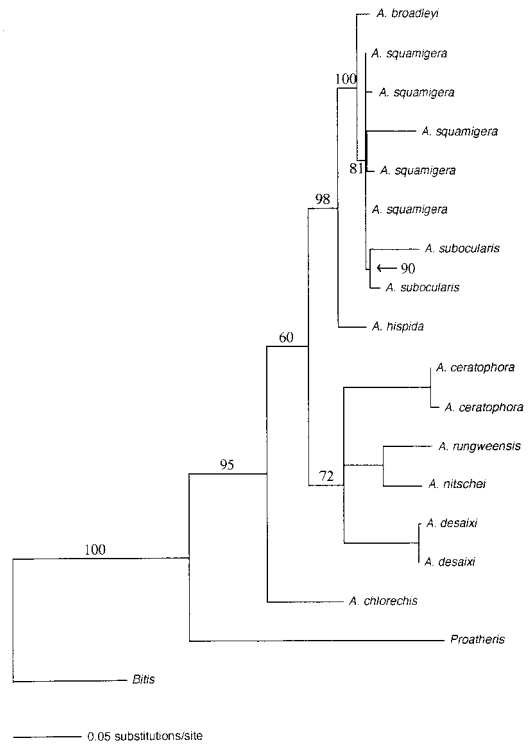


Fig. 1. Hypothesis of relationships of Atherine snakes based on strict consensus of maximum-likelihood and maximum-parsimony analyses of cytochrome *b* gene sequences. Numbers above branches indicate bootstrap support derived from maximum-parsimony analysis with 1000 pseudoreplicates and 100 random taxon addition replicates.

rameter values (optimal model of substitution = HKY + G; G = 0.426).

Institutional abbreviations are as listed in Leviton et al. (1985). The University of Texas at Arlington Live Collection is abbreviated with DPL field numbers.

RESULTS

Cytochrome *b* sequences exhibited relatively little variation among *Atheris* taxa. Maximum sequence divergence was 15.2% between *Atheris ceratophora* and *A. subocularis*. Across all taxa examined, 358 of the 647 positions varied, with 184 of these being parsimony informative. Maximum-parsimony branch-and-bound and maximum-likelihood heuristic analyses produced nearly identical trees, differing only in relationships within the *nitschei* group. A consensus tree with bootstrap values greater than 50% is presented in Figure 1.

Parsimony analysis of cytochrome *b* sequences results in strong support for the monophyly of

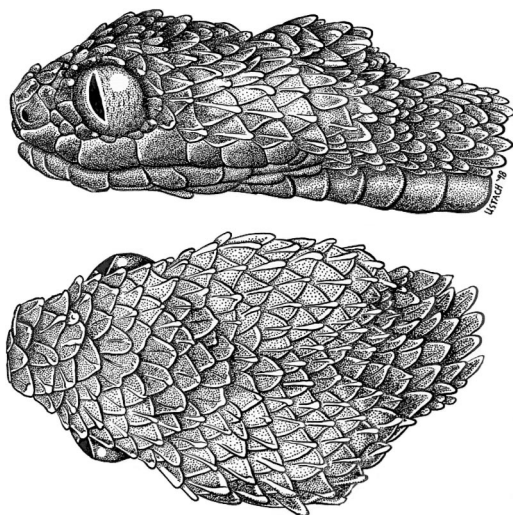


Fig. 2. Left lateral and dorsal aspect of *Atheris subocularis*; vicinity Nguti, Southwest Province, Cameroon; UTA R-45004; head length 14.9 mm. Illustrations by P. C. Ustach.

a Central African *squamigera* group (*A. hispida* (*A. broadleyi* (*A. squamigera*, *A. subocularis*)) (99%), an East African *nitschei* group (*A. ceratophora*, *A. desaixi* (*A. rungweensis*, *A. nitschei*)) (72%), and is consistent with the recent removal of *Proatheris* from *Atheris* (Broadley, 1996). Within the *squamigera* group, the recently described Congo/southeastern Cameroon *A. broadleyi* is well supported as sister to southwestern Cameroon *Atheris*, and this group appears to be monophyletic (82%). Within southwestern Cameroon *Atheris*, there is strong support (90%) for the monophyly of *A. subocularis*, but the relationship between *A. subocularis* and sympatric *A. squamigera* is unclear based on this molecular analysis alone.

Analysis of the cytochrome *b* sequence alone indicates that *A. subocularis* forms a discrete clade possibly within its sympatric sister species, *A. squamigera*. Given the strong molecular support for the monophyly of the two *A. subocularis* specimens examined here, and considering the distinct and consistent morphological differences between *A. subocularis* and sympatric *A. squamigera* (see following taxonomic accounts), we resurrect *A. subocularis* Fischer from the synonymy of *A. squamigera* (Hallowell). Based on four new specimens of *A. subocularis* collected between 1995 and 1997 in the Southwest Province, Cameroon, and the original description by Fischer (1888), we provide the following taxonomic account.



Fig. 3. *Atheris subocularis*; vicinity Manyemen, Southwest Province, Cameroon, 390 mm SVL, DPL 4734. Photo by D. P. Lawson.

Atheris subocularis Fischer

Atheris subocularis Fischer 1888. Jahrb. Hamburg. Wiss. Anst. 5:5, pl. 1 (figs. 2a–e, labeled *A. suborbitalis* in error), pl. 2 (fig. 11, labeled *A. suborbitalis* in error)
Figures 2–3

Holotype.—BMNH 1946.1.20.80 (formerly BMNH 1889.12.16.139). Type locality: “Kamerun.”

Referred material.—UTA R-45003–04; 46529–30.

Diagnosis.—*Atheris subocularis* is distinguished from all other members of the genus by the following combination of characters: (1) one or more supralabials in contact with orbit, or separated by greatly reduced suboculars; (2) 12–15 interrials; and (3) dorsal scales in 14–15 rows anteriorly, 14–16 rows at midbody, and 12–13 rows posteriorly.

Specifically, *A. subocularis* is readily differentiated from sympatric *A. squamigera* by the following suite of characters (male *A. squamigera* in parentheses, females in brackets when different from males): (1) usually fourth or fifth supral-

abial entering orbit (orbit separated from supralabials by oculars) [orbit separated by oculars and a variable number of interoculars]; (2) fourth supralabial longer than high (higher than long); (3) 58–65 subcaudals (55–58) [50–57]; (4) 14–16 scale rows at midbody (18–19) [20–22], 14–15 scale rows on the neck (16–19) [18–20], and 12–13 scale rows posteriorly (14–17) [14–19]; (5) a black chevron or two black spots on dorsum of head (dorsum of head uniform), and; (6) olive background dorsal coloration (green or yellow).

Atheris subocularis may be further differentiated from the putative *A. squamigera robusta* Laurent (1956) of the Ituri by its smaller total length, and by having fewer dorsal scale rows.

Description and variation.—Rostral flattened, subtriangular, about 4.5 times broader than high, contacting anteriormost supralabials, three large unkeeled suprarostrals; medial smaller than lateral suprarostrals, about 1.25 times wider than high; right and left suprarostrals slightly higher than wide; nasal wider than high, partially divided above and below the nares; posterior wall of nares large, comprising about 75% of opening; internasals 4, two innermost only feebly keeled; interrials 12–15; interorbitals 6–7, keeled, relatively uniform in shape; oculars 11–14, supra- and postoculars keeled, terminating in blunt knobs, suboculars absent or greatly reduced and dorsoventrally compressed, often a single minute subocular at the suture of the 4th and 5th supralabial, preoculars enlarged, smooth; oculars separated from nasals by 2–5 smooth or feebly knobbed scales; supralabials 8–10, 4–5 entering orbit; infralabials 8–9, posteriormost feebly knobbed or smooth, anteriormost in contact at the midline, separating mental from 4–5 pairs of chin shields; mental two to three times as wide as deep; gulars keeled; ventrals 154–163; subcaudals 58–65, entire; anal entire; dorsal scales about twice as long as wide, becoming shorter posteriorly, in 14–15 rows anteriorly, 14–16 rows at midbody, 12–13 rows posteriorly; keel on dorsals increasing in height from base, declining rapidly at apex; paraventrals larger than other dorsals, keeled, about as high as long.

Body subtriangular in cross-section; maximum total length of males about 491 mm; females unknown; tail length 19–20% of total; head 1.4–1.7 times as long as wide; eye large, 19–23% of head length; face, from anterior border of orbit to tip of snout, about 25–28% of head length.

Color in preservative as in life or faded to almost uniform black. Color in life: dorsum of

head and body uniform greenish olive or yellowish olive-green broken by 30 or more indistinct olive yellow crossbands; most crossbands bordered anteriorly by diffuse black or dark olive band; crossbands very indistinct posteriorly and on tail; interstitial skin black, olive yellow or citrine beneath crossbands, broadly visible around scale margins throughout body; dorsum of head with incomplete black chevron or several black spots; face slightly paler than dorsum of head; rostrals, labials and mental region smudged with greenish olive; diffuse black post-orbital stripe in DPL 4734; sides of neck from rictus about three scale rows posteriorly, lighter olive-yellow; chin and venter uniformly dull lime green, sparsely smudged with black, becoming slightly darker posteriorly and under the tail; black interstitial skin broadly visible around margins of ventrals; eye yellowish olive-green; tongue red, tips black.

Distribution.—Known only from the Southwest Province of Cameroon, Africa.

Atheris squamigera has a wide distribution in central Africa (Broadley, 1998), and exhibits considerable inter- and intrapopulation variation (see Lawson, 1999; Lawson and Ustach, 2000). Therefore, it is helpful to provide a description of the southwestern Cameroon population of *A. squamigera*. For comparison, selected features of Cameroon *A. squamigera*, *A. broadleyi*, and *A. subocularis* are given in Table 1. Because *A. subocularis* is sympatric with *A. squamigera* in southwestern Cameroon, for comparison and identification, we provide the following taxonomic account specifically for the southwest Cameroon population of *A. squamigera*.

Atheris squamigera (Hallowell)

Echis squamigera Hallowell, 1856, Proc. Acad. Nat. Sci. Philadelphia. 1854:193.

Figure 4

Holotype.—ANSP 6949. Type locality: “near the River Gaboon, Guinea” [= Libreville, Gabon].

Referred material.—UTA R-4704, 4922–24, 5056, 5172, 5176, 5185, 5547–48, 31346.

Description and variation (values for female Atheris squamigera, when different, in parentheses).—Rostral flattened, subtriangular, about 4.7 (4.1) times broader than high, contacting anteriormost supralabials, three large unkeeled suprarostrals; medial suprarostal only slightly smaller than (about the same as) lateral suprarostrals, about as wide as high; right and left suprarostrals slightly higher than wide (about as wide as

TABLE 1. SELECTED FEATURES OF CAMEROON *Atheris*. Mean values in parentheses, mode in brackets. See text for additional diagnostic characters.

Character	<i>Atheris subocularis</i> n = 4	<i>Atheris squamigera</i> males n = 4	<i>Atheris squamigera</i> females n = 7	<i>Atheris broadleyi</i> n = 16
Ventrals	154–163 (158)	156–163 (159)	149–158 (154)	157–169 (162)
Subcaudals	58–65 (59)	55–58 (56)	50–57 (53)	45–61 (51)
Maximum total length (mm)	491	467	629	768
TL/SVL	0.19–0.20 (0.20)	0.16–0.19 (0.18)	0.17–0.18 (0.17)	0.15–0.22 (0.17)
Mid-body scale rows	14–16	18–19 (18.5)	20–22 (21)	17–23 [21]
Anterior-body scale rows	14–15	16–19 (17.5)	18–20 (19)	17–20 [19]
Posterior-body scale rows	12–13	14–17 (15)	14–19 (17)	14–17 (16)
Supralabials	8–10 [8]	9–10 [10]	9–11 [11]	9–12 [10]
Supralabials contacting eye	4 and/or 5	none	none	none
Infralabials	8–9	9–10 [10]	9–12 [11]	9–12 [11]
Infralabials contacting chin shields	2–4	2–3	2–3	2–3
Suprarostrals	3	3–7, median of- ten fused to internasal	3–7, median of- ten fused to internasal	3–7, median never fused to internasal
Interorbitals	6–7	6–7 (6.5)	6–10 (7)	3–8 (5.8)
Total oculars	11–14 [12]	13–15 [14]	14–16 [15]	12–16 [15]
Head scales	keeled	keeled and smooth	keeled and smooth	keeled
Interrictals	12–15	15–16 (16)	16–19 (17)	14–18
HL/SVL	(0.04)	(0.05)	(0.06)	(0.06)
Eye diam./HL	(0.21)	(0.19)	(0.16)	(0.18)
Snout length/HL	(0.26)	(0.25)	(0.23)	(0.24)
Dorsal color pattern	Olive, black and yellow bars, V on head	Green w/ yellow crossbands or uniform yellow	Green w/ yellow crossbands or uniform yellow	Citrine to greenish olive w/ crossbands

high); nasal wider than high, entire or partially divided above and/or below the nares; posterior wall of nares large, comprising about 75% of opening; internasals 4–5, keeled; interrials 15–16 (16–19); interorbitals 6–7 (6–10), keeled and relatively uniform in shape, or enlarged or fused and only feebly keeled; oculars 13–15 (14–16); supra- and postoculars keeled, terminating in blunt knobs, suboculars smooth or terminating in slight knob; oculars separated from nasals by 3–5 (5–10) smooth or feebly knobbed scales; supralabials 9–10 (9–11), separated from orbit by suboculars and 1–3 interoculabials; infralabials 9–10 (9–12), posteriormost knobbed or keeled, anteriormost in contact at the midline, separating mental from 4–6 (4–7) pairs of chin shields; mental about twice as wide as deep; gulars strongly keeled; ventrals 156–163 (149–158); subcaudals 55–58 (50–57), entire; anal entire; dorsal scales about twice as long as high, becoming shorter and relatively higher toward posterior of body, in 16–19 (18–21) rows anteriorly, 18–19 (20–22) rows at midbody, 14–17 (14–19) rows posteriorly; keel on dorsals in-

creasing in height from base, declining rapidly at apex; paraventrals larger than other dorsals, keeled, about as high as long.

Body rounded in cross-section; maximum total length about 467 (629) mm; tail length 16–19% (17%) of total; head about 1.3 times as long as wide; eye large, about 20% (16%) of head length; face, from anterior border of orbit to tip of snout, about 25% (23%) of head length.

Color in preservative is plumbeous or indigo dorsally broken by diffuse or strong buff yellow crossbands, buff yellow or plumbeous or indigo ventrally, or uniform buff yellow flecked with green and brown. Color in life: (1) dorsum of head and body apple green or turquoise green broken by buff- to spectrum yellow crossbands which are indistinct anteriorly, becoming pronounced posteriorly; interstitial skin black and/or buff-yellow, not normally visible around scale margins; face paler than dorsum of head; chin and venter uniformly dull lime green or sulfur yellow; eye lime green; tongue red, tips black;

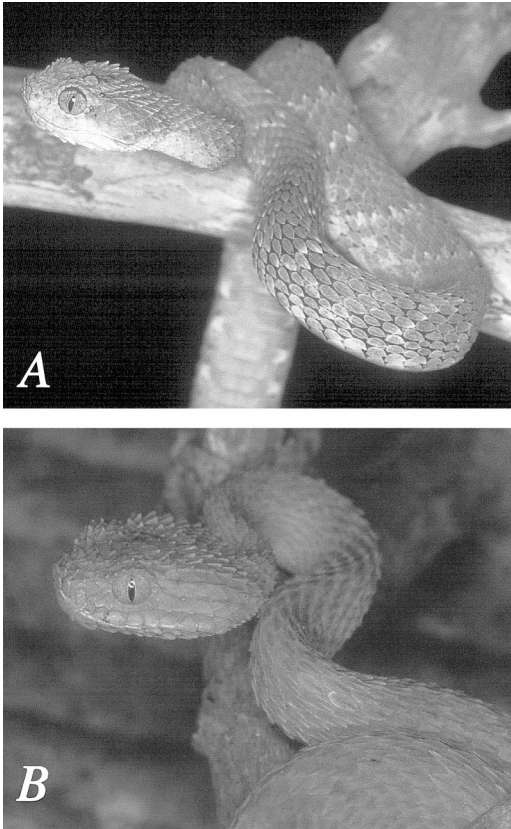


Fig. 4. (A) *Atheris squamigera*: green adult male from vicinity Nguti, Southwest Province, Cameroon, approximately 375 mm SVL, UTA R-50151; (B) *Atheris squamigera*: yellow adult male, vicinity Nguti, Southwest Province, Cameroon, 376 mm SVL, UTA R-44963. Photos by D. P. Lawson.

or (2) uniformly spectrum yellow sparsely flecked with lime green and/or brown.

Distribution.—Eastern Nigeria (Lawson and Ustach, 2000) eastward to western Kenya and Tanzania, south to northern Angola, and the island of Bioko (Broadley, 1998).

DISCUSSION

We appreciate that several problems persist with the recognition of *A. subocularis*. One is the absence of referable female specimens. This lack of female *A. subocularis* is atypical for *Atheris* populations. Southwestern Cameroon collections, as well as collections of other populations and species of *Atheris*, are often female biased (e.g., *A. broadleyi*, Lawson, 1999; pers. obs.). Combined with the sexual dimorphism seen in *A. squamigera* (and probably other *Atheris*), this collecting bias has resulted in the recognition

of at least one nonvalid taxon (Lawson and Ustach, 2000). It may be that female *A. subocularis* are morphologically indistinguishable from female *A. squamigera* or that there are pronounced ecological or behavioral differences between the two closely related taxa that render female *A. subocularis* less susceptible to sampling efforts.

Given the absence of females, there remains a remote possibility that *A. subocularis* is a sex-limited *A. squamigera* polymorphism of unknown causation occurring only in the southwest Cameroon population. A sex-linked basis for *A. subocularis* (with inviable hemizygous females, the heterogametic sex, resulting in the absence of this sex) is unlikely to persist because of strong selection pressure against drastically reduced offspring viability. *Atheris subocularis* may also be explained as a local recessive genetic morph in homozygotic homogametic males. However, one would expect only 25% of males in the population to exhibit the *subocularis* morph rather than the 50% seen in the limited sample here (see below). Sexual dimorphism in snakes is commonplace (Shine, 1993, 1994), and the presence and maintenance of discrete polymorphisms have been well studied in other vertebrate taxa (e.g. Smith, 1993). However, the presence of a discrete intrasexual polymorphism has not been reported in snakes. Polymorphism can theoretically be produced and maintained through hybridization (Ridley, 1993). However, unless a submontane Rumpi Hills/Bakossi Mountain endemic remains to be discovered, there are no other known *Atheris* in the region with which *A. squamigera* could hybridize.

Atheris subocularis appears to be restricted to forests of southwestern Cameroon west of the Cameroon highland chain and, presumably, extreme eastern Nigeria. The holotype of *A. subocularis* is accompanied only by the general locality Cameroon. Because southwestern Cameroon was the political center of the German colonial territory at the time the holotype was collected, and Fischer was German and published through the Hamburg Museum, we believe the type specimen to have also come from this general region. Although the new material was taken below 300 m along the western base of the Cameroon Highlands, this species may be more common at moderate elevations in the Bakossi Mountains and Rumpi Hills, and its scarcity in natural history collections may be attributable to an historical lack of sampling effort in these montane areas.

Although rare in collections, *A. subocularis* may not be uncommon in the wild. The four

new specimens of *A. subocularis* constitute 15% of the total *Atheris* in one of our (DPL) collections from southwestern Cameroon, and *A. subocularis* was taken in equal numbers as male *A. squamigera*. Fischer (1888) based his description on the lone male holotype, and it is unknown whether this represented the entire *Atheris* material in his collection. Although relatively common 110 yr later, the relative frequency of *A. subocularis* in the region is not known. Although Cameroon has been well collected relative to other central African countries, systematic reptile collections for southwestern Cameroon are rare. Stucki-Stirn (1979) reported on a significant collection of snakes from the area, but it is unclear how well *Atheris* was represented. He makes no mention of supralabials entering the orbit in his general account of *A. squamigera*, and unfortunately, his material was left in Cameroon and has since been destroyed (C. Wild, pers. comm.).

The new *A. subocularis* specimens were taken as they crossed a road very near villages or towns on rainy nights. Based on these limited observations, *A. subocularis* may be affiliated with the forest edge, degraded forest habitats, or the "farmbush" of Schiøtz (1967). Lawson (1993) discussed the farmbush snakes in this region of southwestern Cameroon. Portions of southwestern Cameroon are believed to have been Pleistocene forest refugia (Kingdon, 1989), and it may be that the presumed restricted presence of *A. subocularis* is relictual and reflects prior isolation of a portion of the *A. squamigera* population. The phenomenon of a restricted distribution in southwestern Cameroon is not unique. The rare, diminutive bufonid, *Didymanipus sjostedtii*, also shares a forest edge or open forest patch distribution restricted to southwestern Cameroon and the island of Bioko.

Because there are so few specimens, and fewer in situ observations, it is not possible to ascertain differences (if any) in the ecology or behavior between *A. subocularis* and *A. squamigera* in Cameroon. However, if *A. subocularis* proves to predominate at the forest edge, then this species may be an anthropogenically maintained ecotone taxon persisting through polymorphic resource use/disruptive selection in the sense of Smith and Skúlason (1996) and Smith et al. (1997). Broadley (1998) recently described *A. acuminata* on the basis of a single male specimen taken in gallery forest. In a situation analogous to that seen between *A. squamigera* and *A. subocularis*, *A. acuminata* exhibits reduced scale counts relative to its sympatric and presumed sister taxon, *A. hispida* (Broadley, 1998). Mor-

phological and molecular divergence occurring at the forest edge between sister species may be widespread within the *A. squamigera* clade and related taxa. The repeated fluctuations of Africa's mesic forests over the last 40,000 yr overlap with continuous human alterations of this habitat call for additional research on the evolution and maintenance of these ecotone *Atheris*. That both *A. acuminata* and *A. subocularis* are known only from male specimens is intriguing. Clearly, additional specimens of male and female *A. squamigera*, tissue samples, field studies, and captive propagation trials are needed to determine the genetic basis and status of these putative species.

MATERIALS EXAMINED

Alcoholic specimens examined: *Atheris broadleyi*, Cameroon, East Province, UTA R-37798–37801 and 44911–21. *Atheris squamigera*, Cameroon, Southwest Province, UTA R-31346, 4704, 4922–24, 5056, 5172, 5176, 5185, 5547–48. *Atheris subocularis*, Cameroon, Southwest Province, UTA R-45003–04; 46529–30.

Tissue samples used: *Atheris broadleyi*, DPL 3646; *Atheris chlorechis*, *Atheris ceratophora*, *Atheris desaixi*, and *Proatheris superciliaris*, all DPL live collection. *Atheris hispida*, Dallas Zoo, no number. *Atheris nitschei*, no number, shed skin courtesy Jan Slapeta. *Atheris rungweensis*, sequence courtesy C. Parkinson. *Atheris squamigera*, Cameroon, Southwest Province, UTA R-50151; UTA R-44929; DPL 5179 and 5339, live collection. *Atheris subocularis*, UTA R-45003, 46530. *Bitis gabonica*, Cameroon, Southwest Province, UTA R-45532. *Bitis nasicornis*, Cameroon, Southwest Province, UTA R-45515.

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LITERATURE CITED

- BOULENGER, G. A. 1896. Catalogue of the snakes in the British Museum (Natural History). Vol. 3. Trustees of the British Museum (Natural History), London.
- . 1919. Batraciens et reptiles recueillis par le Dr. C. Christy au Congo Belge, dans les districts de Stanleyville, Haut-Uele et Ituri en 1912–1914. *Rev. Zool. Afr.* 7:1–29.
- BROADLEY D. G. 1996. A review of the tribe Atherini (Serpentes: Viperidae), with the description of two new genera. *Afr. J. Herpetol.* 45:40–48.
- . 1998. A review of the genus *Atheris* Cope (Serpentes: Viperidae), with the description of a new species from Uganda. *Herpetol. J.* 8:117–135.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39:783–791.
- FISCHER, J. G. 1888. Über zwei neue schlangen und einen neuen laubfrosch von Kamerun. *Jahrb. Hamb. Wiss. Anst.* 5:1–52.
- HILLIS, D. M., AND J. J. BULL. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Syst. Biol.* 42:182–192.
- , C. MORITZ, AND B. K. MABLE (EDS.). 1996. *Molecular systematics*. 2d ed. Sinauer Associates, Inc., Sunderland, MA.
- KINGDON, J. 1989. *Island Africa: the evolution of Africa's rare animals and plants*. Princeton Univ. Press, Princeton, NJ.
- KLAUBER, L. M. 1956. *Rattlesnakes: their habits, life histories, and influence on mankind*. Vol. 1. Univ. of California Press, Berkeley.
- LAWSON, D. P. 1993. The reptiles and amphibians of the Korup National Park project, Cameroon. *Herpetol. Nat. Hist.* 1:27–90.
- . 1999. A new species of arboreal viper (Serpentes: Viperidae: *Atheris*) from Cameroon, Africa. *Proc. Biol. Soc. Wash.* 112:793–803.
- , AND P. C. USTACH. 2000. A redescription of *Atheris squamigera* (Serpentes: Viperidae) with comments on the validity of *Atheris anisolepis*. *J. Herpetol.* 34:386–389.
- LEVITON, A. E., R. H. GIBBS JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology. Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802–821.
- MCDIARMID, R. W., J. A. CAMPBELL, AND T. A. TOURÉ. 1999. *Snake species of the world. A taxonomic and geographic reference*. Vol. 1. Herpetologists' League, Washington, DC.
- PALUMBI, S. R. 1996. Nucleic acids II: the polymerase chain reaction, p. 205–247. *In*: D. M. Hillis, C. Moritz, and B. K. Mable (eds.). *Molecular systematics*. 2d ed. Sinauer Associates, Inc., Sunderland, MA.
- POSADA, D. AND K. A. CRANDALL. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817–818.
- RIDLEY, M. 1993. *Evolution*. Blackwell Scientific Publ., Boston, MA.
- SCHIØTZ, A. 1967. The treefrogs (Rhacophoridae) of West Africa. *Spolia zool. Mus. haun.* 25:1–346.
- SHINE, R. 1993. Sexual dimorphism in snakes, p. 49–86. *In*: Snakes: ecology and behavior. R. A. Seigel and J. T. Collins (eds.). McGraw-Hill Inc., New York.
- . 1994. Sexual size dimorphism in snakes revisited. *Copeia* 1994:326–346.
- SMITH, T. B. 1993. Disruptive selection and the genetic basis of bill size polymorphism in the African finch *Pyrenestes*. *Nature* 363:618–620.
- , AND S. SKÚLASON. 1996. Evolutionary significance of resource polymorphism in fishes, amphibians, and birds. *Annu. Rev. Ecol. Syst.* 27:111–133.
- , R. K. WAYNE, D. J. GIRMAN, AND M. W. BRUFORD. 1997. A role for ecotones in generating rainforest biodiversity. *Science* 276:1855–1857.
- SMITHE, F. B. 1975. *Naturalist's color guide*. American Museum of Natural History, New York.
- STUCKI-STIRN, M. C. 1979. Snake report 721. Herpeto-Verlag, Teuffenthal, Switzerland.

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