

A NEW SQUEAKER FROG (ARTHROLEPTIDAE: *ARTHROLEPTIS*) FROM THE MOUNTAINS OF CAMEROON AND NIGERIA

DAVID C. BLACKBURN^{1,5}, VÁCLAV GVOŽDÍK^{2,3}, AND ADAM D. LEACHÉ⁴

¹Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence, KS 66045, USA

²Department of Vertebrate Evolutionary Biology and Genetics, Institute of Animal Physiology and Genetics, Academy of Sciences of the Czech Republic, 277 21 Liběchov, Czech Republic

³Department of Zoology, National Museum, 115 79 Prague, Czech Republic

⁴Genome Center and Department of Evolution and Ecology, University of California, Davis, CA 95616, USA

ABSTRACT: A new species of squeaker frog (genus *Arthroleptis*) is described from the northern mountains of the Cameroon Volcanic Line, a species-rich region within the West African biodiversity hotspot. This new species is associated with human-altered landscapes, including farms and grasslands, and is known from the highland areas near Bamenda, including Mt. Oku, Cameroon, as well as the Obudu and Mambilla Plateaus of eastern Nigeria. The known distribution suggests that it may eventually also be found throughout the Acha-Tugi Ridge that traverses the Cameroon–Nigeria border. More than 40 years ago, a specimen from one of these populations was recognized as probably representing a new species, but no further work was published on this material. We posit that the taxonomy of this new species has proven problematic because of morphological similarity to *Arthroleptis poecilnotus*. Although in some ways resembling *A. poecilnotus*, a molecular phylogeny based on mitochondrial gene sequence data demonstrates that the new species is not closely related to *A. poecilnotus* and, instead, forms a clade with *A. krokosua*, *A. perreti*, and *A. variabilis*. The new species is diagnosable by the combination of medium–small body size (24–29 mm snout–vent length in adult females), the color patterns of the venter and head, and a relatively stout hindlimb with a prominent inner metatarsal tubercle. The description of this new species further highlights these mountains as an important region of endemism within the Cameroon Volcanic Line.

Key words: Amphibia; Anura; Biodiversity hotspot; Federal Republic of Nigeria; Gulf of Guinea; New species; Republic of Cameroon

WITHIN THE West African biodiversity hotspot (sensu Myers et al., 2000), the mountains of the Cameroon Volcanic Line form an important region of endemism for amphibians (Stuart et al., 2004). This geological structure comprises three ecoregions as defined by Burgess et al. (2004) and consists of the islands of the Gulf of Guinea (Bioko, Príncipe, São Tomé, and Annobón) and the mountains of Cameroon and eastern Nigeria (Déruelle et al., 1991; Marzoli et al., 2000). During the past 40 years, many new species of amphibians have been described from these mainland and island mountains (Amiet, 1971*a,b*, 1972*a,b*, 1973, 1977, 1980*a,b*, 1981, 2000, 2001, 2004*a,b*; Amiet and Dowsett-Lemaire, 2000; Blackburn, 2008*a*, 2010*a,b*; Blackburn et al., 2009; Boistel and Amiet, 2001; Drewes and Wilkinson, 2004; Herrmann et al., 2004; Kobel et al., 1980; Lawson, 2000; Loumont and Kobel, 1991; Nussbaum, 1985; Nussbaum and Pfrender, 1998; Perret, 1971; Plath et al.,

2006; Rödel et al., 2004; Uyeda et al., 2007; Zimkus, 2009). Although the islands and mountains near the coast contain many endemic species, there are also many amphibian species endemic to mountains to the north that are associated with the Bamiléké, Adamawa, Mambilla, and Obudu Plateaus (e.g., Amiet, 1972*a,b*, 1977, 1980*a*, 1981; Blackburn, 2010*a*; Boistel and Amiet, 2001; Herrmann et al., 2004; Lawson, 2000; Loumont and Kobel, 1991; Perret, 1971; Zimkus, 2009).

We describe a new species of squeaker frog (genus *Arthroleptis*) that is endemic to the mountains of the Cameroon Volcanic Line; moreover, it seems to be localized to the northern mountains found in Cameroon and Nigeria (Fig. 1). Recent studies of *Arthroleptis* (sensu Blackburn, 2008*b*) have revealed many new species found in locations as distant as Liberia and Tanzania (Blackburn, 2008*b*, 2009*a*, 2010*b*; Blackburn et al., 2009; Ernst et al., 2008; Poynton, 2003; Poynton et al., 2008; Rödel et al., 2009). The new species that we describe here was first known based on a specimen collected on the Obudu Plateau in

⁵ CORRESPONDENCE: e-mail, david.c.blackburn@gmail.com

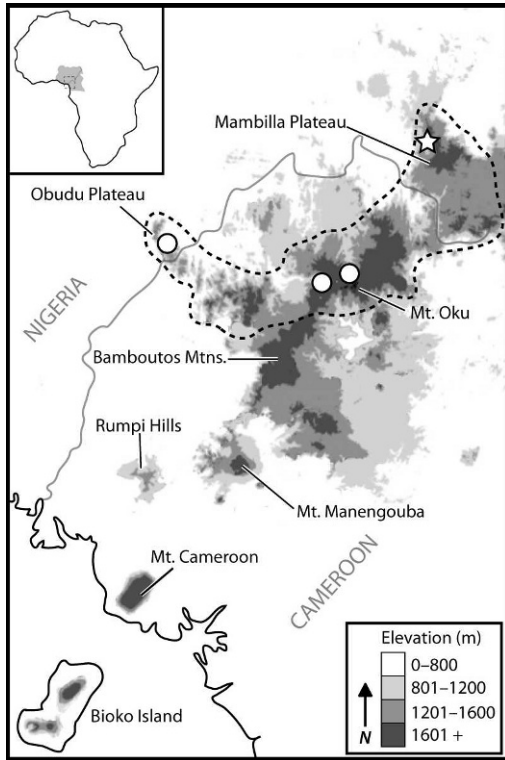


FIG. 1.—Distribution of *Arthroleptis palava* in the mountains of Cameroon and Nigeria; inset indicates region depicted in figure. Star designates type locality; circles designate localities where other paratypes were collected. Dotted line indicates possible area of occurrence of *A. palava*. Elevational gradient based on fig. 1 of Bergl et al. (2007).

1959 that Schiøtz (1963) noted “seems to represent an undescribed species,” although no further details were provided in subsequent publications. That this species was never described is probably due, at least in part, to its morphological similarity to *A. poecilonotus*, a taxon with a difficult taxonomic history (Blackburn, 2008b, 2010b; Rödel, 2000; Rödel and Bangoura, 2004). A recent phylogenetic analysis revealed that specimens morphologically similar to that reported by Schiøtz (1963) were distantly related to *A. poecilonotus* and instead formed a clade with *A. variabilis* and the recently described *A. perreti* (Blackburn, 2008b; Blackburn et al., 2009). Here, we add more specimens of the new species to a phylogenetic analysis of molecular sequence data that further supports the distinctness of this historically problematic new species.

MATERIALS AND METHODS

Specimens were collected during visual encounter surveys conducted by the authors during fieldwork in Cameroon (Gvoždík in 2005; Blackburn in 2006) and Nigeria (Leaché in 2006; Blackburn in 2009). Type material was examined of all species discussed (by D. C. Blackburn; see Appendix I), except those of the recently described *A. nguruensis* Poynton, Menegon, and Loader 2008 and *A. stenodactylus* Pfeffer, 1893, the latter having been destroyed during World War II (Frost, 2009). All measurements (± 0.1 mm) were taken by DCB using digital calipers and a dissecting microscope; limb measurements were taken on the right side. Measurements follow Blackburn (2005), which is a modification of Matsui (1984); tympanum height was measured as the vertical diameter of the tympanum. Museum abbreviations follow Leviton et al. (1985), with the exception of Museums of Malawi, Blantyre (MMB) and National Museum, Prague (NMP).

We extend the phylogenetic analysis of Blackburn (2008b) by including additional specimens of the new species, *A. bioko* (Blackburn, 2010b), and *Arthroleptis* “*poecilonotus*.” Genetic data were obtained for seven additional specimens of the new species and three *A. “poecilonotus”* from the Oban Hills of eastern Nigeria (Table 1). We view the inclusion of the additional *A. “poecilonotus”* specimens as particularly important because they were collected near to the Obudu Plateau and allow us to test species boundaries and the geographic distribution of the new species. Evolutionary relationships were determined through phylogenetic analyses of DNA sequence data for the mitogenomic region containing the genes encoding for 12S and 16S ribosomal RNA and the intervening transfer RNA for valine; phylogenetic relationships among this and other *Arthroleptis* based on multilocus nuclear data will be presented elsewhere (D. C. Blackburn, unpublished data). Genomic DNA was extracted from tissue samples using a guanidine thiocyanate method following the protocol of Esselstyn et al. (2008). Polymerase chain reaction (PCR) was used to amplify the target region; primer pairs and PCR conditions follow Darst and Cannatella (2004). Purification and sequencing follows Esselstyn et al.

TABLE 1.—*Arthroleptis* and *Cardioglossa* specimens analyzed in the phylogenetic analysis. Asterisk indicates those GenBank accessions to which minor corrections were made during this study.

| Species | Collection no. | GenBank no. | Country | Reference | |
|---------------------------|------------------------|--------------|-------------------|----------------------------|----------------------------|
| <i>A. adelphus</i> | CAS 207922 | FJ15055* | Equatorial Guinea | Blackburn (2008 <i>b</i>) | |
| | MCZ A-136847 | FJ151092* | Cameroon | Blackburn (2008 <i>b</i>) | |
| <i>A. bioko</i> | CAS 207283 | HM238196 | Equatorial Guinea | This study | |
| | CAS 207285 | FJ151053* | Equatorial Guinea | Blackburn (2008 <i>b</i>) | |
| <i>A. brevipes</i> | MVZ 244891 | FJ151107* | Ghana | Blackburn (2008 <i>b</i>) | |
| | MVZ 244892 | FJ151108* | Ghana | Blackburn (2008 <i>b</i>) | |
| <i>A. krokosua</i> | SMNS 12555 | EU350211 | Cameroon | Ernst et al. (2008) | |
| <i>A. palava</i> sp. nov. | MCZ A-137983 | FJ151150 | Cameroon | Blackburn (2008 <i>b</i>) | |
| | MCZ A-139527 | HM238186 | Nigeria | This study | |
| | MCZ A-139528 | HM238187 | Nigeria | This study | |
| | MVZ 253131 | HM238188 | Nigeria | This study | |
| | MVZ 253132 | HM238189 | Nigeria | This study | |
| | MVZ 253140 | HM238193 | Nigeria | This study | |
| | MVZ 253141 | HM238194 | Nigeria | This study | |
| | NMP6V 73343/3 | FJ151142 | Cameroon | Blackburn (2008 <i>b</i>) | |
| | NMP6V 73343/4 | FJ151143 | Cameroon | Blackburn (2008 <i>b</i>) | |
| | NMP6V 73368 | HM238195 | Cameroon | This study | |
| | NMP6V 73437 | FJ151132 | Cameroon | Blackburn (2008 <i>b</i>) | |
| | <i>A. perreti</i> | MCZ A-136931 | FJ151094 | Cameroon | Blackburn (2008 <i>b</i>) |
| | | MCZ A-136932 | FJ151095 | Cameroon | Blackburn (2008 <i>b</i>) |
| | <i>A. poecilonotus</i> | CAS 230190 | FJ151119* | Sierra Leone | Blackburn (2008 <i>b</i>) |
| MCZ A-136750 | | FJ151084* | Cameroon | Blackburn (2008 <i>b</i>) | |
| MCZ A-136751 | | FJ151085 | Cameroon | Blackburn (2008 <i>b</i>) | |
| MVZ 244895 | | FJ151110* | Ghana | Blackburn (2008 <i>b</i>) | |
| MVZ 244896 | | FJ151111* | Ghana | Blackburn (2008 <i>b</i>) | |
| MVZ 253134 | | HM238190 | Nigeria | This study | |
| MVZ 253135 | | HM238191 | Nigeria | This study | |
| MVZ 253139 | | HM238192 | Nigeria | This study | |
| <i>A. stenodactylus</i> | CAS 168455 | FJ151054 | Tanzania | Blackburn (2008 <i>b</i>) | |
| | MCZ A-137021 | FJ151098 | Malawi | Blackburn (2008 <i>b</i>) | |
| <i>A. variabilis</i> | AMCC 117638 | FJ151069 | Cameroon | Blackburn (2008 <i>b</i>) | |
| | MCZ A-136722 | FJ151086 | Cameroon | Blackburn (2008 <i>b</i>) | |
| <i>C. gracilis</i> | MCZ A-136796 | FJ151088 | Ghana | Blackburn (2008 <i>b</i>) | |

(2008). Consensus sequences were generated in Sequencer version 4.7 (Gene Codes Corporation) and manually vetted. After alignment (see below), autapomorphic states (base pair changes, insertions, or deletions) for both new data and those presented in Blackburn (2008*b*) were verified by inspection of chromatograms; in some cases, changes were made to previously published sequences (Table 1), and these corrections have been submitted to GenBank. Resulting sequence lengths are as follows: *A. sp. nov.* (MCZ A-139527, 1957 base pairs [bp]; MCZ A-139528, 1955 bp; MVZ 253131, 1945 bp; MVZ 253132, 1939 bp; MVZ 253140, 1932 bp; MVZ 253141, 1937 bp; NMP6V 73368, 1885 bp) and *A. "poecilonotus"* (MVZ 243134, 1948 bp; MVZ 253135, 1887 bp; MVZ 253139, 1934 bp). Newly collected sequences were accessioned in GenBank (Table 1).

For phylogenetic analysis, these newly collected sequences were included in an analysis with representatives of other *Arthroleptis* species based on the results of Blackburn (2008*b*; Table 1). The data set was restricted to members of the *A. poecilonotus* species complex (*A. bioko*, *A. brevipes*, and *A. "poecilonotus"*), *A. adelphus*, *A. variabilis*, and *A. perreti* (the latter corresponds to "*A. sp. nov. 1*" of Blackburn, 2008*b*; see Blackburn et al., 2009); we follow Blackburn (2010*b*) in assigning populations from the Togo Hills of eastern Ghana to *A. brevipes*. These species formed a clade in the phylogenetic analysis of Blackburn (2008*b*), which included many other *Arthroleptis* species from elsewhere in sub-Saharan Africa. Based on morphological similarities, we also included data from *A. krokosua*, which is known from a single specimen collected in western Ghana (Ernst

et al., 2008). Because Blackburn (2008b) found *A. stenodactylus* to be sister to the clade of the above-mentioned species, we also included this species in the analysis. A multiple alignment of the resulting data set, comprising DNA sequences of unequal length for 33 terminal taxa, was generated using default parameters in Clustal X version 1.83.1 (Thompson et al., 1997). The resulting alignment was trimmed such that it corresponds to positions 2526–4587 of the *Xenopus laevis* mitochondrial genome (GenBank NC-001573).

The best-fit model of sequence evolution (GTR + I + Γ) was selected using the Akaike information criterion (AIC = 16657.07) as implemented in MrModeltest version 2.3 (Nylander, 2004). Both maximum-likelihood (ML) and Bayesian estimates of phylogeny were generated. ML analyses were conducted on the aligned sequence data in Garli version 0.96b8 (Zwickl, 2006) using a random starting tree and a GTR + I + Γ model of sequence evolution with all parameters estimated. Fifty search repetitions of ML analysis were carried out and the estimate with the lowest $-\ln$ likelihood score used as the preferred ML phylogeny; each search was terminated 10×10^5 generations after the last topological improvement. One thousand non-parametric bootstrap replicates were performed in Garli using the same model of sequence evolution; each bootstrap replicate contained one search replicate that was terminated 2×10^4 generations after the last topological improvement. Branches present in $\geq 70\%$ of the bootstrap replicate phylogenies were considered well supported following Hillis and Bull (1993). A Bayesian estimate of phylogeny was obtained using MrBayes version 3.1.2 and GTR + I + Γ model of sequence evolution. Four runs of four MCMC chains were run for 20 million generations, sampled every 2000 generations, using a temperature of 0.2 and default priors. Convergence was assessed by examining correlations of split frequencies among runs in AWTY (Nylander et al., 2008). The first two million generations were discarded as burn-in following examination of trends and distributions of log-likelihoods and parameter values using Tracer version 1.4 (Rambaut and Drummond, 2007); estimated sample sizes from the four combined

runs were all above 22,000. The phylogeny and posterior probabilities were then estimated from the remaining trees; split support was calculated using SumTrees (Sukumaran and Holder, 2008). In addition, the maximum clade credibility tree (the post burn-in tree with the maximum product of the posterior clade probabilities) was estimated using TreeAnnotator version 1.5.3 (Rambaut and Drummond, 2009). Topologies with posterior probabilities ≥ 0.95 were considered well supported following Wilcox et al. (2002). Parsimony analyses of these data resulted in a similar topology of interspecific relationships (data not shown). Based on Blackburn (2008b), *Cardioglossa gracilis* was used as an outgroup to root the phylogeny.

RESULTS

The phylogenetic analyses (Fig. 2) resulted in a pattern of interspecific relationships that is identical to that found by Blackburn (2008b). The topologies of the maximum likelihood and the maximum clade credibility trees are nearly identical. The single exception is that MCZ A-137983 from Mt. Oku is more closely related to two specimens from the Mambilla Plateau (MCZ A-138527–8) in the maximum likelihood topology but more closely related to other specimens from Cameroon (NMP6V 73368, 73343/3–/4, 73437) in the maximum clade credibility tree. Interspecific relationships exhibit high support from both nonparametric bootstrapping and Bayesian posterior probabilities. The additional specimens of *A. "poecilonotus"* from the Oban Hills of eastern Nigeria form a highly supported clade with morphologically similar specimens from Cameroon; genetic divergence among *A. "poecilonotus"* from Cameroon and Nigeria is very low ($< 0.01\%$ uncorrected p -distance). The topology within the *poecilonotus* species complex (sensu Blackburn, 2010b) is similar to that found by Blackburn (2008b), but there is low support for the sister relationship between *A. "poecilonotus"* from Sierra Leone and western Ghana. There is strong support that *A. perreti* is sister to a well supported clade (bootstrap = 70%; posterior probability = 0.99; Fig. 2) comprising *A. variabilis*, *A. krokosua*, and the new species described below. There is strong support (bootstrap =

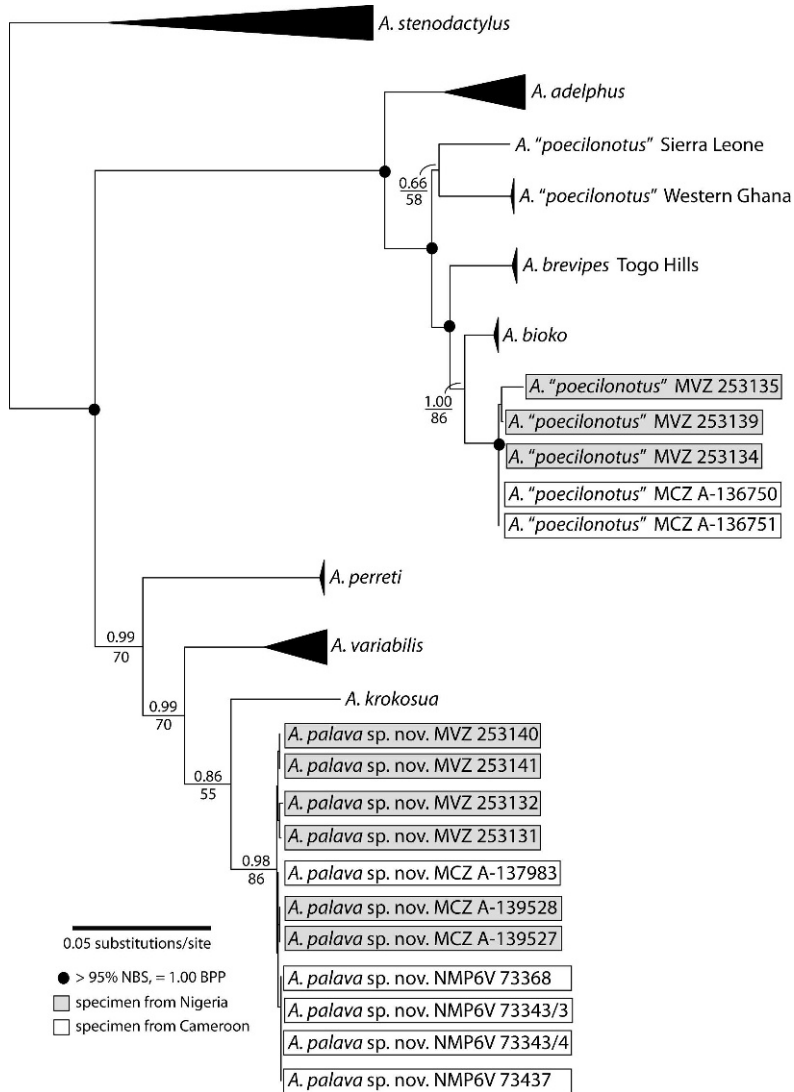


FIG. 2.—Maximum-likelihood phylogram estimated from mitochondrial DNA sequences depicting the phylogenetic relationships of *Arthroleptis palava*. All species are monophyletic with high support. Nodes with black circles indicate Bayesian posterior probability (BPP) of 1.00 and non-parametric bootstrap (NBS) \geq 95%. For nodes with lower support values, numbers above branches are BPP and below are NBS. The outgroup, *Cardioglossa gracilis*, is not shown.

86%; posterior probability = 0.98; Fig. 2) for a clade comprising morphologically similar specimens that we refer to this new species. Genetic divergence within the new species is very low ($<0.01\%$). Because the populations from the northern mountains of the Cameroon Volcanic Line are genealogically exclusive (with respect to mitochondrial DNA) and are morphologically diagnosable, we describe these as a new species.

SPECIES DESCRIPTION

Arthroleptis palava sp. nov.

The Problem Squeaker Frog

(Figs. 3 and 4; Table 2)

Arthroleptis "sp. nov. 2." Blackburn, 2008b, *Molecular Phylogenetics and Evolution* 49.

Holotype.—MCZ A-139528 (field no. DCB 34672), adult female, 9 April 2009, Federal Republic of Nigeria, Taraba State, Mambilla

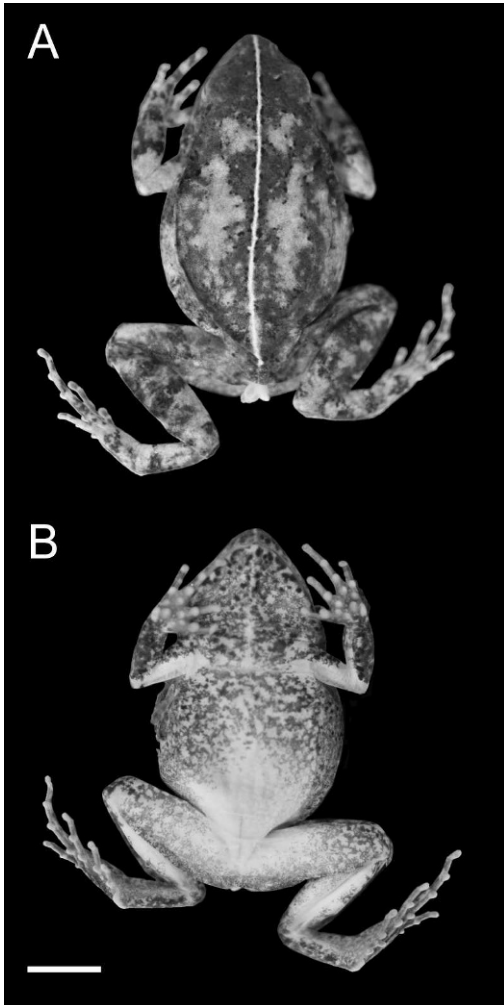


FIG. 3.—*Arthroleptis palava* holotype (MCZ A-139528) in life: right dorsolateral (A) and ventral (B) views (photo by DCB). Scale bar, approximately 5 mm.

Plateau, Ngel Nyaki Forest Reserve, Nigerian Montane Forest Project Field Station, 7.08611 11.06664 (WGS84), ca. 1590 m, collected by H. Chapman and M. Amadu (Fig. 4).

Paratypes.—MCZ A-137983 (DCB 34581), juvenile, 16 August 2006, Republic of Cameroon, Northwest Province, Mount Oku, Elak-Oku Village, 6.24583 10.50000 (WGS84), ca. 1900 m, collected by DCB, K. S. Blackburn, P. Huang, and M. K. Talla; MCZ A-139527 (DCB 34671), adult female, 9 April 2009, Federal Republic of Nigeria, Taraba State, Mambilla Plateau, near Yelwa Village, 7.08611



FIG. 4.—*Arthroleptis palava* holotype (MCZ A-139528) in right dorsolateral view. Scale bar, approximately 5 mm.

11.06664 (WGS84), ca. 1580 m, collected by DCB and M. Zubairu; ZMUC R072268, adult male, January 1959, Federal Republic of Nigeria, Cross River State, Obudu Plateau, along road near Obudu Cattle Ranch, 6.35000 9.43000 (datum unavailable), ca. 1520–1680 m, collected by A. Schiøtz; MVZ 253131–2 (ADL 3258–9), adult males, 8 April 2006, Federal Republic of Nigeria, Cross River State, Obudu Plateau, Obudu Cattle Ranch, 6.42087 9.35961 (WGS84), ca. 1580 m, collected by ADL, E. A. Eniang, A. M. Leaché; MVZ 253140–1 (ADL 3269–70), adult females, 8 April 2006, Federal Republic of Nigeria, Cross River State, Obudu Plateau, Obudu Cattle Ranch, 6.42517 9.36238 (WGS84), ca. 1400 m, collected by ADL, E. A. Eniang, A. M. Leaché; NMP6V 73343/3 (VG-C122), juvenile, 1 December 2005, Republic of Cameroon, Northwest Province, Bamenda Highlands, Mejung Village, 6.12869 10.24402 (WGS84), ca. 1090 m, collected by VG; NMP6V 73343/4 (VG-C060), subadult female, 3 December 2005, Republic of Cameroon, Northwest Province, Bamenda Highlands, Mejung Village, 6.12400 10.24801 (WGS84), ca. 1120 m, collected by VG; NMP6V 73368 (VG-C044), adult female, 29 November 2005, Republic of Cameroon, Northwest Province, Bamenda Highlands, Kedjom Keku Village (“Big Babanki”), 6.10229 10.27408 (WGS84), ca. 1310 m, collected by VG; NMP6V 73437 (VG-C124), juvenile, 3 December 2005, Republic of Cameroon, Northwest Province, Bamenda Highlands, Kedjom Keku Village (“Big Babanki”), 6.11506 10.27335 (WGS84), ca. 1390 m, collected by VG.

TABLE 2.—Measurements (in millimeters) of adult type specimens of *Arthroleptis palava*.

| | MCZ A-139528 | MCZ A-139527 | ZMUC R072268 | MVZ 253131 | MVZ 253132 | MVZ 253140 | MVZ 253141 | NMP6V 73368 |
|---------------------------------|------------------|-----------------|-----------------|---------------|---------------|---------------|---------------|----------------|
| | Holotype | Paratype | Paratype | Paratype | Paratype | Paratype | Paratype | Paratype |
| | Female | Female | Male | Male | Male | Female | Female | Female |
| Snout-vent length | 24.9 | 23.7 | 22.2 | 24.2 | 24.0 | 28.2 | 29.1 | 28.8 |
| Head width | 9.1 | 8.7 | 7.5 | 9.6 | 9.2 | 11.4 | 11.4 | 11.2 |
| Tympanum height | 1.3 | 1.3 | 1.1 | 1.6 | 1.3 | 1.7 | 1.7 | 1.9 |
| Eye diameter | 3.2 | 3.1 | 3.5 | 3.6 | 3.0 | 4.3 | 3.9 | 4.0 |
| Snout length | 2.6 | 2.7 | 2.5 | 2.6 | 2.5 | 3.1 | 2.6 | 2.2 |
| Forearm length | 5.7 | 5.3 | 5.2 | 6.7 | 6.6 | 7.5 | 7.2 | 7.0 |
| Manual digit I | 2.1 | 2.1 | 2.1 | 2.0 | 2.1 | 2.5 | 2.6 | 2.8 |
| Manual digit II | 2.2 | 2.1 | 2.1 | 2.4 | 2.7 | 2.6 | 2.8 | 3.0 |
| Manual digit III | 3.7 | 3.5 | 4.1 | 4.7 | 5.1 | 4.7 | 4.7 | 4.8 |
| Manual digit IV | 2.2 | 1.9 | 2.5 | 2.9 | 2.8 | 3.2 | 3.1 | 3.1 |
| Thigh length | 11.8 | 11.2 | 10.2 (L) | 11.4 | 11.8 | 13.9 | 13.7 | 13.5 |
| Crus length | 10.7 | 10.5 | 10.7 (L) | 11.4 | 11.5 | 13.5 | 13.5 | 14.4 |
| Pedal digit I | 1.5 | 1.6 | 1.5 | 1.5 | 1.6 | 1.9 | 1.7 | 1.9 |
| Pedal digit II | 2.3 | 2.0 | 2.3 (L) | 2.3 | 2.3 | 2.9 | 2.7 | 2.9 |
| Pedal digit III | 3.6 | 3.6 | 3.9 | 4.0 | 4.1 | 4.6 | 4.2 | 4.9 |
| Pedal digit IV | 6.1 | 5.8 | 6.2 | 6.4 | 6.7 | 7.9 | 7.7 | 7.9 |
| Pedal digit V | 3.2 | 2.8 | 3.4 | 3.5 | 3.4 | 4.1 | 3.7 | 4.2 |
| Inner metatarsal length | 1.6 | 1.2 | 1.3 | 1.3 | 1.5 | 1.7 | 1.7 | 1.6 |
| No. of spines, manual digit II | n/a ^a | n/a | R-4; L-3 (weak) | R-10; L-8 | R-10; L-10 | n/a | n/a | n/a |
| No. of spines, manual digit III | n/a | n/a | R-13; L-13 | R-10; L-14 | R-15; L-16 | n/a | n/a | n/a |

^a n/a, not applicable.

Diagnosis.—A medium-small *Arthroleptis* that is distinguished from other *Arthroleptis* by the combination of body size, the color patterns of the venter and head, and a relatively stout hindlimb with a prominent inner metatarsal tubercle. Adult female body size of *A. palava* is smaller (26.9 ± 2.5 mm; $n = 5$) than the other *Arthroleptis* from Central and western Africa with which it forms a clade: *A. krokosua* (43.3 mm; $n = 1$; from Ernst et al., 2008), *A. perreti* (37.5 ± 4.3 mm; $n = 25$; from Blackburn et al., 2009), and *A. variabilis* (33.1 ± 3.0 mm; $n = 27$; from Blackburn et al., 2009). *Arthroleptis palava* differs in the following ways from other *Arthroleptis* species that are “medium-small” to large (i.e., species larger than maximum snout-vent length [SVL] ≥ 25 mm): from *A. adelphus* by having a more defined (although sometimes fragmented) supratympanic band, generally smoother skin on the dorsal and lateral surfaces, and smaller body size (female *A. adelphus*: 32.5 ± 0.90 mm; $n = 5$); from *A. adolfifriederici* by a more flange-like inner metatarsal tubercle and smaller body size (female *A. adolfifriederici*: 37.8 ± 4.1 mm; n

= 6); from *A. affinis* by lacking well-defined supernumerary tubercles on the feet (although some specimens of *A. palava* have a weakly developed supernumerary tubercle at the base of the second toe) and smaller body size (>30 mm in *A. affinis*); from *A. bioko* and *A. francei* by having a relatively larger inner metatarsal tubercle and by generally having a fragmented supratympanic band; from *A. krokosua* by lighter pigmentation on throat and vent, lacking large well-defined black spots on the lateral surface of the body, and by a fourth finger that is nearly always longer than the first and second fingers; from *A. perreti* by lacking a darkly colored posterior thigh with many well-defined white spots; from *A. reichei* by having generally less expanded finger and toe tips; from *A. stenodactylus* by generally having a fragmented supratympanic band and more pigmentation on the venter; from *A. nikeae* by much smaller adult body size (>50 mm in *A. nikeae*); from *A. tanneri* and *A. nguruensis* by smaller adult body size (>40 mm in *A. tanneri* and *A. nguruensis*) and a relatively narrower head; from *A. tuberosus* by less

tuberculate skin; from *A. variabilis* by lacking a well-defined pale stripe on the midline of the throat (although it is incipient in some specimens of *A. palava*); from *A. wahlbergii* by having a more prominent inner metatarsal tubercle, by lacking a prominent well-defined dark inguinal spot, and by lacking well-defined supernumerary metatarsal tubercles.

Description of holotype.—Medium-small (SVL 24.9 mm), robust and slightly globular female with stout limbs (Figs. 3 and 4; Table 2); head roughly triangular, length approximately equal to width; snout projecting approximately 0.8 mm beyond lower jaw; snout triangular in dorsal view with rounded rostral tip, blunt and sharply curving posteroventrally in lateral view; eyes just projecting beyond eyelids in dorsal view; eyes not projecting laterally beyond margins of head in dorsal view; eyes projecting just above dorsal margin of head in lateral view; eye diameter approximately 1.1 times interorbital distance; pupil large, round in preservative; loreal region weakly concave; naris small, elliptical, directed laterally, and nearly entirely visible in dorsal view; canthus rostralis short and rounded; eye diameter 2.3 times eye-narial distance; eye diameter 2.1 times distance from naris to rostral tip; internarial region flat to weakly concave with rounded lateral margin; internarial distance 86% interorbital distance; tympanum small, round, height approximately 40% diameter of eye; tympanic annulus poorly defined but still visible; supratympanic fold absent; tongue robust, broad, cordiform, and covered with many small pustules; anterior attachment of tongue broad; posterior notch of tongue approximately one sixth anteroposterior length of tongue; indistinct, rounded median papilla on dorsal tongue surface near anterior attachment; choana small, rounded, and completely hidden by maxillary shelf in ventral view; premaxillary and maxillary teeth present, but hidden by lips; vomerine teeth absent.

Skin of limbs, dorsal and lateral surfaces of head and body, and ventral head smooth (somewhat more tuberculate in life; Fig. 3); median skin raphe indistinct; posterior surface of venter glandular and wrinkled (i.e., "seat-patch" region).

Limbs and digits well developed; digits of both manus and pes stout and somewhat

robust; relative length of fingers: $III > II \approx IV > I$; finger tips rounded and swollen, approximately equal to width of the subarticular tubercles; finger with large rounded, prominent, globular, single subarticular tubercles; palmar and metacarpal tubercles present and strongly developed, projecting from palmar surface as well-defined globules; metacarpal tubercles more prominent than four palmar tubercles; webbing between manual digits (fingers) absent; thigh length 110% of crus length; relative length of toes: $IV > III > V > II > I$; toe tips swollen and rounded, approximately equal to width of subarticular tubercles; toes with prominent, single subarticular tubercles; weakly developed and plaque-like supernumerary tubercle on pedal surface proximal to most proximal subarticular tubercle of second toe; webbing between pedal digits (toes) absent; prominent, well developed flange-like inner metatarsal tubercle, length 110% of first toe length.

Measurements.—See Table 2.

Coloration of holotype (in alcohol).—Dorsal ground color pale medium brownish gray with prominent tan to pale gray spots and many small dark gray spots (Fig. 4); prominent well-defined white line along dorsal midline from snout to cloaca; iris dark gray with pale creamy gray pupil; loreal and suborbital regions with numerous small dark gray spots, but otherwise similar to dorsal head; interorbital bar absent; supratympanic band broken into many small dark spots (almost indiscernible as a band), extending posteroventrally towards arm; tympanum essentially opaque, dark gray, with many small metallic gray flecks; dorsal surface of arm pale gray shading to more brownish on forearm and wrist; two prominent, but broken, dark brown transverse bands on forearm, one near wrist and one at mid-forearm; dorsal surface of hands pale gray with dark brownish gray markings; interphalangeal knuckles tend to pale gray with dark gray in between giving appearance of banded digits; pair of pale gray markings posterior to head and posterior to these pair of elongate pale gray markings, within pairs of markings typical "hour-glass" pattern somewhat discernible; lateral surface pale gray with scattered small dark gray and smaller white spots; dorsal surface of hindlimbs (thighs and crus) mottled brownish gray

with dark gray markings; single, but broken, transverse dark gray band on dorsal surface of distal thigh; posterior surface of thigh pale gray base color, densely covered with small dark gray melanophores forming no obvious pattern; base color of dorsal foot pale gray with dark gray markings; pedal digits with similar "banding" pattern as manual digits, but less well-defined; region surrounding cloaca similar in coloration to adjacent dorsal surface of thighs.

Lateral margin of lower jaw with prominent dark brownish gray spots and few interdigitated white spots along the anterior two-thirds of jaw; throat pale gray base with brown melanophores concentrated into clumps; scattered white blotches on throat, concentrated along midline to form incipient line at gular midline; gular color pattern continues across venter, with pronounced disruption at posterior border of coracoids; medial surfaces of arm and forearm pale gray (unpigmented) with medium to dark brown markings; ventral surface of arm pale gray with no markings; ventral surface of forearm mottled medium and dark brown; ventral surface of hand and fingers pale brown; palmar, metacarpal, subarticular tubercles, and finger tips pale gray (unpigmented); posterior-most venter (near "seat-patch") pale creamy gray with no dark markings; ventral and anterior thigh and ventral crus with similar pattern to venter; plantar surface dark brownish gray with few small pale gray spots; subarticular tubercles on toes, inner metatarsal tubercle, and ventral toe tips pale gray (unpigmented).

Coloration in life.—Dorsal coloration ranging pale to medium brown with small dark brown markings (Fig. 4); when present, dorsal midline stripe pale cream in life (i.e., specimens from Mambilla Plateau and Bamenda Highlands; MCZ A-139527–8, NMP6V 73343/4, 73437); darker markings on dorsal and lateral surfaces ranging from dark brown to almost black; paler markings on lateral surface ranging from pale brown to creamy tan; ventral surface of throat and body gray to white with dark brown markings (Fig. 4); iris golden with black vermiculations and black pupil (Fig. 4).

Variation.—Morphometric and meristic variation is documented in Table 2. Adult females exhibit larger body size than adult males (mean female SVL: 26.9 mm \pm 2.5;

mean male SVL: 23.5 \pm 1.1; two-tailed test with unequal variance $P = 0.04$). Specimens of *A. palava* exhibit variation in color patterns. Most specimens exhibit a pale interorbital bar that is lined along both the anterior and posterior margin with small dark spots, sometimes forming a line. In some specimens this pale interorbital bar blends seamlessly into the pale coloration of the snout (MVZ 253140), whereas in others this bar is entirely absent (MCZ A-139528). Several specimens exhibit a pale stripe running along the dorsum from the rostral tip to the vent (Mambilla Plateau: MCZ A-139527–8; Bamenda Highlands: NMP6V 73343/4, 73437). In addition, specimens from the Mambilla (MCZ A-139527–8) and Obudu (MVZ 243132) Plateaus exhibit an incipient pale stripe along the gular midline. In most specimens of *A. palava*, the supratympanic band, extending from the posterior corner of the eye to behind the tympanum, is fragmented, although several specimens from the Obudu Plateau and most specimens from the Bamenda Highlands exhibit a more-or-less continuous band on one or both sides (MVZ 253131–2; NMP6V 73343/3–4, 73437; ZMUC R072268). The intensity of pigmentation on the venter varies among specimens of *A. palava* with those from the Mambilla Plateau and Bamenda Highlands exhibiting the darkest pigmentation; however, all specimens exhibit pigmentation on the venter.

Secondary sexual characters.—Male specimens of *A. palava* have a hypertrophied third finger (range: 18.5–21.3% SVL [$n = 3$]; 15.8 \pm 0.01% SVL in females [$n = 5$]) with small spines lining the medial surface of the second and third fingers. Ranges of the number of spines on the digits (Table 2) are similar to those reported for *A. perreti* and *A. variabilis* (Blackburn, 2009b; Blackburn et al., 2009). One male (ZMUC R072268) has fewer spines on the second finger than other specimens, but this may be an indication of having not attained full maturity because these spines are only weakly developed and the specimen is slightly smaller than other male specimens. Furthermore, males exhibit spines extending from the inguinal region, on the dorsal surface just anterior to the vent, and extending along the lateral body surface at least past the snout–vent midpoint.

Distribution and natural history.—Specimens were collected at various sites in human-modified landscapes, including a field station at Ngel Nyaki Forest Reserve and a eucalyptus plantation near Yelwa (both on the Mambilla Plateau), and farmland near Elak-Oku Village on Mt. Oku as well as elsewhere in the Bamenda Highlands (Fig. 1). The call of this species has not yet been recorded. If the known localities are taken to define the elevational range of this species (1000–1900 m) and it has a uniform distribution throughout the northern mountains of the Cameroon Volcanic Line, then the estimated extent of occurrence of *A. palava* may exceed 30,000 km².

Conservation.—At present, *A. palava* is known only from sites in obviously human-modified landscapes. Forests at many of these sites have been degraded by human use (Ash and Dowsett-Lemaire, 1989; Ash and Sharland, 1986; Chapman et al., 2004; Gartshore, 1986; Lea et al., 2005; Stuart, 1986), but it is unlikely that this threatens *A. palava*. Because of its large estimated area of occurrence and lack of conservation concerns, we recommend that *A. palava* be considered Least Concern according to IUCN (2008) criteria.

Etymology.—The specific epithet is a noun in apposition and, in recognition of the likely past confusion of this new species with *A. poecilonotus*, is a word meaning “problem” in the pidgins of Central and West Africa.

DISCUSSION

In January 1959, A. Schiøtz collected the first specimen of *A. palava* on the Obudu Plateau. Despite the suggestion that this represented a new species (Schiøtz, 1963) and a brief later reference to this specimen (Schiøtz, 1966), we know of no further mention of either this specimen or that it may have represented a new species. We suggest that this is due, at least in part, to morphological similarity to *A. poecilonotus*, which is a complex of morphologically similar species (Blackburn, 2010*b*; Rödel, 2000; Rödel and Bangoura, 2004). *Arthroleptis palava* exhibits similar dorsal coloration to members of the *poecilonotus* species complex and is similar in body size (“*poecilonotus*”

mean male SVL: 24.0 ± 2.2 mm; *n* = 13; from Blackburn, in press, *b*). Until recently, the systematics of the *poecilonotus* species complex has been impenetrable because of a lack of genetic or acoustic resources. However, both molecular phylogenetic (Blackburn, 2009*a*; this study) and morphological studies (Blackburn, 2010*b*) are now facilitating the delimitation of taxa within this species complex, including the discovery of morphologically distinctive taxa (Blackburn, 2010*b*). For example, a combination of molecular and morphological data (Blackburn, 2009*a*, 2010*b*) reveals that *A. brevipes*, previously known only from one specimen, is probably a valid taxon found in the region of western Togo and eastern Ghana. Before the past 20 years, there have been few, if any, thorough surveys of populations throughout the range attributed to *A. poecilonotus*, and some of these populations can be quite variable morphologically (e.g., Rödel, 2000). Because of the similarity in body size and coloration, it was not until a recent molecular phylogenetic analysis (Blackburn, 2009*a*) that it was apparent that populations in the northern mountains of Cameroon represented a new taxon that is only distantly related to the *poecilonotus* species complex. Further search for specimens revealed that this new species is morphologically distinct from the *poecilonotus* species complex, is also found in the mountains of eastern Nigeria, and corresponds to the specimen first collected by A. Schiøtz more than 50 years ago.

Although Ernst et al. (2008) provided a cursory study of the relationships of *A. krokosua*, this is the first phylogenetic analysis including this recently described species. The hierarchical clustering analysis of morphometric data presented by Ernst et al. (2008) found *A. krokosua* to be similar to *A. variabilis*. Thus, it is not surprising that the phylogenetic results presented here demonstrate *A. krokosua* to form a clade with *A. variabilis*. Although the ML estimate of phylogeny places *A. krokosua* as sister to *A. palava*, this branching pattern receives low support (bootstrap = 55%; posterior probability = 0.86; Fig. 2). However, if true, this topological pattern would suggest a more complicated pattern of spatial diversification than one in

which vicariance results in two lowland or two montane species. Instead, the pattern is suggestive that vicariance might have occurred along elevational gradients, resulting in a pair of sister species, one species in the lowlands and one species in montane areas.

Morphological similarities between *A. palava* and several distantly related *Arthroleptis* species may be indicative of ecological convergence. *Arthroleptis palava* is similar to both *A. francei* and *A. stenodactylus* in having stocky hindlimbs in which the length of the crus (i.e., tibiofibula) is less than half of snout-vent length. Also similar to *A. stenodactylus*, the length of the inner metatarsal tubercle is typically >80% of the length of the first toe. Both *A. francei* and *A. stenodactylus* can be found in a variety of habitat types, including grasslands and forests or woodlands, and the latter is known to burrow in loose soil (Channing, 2001; D. C. Blackburn, personal observation). Emerson (1988) found a correlation between relative hindlimb length and locomotor mode with taxa with shorter hindlimbs tending toward walking and burrowing. Similar to the three species most closely related to it (*A. krokosua*, *A. perreti*, and *A. variabilis*), *A. palava* exhibits a large flange-like inner metatarsal tubercle that ranges from 60% to 110% of the length of the first toe. However, unlike the other three species, the hindlimb of *A. palava* is stocky; the crus is >50% of snout-vent length in *A. krokosua*, *A. perreti*, and *A. variabilis* (e.g., Blackburn et al., 2009; Ernst et al., 2008). Because *A. palava* is found in habitats unlike those of these other species, including grasslands, it suggests that these morphological differences are associated with a divergent ecology. Furthermore, the lack of sister-taxon relationships among *A. francei*, *A. palava*, and *A. stenodactylus* suggest that the morphological similarities among these species represent convergence, probably driven by transitions to similar habitat types.

Acknowledgments.—Individuals at many institutions shared resources and loaned specimens that were integral to the completion of this project: B. Clarke (BM), R. Drewes and J. Vindum (CAS), A. Resetar (FMNH), R. Brown, A. Campbell, J. Simmons, and L. Trueb (KU), J. Losos and J. Rosado (MCZ), L. Mazibuko (MMB), A. Schmitz (MHNG), J. McGuire and C. Spencer (MVZ), R. Winkler and U. Wüest (NHMB), P. Malonza and J.

Measey (NMK), E. Prendini (formerly TMP), D. Cannatella and T. Laduc (TNHC), A. Wynn (USNM), C. Franklin and J. Campbell (UTA), R. Günther and M.-O. Rödel (ZMB), and M. Anderson (ZMUC). A. Schiøtz kindly shared collection data for specimens collected by him on the Obudu Plateau in 1959 and 1965. We also thank V. Che for advice and assistance over the years with Cameroonian Pidgin English. For facilitating fieldwork in Nigeria, E. A. Eniang and the Biodiversity Preservation Center as well as H. M. Chapman, the Nigerian Montane Forest Project, and Gombe State University. Many people assisted with the fieldwork, logistics, or both in Cameroon that made this research possible: K. S. Blackburn, M. Che, V. Che, J. L. Diffo, D. Fotibu, L. N. Gonwouo, P. Huang, M. T. Kouete, and M. LeBreton. VG extends special thanks to E. Vunan (SATEC, Kedjom Keku) for assistance and hospitality. The Cameroonian ministry of forestry and wildlife supplied research and collection permits (0173PR/MINEF/SG/DFAP, 0588/PRBS/MINFOF/SG/DFAP/SDVEF/SC, 1010/PRBS/MINFOF/SG/DFAP/SDVEF/SC) and permissions to export specimens. Funding came from the Department of Organismic and Evolutionary Biology (Harvard University), NSF grant EF-0334939 (AmphibiaTree) to J. Hanken, and the University of Kansas Biodiversity Institute (DCB); a grant from the Ministry of Education, Youth and Sports of the Czech Republic (No. LC06073; Biodiversity Research Centre) and grants IRP IAPG AVOZ 50450515 and MK00002327201 (VG); and the Museum of Vertebrate Zoology, University of California, Berkeley (ADL). Collection of sequence data by J. Witters was supported by a Research Experience for Teachers supplement (NSF-0334928; AmphibiaTree) to L. Trueb. J. Esselstyn, C. Linkem, and C. Siler provided valuable comments on a draft of this manuscript.

LITERATURE CITED

- AMIET, J.-L. 1971a. Espèces nouvelles ou mal connues de *Leptodactylodon* (Amphibiens Anoures) de la Dorsale camerounaise. *Annales de la Faculté des Sciences du Cameroun* 5:57–81.
- AMIET, J.-L. 1971b. *Leptodactylodon* nouveaux du Cameroun (Amphibiens Anoures). *Annales de la Faculté des Sciences du Cameroun* 7–8:141–172.
- AMIET, J.-L. 1972a. Description de cinq nouvelles espèces camerounaises de *Cardioglossa* (Amphibiens Anoures). *Biologia Gabonica* 8:201–231.
- AMIET, J.-L. 1972b. Description de trois Bufonidés orophiles du Cameroun appartenant au groupe de *Bufo preussi* Matschie (Amphibiens Anoures). *Annales de la Faculté des Sciences du Cameroun* 11:121–140.
- AMIET, J.-L. 1973. Caractères diagnostiques de *Petropedetes perreti*, nov. sp. et notes sur les autres espèces camerounaises. *Bulletin de l'Institut Français Afrique Noire* 35:462–474.
- AMIET, J.-L. 1977. Les *Astylosternus* du Cameroun (Amphibia Anura, Astylosterninae). *Annales de la Faculté des Sciences de Yaoundé* 23–24:99–227.
- AMIET, J.-L. 1980a. Révision du genre *Leptodactylodon* Andersson (Amphibia, Anura, Astylosterninae). *Annales de la Faculté des Sciences de Yaoundé* 27:69–224.
- AMIET, J.-L. 1980b. Un *Hyperolius* nouveau du Cameroun: *Hyperolius endjami* n. sp. (Amphibia Anura, Hyperoliidae). *Revue Suisse de Zoologie* 87:445–460.

- AMIET, J.-L. 1981. Une nouvelle *Cardioglossa* orophile de la Dorsale camerounaise: *C. schioetzi* nov. sp. (Amphibia, Anura, Arthroleptidae). *Annales de la Faculté des Sciences de Yaoundé* 28:117–131.
- AMIET, J.-L. 2000. Les *Alexeroon* du Cameroun (Amphibia, Anura, Hyperoliidae). *Alytes* 17:125–164.
- AMIET, J.-L. 2001. Un nouveau *Leptopelis* de la zone forestière camerounaise (Amphibia, Anura, Hyperoliidae). *Alytes* 19:29–44.
- AMIET, J.-L. 2004a. A propos de deux *Leptopelis* nouveaux pour la faune du Cameroun (Anura, Hyperoliidae). *Alytes* 21:111–170.
- AMIET, J.-L. 2004b. Une nouvelle espèce d'*Hyperolius* du Cameroun (Amphibia, Anura, Hyperoliidae). *Revue Suisse de Zoologie* 11:567–583.
- AMIET, J.-L., AND F. DOWSETT-LEMAIRE. 2000. Un nouveau *Leptodactylodon* de la Dorsale camerounaise (Amphibia, Anura). *Alytes* 18:1–14.
- ASH, J. S., AND F. DOWSETT-LEMAIRE. 1989. The Nigerian Conservation Foundation expedition to eastern Nigeria, 1988: Itinerary and recommendations. *Tauraco Research Report* 1:1–5.
- ASH, J. S., AND R. E. SHARLAND. 1986. Nigeria: Assessment of bird conservation priorities. I.C.B.P. Study Report 11:1–59.
- BERGL, R. A., J. F. OATES, AND R. FOTSO. 2007. Distribution and protected area coverage of endemic taxa in West Africa's Biafran forests and highlands. *Biological Conservation* 134:195–208.
- BLACKBURN, D. C. 2005. *Cardioglossa liberiensis* Barbour & Loveridge 1927 is a junior synonym of *Phrynobatrachus fraterculus* (Chabanaud 1921). *African Journal of Herpetology* 54:171–179.
- BLACKBURN, D. C. 2008a. A new species of *Cardioglossa* (Amphibia: Anura: Arthroleptidae) endemic to Mount Manengouba in the Republic of Cameroon, with an analysis of morphological diversity in the genus. *Zoological Journal of the Linnean Society* 154:611–630.
- BLACKBURN, D. C. 2008b. Biogeography and evolution of body size and life history of African frogs: Phylogeny of squeakers (*Arthroleptis*) and long-fingered frogs (*Cardioglossa*) estimated from mitochondrial data. *Molecular Phylogenetics and Evolution* 49:806–826.
- BLACKBURN, D. C. 2009a. Description and phylogenetic relationships of two new species of miniature *Arthroleptis* (Anura: Arthroleptidae) from the Eastern Arc Mountains of Tanzania. *Breviora* 517:1–17.
- BLACKBURN, D. C. 2009b. Diversity and evolution of male secondary sexual characters in African squeakers and long-fingered frogs. *Biological Journal of the Linnean Society* 96:553–573.
- BLACKBURN, D. C. 2010a. A new puddle frog (Phrynobatrachidae: *Phrynobatrachus*) from the Mambilla Plateau in eastern Nigeria. *African Journal of Herpetology* 59:33–52.
- BLACKBURN, D. C. 2010b. A new squeaker frog (Arthroleptidae: *Arthroleptis*) from Bioko Island, Equatorial Guinea. *Herpetologica* 66:320–334.
- BLACKBURN, D. C., L. N. GONWOUO, R. ERNST, AND M.-O. RÖDEL. 2009. A new squeaker frog (Arthroleptidae: *Arthroleptis*) from the Cameroon Volcanic Line with red descriptions of *Arthroleptis adolfriederici* Nieden, 1911 "1910" and *A. variabilis* Matschie, 1893. *Breviora* 515:1–22.
- BOISTEL, R., AND J.-L. AMIET. 2001. Une nouvelle espèce de *Wolterstorffina* (Amphibia, Anura, Bufonidae) de l'étage afro-subalpin du Mont Okou (Cameroun). *Alytes* 18:127–140.
- BURGESS, N., J. D. HALES, E. UNDERWOOD, E. DINERSTEIN, D. OLSON, I. ITOUA, J. SCHIPPER, T. RICKETTS, AND K. NEWMAN. 2004. *Terrestrial Ecoregions of Africa and Madagascar*. Island Press, Washington, DC, USA.
- CHAPMAN, H. M., S. M. OLSON, AND D. TRUMM. 2004. An assessment of changes in the montane forests of Taraba State, Nigeria, over the past 30 years. *Oryx* 38:282–290.
- CHANNING, A. 2001. *Amphibians of Central and Southern Africa*. Cornell University Press, Ithaca, New York, USA.
- DARST, C. R., AND D. C. CANNATELLA. 2004. Novel relationships among hyloid frogs inferred from 12S and 16S mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 31:462–475.
- DÉRUELLE, B., C. MOREAU, C. NKOUMBOU, R. KAMBOU, J. LISSOM, E. NJONFANG, R. T. GHOGOMU, AND A. NONO. 1991. The Cameroon Line: A review. Pp. 274–327. *In* A. B. Kampunzu and R. T. Lubala (Eds.), *Magmatism in Extensional Structural Settings*. Springer-Verlag, Berlin, Germany.
- DREWEES, R. C., AND J. A. WILKINSON. 2004. The California Academy of Sciences Gulf of Guinea Expedition (2001). I. The taxonomic state of the genus *Nesionixalus* Perret, 1976 (Anura: Hyperoliidae), treefrogs of São Tomé and Príncipe, with comments on the genus *Hyperolius*. *Proceedings of the California Academy of Sciences* 55:395–407.
- EMERSON, S. B. 1988. Convergence and morphological constraint in frogs: Variation in postcranial morphology. *Fieldiana* 43:1–19.
- ERNST, R., A. C. ACYEI, AND M.-O. RÖDEL. 2008. A new giant species of *Arthroleptis* (Amphibia: Anura: Arthroleptidae) from the Krokosua Hills Forest Reserve, south-western Ghana. *Zootaxa* 1697:58–68.
- ESSELSTYN, J. A., H. J. D. GARCIA, M. G. SAULOG, AND L. R. HEANEY. 2008. A new species of *Desmalopex* (Pteropodidae) from the Philippines, with a phylogenetic analysis of the Pteropodini. *Journal of Mammalogy* 89:815–825.
- FROST, D. R. 2009. *Amphibian species of the world: An online reference*. Version 5.3. Available at: <http://research.amnh.org/herpetology/amphibia/index.php>. American Museum of Natural History, New York, New York, USA.
- GARTSHORE, M. 1986. The status of the montane herpetofauna of the Cameroon highlands. Pp. 204–240. *In* S. N. Stuart (Ed.), *Conservation of Cameroon Montane Forests*. International Council for Bird Preservation, London, UK.
- HERRMANN, H.-W., P. A. HERRMANN, A. SCHMITZ, AND W. BÖHME. 2004. A new frog species of the genus *Cardioglossa* from the Tchabal Mbabo Mtns, Cameroon. *Herpetozoa* 17:119–125.
- HILLIS, D. M., AND J. J. BULL. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology* 42:182–192.
- IUCN. 2008. *Guidelines for Using the IUCN Red List Categories and Criteria*. Version 7.0. Available at: <http://intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf>.

- KOBEL, H. R., L. DU PASQUIER, M. FISCHBERG, AND H. GLOOR. 1980. *Xenopus amieti* sp. nov. (Anura: Pipidae) from the Cameroons, another case of tetraploidy. *Revue Suisse de Zoologie* 87:919–926.
- LAWSON, D. P. 2000. A new caecilian from Cameroon, Africa (Amphibia: Gymnophiona: Scolecomorphidae). *Herpetologica* 56:77–80.
- LEA, J. M., L. LUISSELLI, AND E. POLITANO. 2005. Are there shifts in amphibian faunal composition in Nigerian landscapes undergoing long-term degradation? A case study from a montane environment. *Terre et la Vie* 60:65–76.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802–832.
- LOUMONT, C., AND H. R. KOBEL. 1991. *Xenopus longipes* sp. nov., a new polyploid pidid from western Cameroon. *Revue Suisse de Zoologie* 98:731–738.
- MARZOLI, A., E. M. PICCIRILLO, P. R. RENNE, G. BELLINI, M. IACUMIN, J. B. NYOBE, AND A. T. TONGWA. 2000. The Cameroon Volcanic Line revisited: Petrogenesis of continental basaltic magmas from lithospheric and asthenospheric mantle sources. *Journal of Petrology* 41:87–109.
- MATSUI, M. 1984. Morphometric variation analysis and revision of the Japanese toads (genus *Bufo*, Bufonidae). *Contributions from the Biological Laboratory, Kyoto University* 26:209–428.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. DA FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- NUSSBAUM, R. A. 1985. Systematics of caecilians (Amphibia: Gymnophiona) of the family Scolecomorphidae. *Occasional Papers of the Museum of Zoology, University of Michigan* 713:1–49.
- NUSSBAUM, R. A., AND M. E. PFRENDER. 1998. Revision of the African caecilian genus *Schistometopum* Parker (Amphibia: Gymnophiona: Caeciliidae). *Miscellaneous Publications of the Museum of Zoology, University of Michigan* 187:1–32, i–iv.
- NYLANDER, J. A. A. 2004. MrModeltest v.2.3. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.
- NYLANDER, J. A. A., J. C. WILGENBUSCH, D. L. WARREN, AND D. L. SWOFFORD. 2008. AWTY (are we there yet?): A system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics* 24:581–583.
- PERRET, J.-L. 1971. Les espèces du genre *Nectophrynoïdes* d'Afrique (Batraciens Bufonidés). *Annales de la Faculté des Sciences du Cameroun* 6:99–109.
- PFEFFER, G. 1893. Ostafrikanische Reptilien und Amphibien, gesammelt von Herrn Dr. F. Stuhlmann im Jahre 1888 und 1889. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten* 10:69–105.
- PLATH, M., H.-W. HERRMANN, AND W. BÖHME. 2006. New frog species of the genus *Phrynobatrachus* (Anura: Phrynobatrachidae) from Mt. Nlonako, Cameroon. *Journal of Herpetology* 40:486–495.
- POYNTON, J. C. 2003. A new giant species of *Arthroleptis* (Amphibia: Anura) from the Rubeho Mountains, Tanzania. *African Journal of Herpetology* 52:107–112.
- POYNTON, J. C., M. MENEGON, AND S. P. LOADER. 2008. A new giant species of *Arthroleptis* (Amphibia: Anura) from the forests of the Nguru Mountains, Tanzania. *African Journal of Herpetology* 57:63–74.
- RAMBAUT, A., AND A. J. DRUMMOND. 2007. Tracer. Version 1.4. Available at: <http://beast.bio.ed.ac.uk/Tracer>.
- RAMBAUT, A., AND A. J. DRUMMOND. 2009. TreeAnnotater. Version 1.5.3. Available at: <http://beast.bio.ed.ac.uk/TreeAnnotater>.
- RÖDEL, M.-O. 2000. *Herpetofauna of West Africa Vol. I. Amphibians of the West African Savanna*. Edition Chimaira, Frankfurt am Main, Germany.
- RÖDEL, M.-O., AND M. A. BANGOURA. 2004. A conservation assessment of amphibians in the Forêt Classée du Pic de Fon, Simandou Range, southeastern Republic of Guinea, with the description of a new *Ammirana* species (Amphibia Anura Ranidae). *Tropical Zoology* 17:201–232.
- RÖDEL, M.-O., A. SCHMITZ, O. S. G. PAUWELS, AND W. BÖHME. 2004. Revision of the genus *Werneria* Poche, 1903, including descriptions of two new species from Cameroon and Gabon (Amphibia: Anura: Bufonidae). *Zootaxa* 720:1–28.
- RÖDEL, M.-O., J. DOUMBIA, A. T. JOHNSON, AND A. HILLERS. 2009. A new small *Arthroleptis* (Amphibia: Anura: Arthroleptidae) from the Liberian part of Mount Nimba, West Africa. *Zootaxa* 2302:19–30.
- SCHIÖTZ, A. 1963. The amphibians of Nigeria. *Videnskabelige meddelelser fra Dansk Naturhistorisk Forening* 125:1–92.
- SCHIÖTZ, A. 1966. On a collection of Amphibia from Nigeria. *Videnskabelige meddelelser fra Dansk Naturhistorisk Forening* 129:44–48.
- STUART, S. N. (Ed.). 1986. *Conservation of Cameroon Montane Forests*. International Council for Bird Preservation, London, UK.
- STUART, S. N., J. S. CHANSON, N. A. COX, B. E. YOUNG, A. S. L. RODRIGUES, D. L. FISCHMAN, AND R. W. WAILER. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.
- SUKUMARAN, J., AND M. T. HOLDER. 2008. SumTrees: Summarization of Split Support on Phylogenetic Trees. Version 1.0.2. Available at: <http://packages.python.org/DendroPy/>.
- THOMPSON, J. D., T. J. GIBSON, F. PLEWNIAC, F. JEANMOUGIN, AND D. G. HIGGINS. 1997. The ClustalX windows interface: Flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 24:4876–4882.
- UYEDA, J. C., R. C. DREWES, AND B. M. ZIMKUS. 2007. The California Academy of Sciences Gulf of Guinea Expedition (2001, 2006). VI. A new species of *Phrynobatrachus* from the Gulf of Guinea Islands and a reanalysis of *Phrynobatrachus dispar* and *P. feae* (Anura: Phrynobatrachidae). *Proceedings of the California Academy of Sciences* 58:367–385.
- WILCOX, T. P., D. J. ZWICKL, T. A. HEATH, AND D. M. HILLIS. 2002. Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution* 25:361–371.
- ZIMKUS, B. M. 2009. Biogeographical analysis of Cameroonian puddle frogs and description of a new species of *Phrynobatrachus* (Anura: Phrynobatrachidae) endemic

to Mount Oku, Cameroon. Zoological Journal of the Linnean Society 157:795–813.

ZWICKL, D. J. 2006. Genetic Algorithm Approaches for the Phylogenetic Analysis of Large Biological Sequence Datasets under the Maximum Likelihood Criterion. Ph.D. Dissertation. University of Texas, Austin, Texas, USA.

Accepted: 21 May 2010

Associate Editor: Richard Lehtinen

APPENDIX I

Specimens Examined

Type material, sex, and snout–vent length (in mm) indicated in parentheses. *Arthroleptis adelphus*.—CAMEROON: CAS 103889 (female, 32.1), MCZ A-2646 (female, 31.3), A-136732 (female, 33.1), MHNG 1042.18 (female, 32.2), 1042.21 (male, 30.7), TNHC 47895 (male, 28.2). EQUATORIAL GUINEA: CAS 207922 (unknown, 22.8). GABON: KU 17193 (female, 33.6). *Arthroleptis adolfifriederici*.—DEMOCRATIC REPUBLIC OF CONGO: MCZ A-14696 (female, 37.3). RWANDA: FMNH 73836 (syntype [formerly ZMB 21789]; female, 40.1); ZMB 21787 (syntype; female, 42.0); KU 154322 (male, 32.3), 154323–25 (females, 30.1, 38.0, 39.1). UGANDA: CAS 177029 (female, 35.8), 177031 (female, 43.4), 177032 (juvenile, 22.2), 177033 (male, 27.6). *Arthroleptis affinis*.—TANZANIA: MCZ A-13145–146 (females, 37.2, 37.6), A-13150–151 (males, 23.4, 25.3), A-13152–153 (females, 35.8, 40.5), A-13157–160 (females, 32.8, 33.7, 34.7, 36.6), A-13162–163 (females, 36.6, 35.7), A-13165 (female, 35.6), A-13167 (male, 27.8), A-13169 (male, 29.2), A-25400–401 (females, 35.5, 30.5), A-138241–244 (female, 36.2, 33.8, 42.9, 37.4); TNHC 38577 (female, 38.0); ZMB 23093 (holotype; female, 35.6). *Arthroleptis bioko*.—EQUATORIAL GUINEA: CAS 207285 (holotype; male, 31.3), CAS 207283–4 (paratypes; males, 26.7, 32.3, 27.2), CAS 207286 (paratype; male, 33.4). *Arthroleptis bivittatus*.—GUINEA: NHMB 1257 (holotype; female, 25.5). *Arthroleptis brevipes*.—TOGO: ZMB 26978 (holotype; female, 28.3). GHANA: MVZ 244891 (male, 23.0), 244892 (female, 26.7), 244894 (female, 29.1). *Arthroleptis franței*.—MALAWI: BM 1954.1.13.74 (paratype; female, 32.4); MCZ A-27474–476 (paratypes; males, 25.4, 28.2, 28.0), A-27477–478 (paratypes; females, 38.7, 41.0), A-27479 (holotype; female, 41.9), A-137038 (female, 37.3); TMP 48089 (female, 43.0), 48092 (male, 27.8). *Arthroleptis nikeae*.—TANZANIA: BM 2002.101 (holotype; female, 52.5), 2002.102 (paratype; female, 53.7). *Arthroleptis perreti*.—CAMEROON: MCZ A-137978 (holotype; female, 37.4), A-136931 (paratype; female, 29.1), A-136932 (paratype; juvenile, 19.1), A-137980 (paratype; female, 33.5). *Arthroleptis poecilnotus*.—CAMEROON: MCZ A-2663 (female, 27.1), A-3430 (female, 24.4), A-5607 (female, 25.0), A-13211 (female, 25.0), A-20965 (female, 22.9), A-20967 (female, 26.3), A-136750–2 (males, 25.1, 25.0, 25.6); USNM 563687 (female, 25.0); UTA A-52325 (female, 26.6), A-52328 (male, 24.6). CENTRAL AFRICAN REPUBLIC: MCZ A-27780 (female?, 25.6).

CONGO (BRAZZAVILLE): MCZ A-136027 (female, 29.4). DEMOCRATIC REPUBLIC OF CONGO: MCZ A-21771 (male, 27.8), A-21772 (female, 29.2). GABON: BM 1875.10.15.3 (holotype of *A. macrodactylus*; male, 24.1); KU 155110–15 (females, 19.6, 18.7, 20.2, 18.0, 19.9, 16.9), 171781–3 (female, 27.9, 26.8, 26.9); PL 207 (M. Burger field series; male, 22.8). GHANA: MVZ 244895–6 (females, 25.0, 24.9), 244898 (female, 25.0), 244900 (male, 19.8), 244901 (female, 21.4); ZMB 3345 (holotype; unknown, 20.6). GUINEA: KU 291916 (unknown, 21.0). IVORY COAST: MCZ A-28152 (female, 24.2), A-28154–56 (males, 20.7, 24.5, 22.5), A-28157–59 (females, 25.8, 27.1, 27.0). LIBERIA: MCZ A-11974 (female, 27.9), A-22461 (female, 25.1), A-24489 (female?, 24.8), A-26992 (unknown, 25.2), A-137184 (female, 22.7), A-137265 (female, 21.6). NIGERIA: MCZ A-26128 (unknown, 20.7); MVZ 253134 (female, 26.8), 253135 (male, 23.1), 253129 (male, 21.4). SIERRA LEONE: CAS 230190 (female, 26.2); MCZ A-27761 (female?, 21.6). SUDAN: MCZ A-23211 (female?, 23.6). UGANDA: MCZ A-25402 (unknown, 20.6). *Arthroleptis reichei*.—MALAWI: MCZ A-27456 (female, 30.7). TANZANIA: BM 2005.664 (female, 28.1); MCZ A-16957 (male, 23.1), A-16958–59 (females, 27.8, 32.1), A-16961 (female, 27.7), A-16965 (female, 28.8), A-16967–9 (females, 30.1, 29.7, 30.3), A-16973 (female, 28.6), A-16975 (female, 28.8), A-137210 (female, 30.2), A-137214 (female, 27.8), A-137215–6 (males, 25.0, 25.8), A-137233 (female, 27.3), A-137236 (female, 28.9), A-138365 (juvenile, 23.7); ZMB 21722 (holotype; female, 29.6), 21780 (paratype; female, 25.9), 69932 (paratype; juvenile, 19.0). *Arthroleptis stenodactylus*.—MALAWI: MMB HA2002.1.13 (female, 37.0), HA2002.1.60 (male, 32.7), HA2002.4.17 (female, 38.4). TANZANIA: BM 2002.596 (female, 33.0); CAS 168455 (male, 35.6); MCZ A-21715 (male, 27.6), A-25387 (female, 28.6), A-27447 (female, 39.5). KENYA: NMK A/4251 (male, 33.0), A/4251/3 (female, 40.0), A/4251/4 (male, 31.0), A/4401/3 (female, 25.7), A/4401/6 (female, 26.2). *Arthroleptis tanneri*.—TANZANIA: CAS 168823 (male; 41.9), 168825 (female; 54.7); MCZ A-13166 (paratype; female; 36.5). *Arthroleptis variabilis*.—CAMEROON: MCZ A-2654 (female, 34.6), A-3428–29 (females, 30.5, 29.4), A-46985 (male?, 35.0) A-136744 (female, 35.8), A-136775 (female, 28.7), A-136777–79 (females, 29.0, 29.0, 29.4), A-136820 (female, 34.6), A-136823–25 (females, 31.8, 29.6, 29.4), A-136827 (female, 33.5), A-136830 (female, 35.0), A-137297 (female, 35.6); USNM 563684 (female, 37.8), 563685 (male?, 26.3), 563686 (juvenile, 20.8), 563688 (male, 31.0), 563689 (female, 37.8); UTA A-35924 (female, 32.3), A-35933 (male, 32.1), A-35940 (female, 36.0), A-35949–50 (females, 34.7, 37.4), A-44447 (female, 35.4), A-44451 (female, 37.7); ZMB 15206 (syntype; female, 36.7), 70085–86 (syntypes; females, 30.8, 32.1). EQUATORIAL GUINEA: CAS 207817–819 (females, 34.0, 30.6, 35.4), 207820 (female?, 26.2), 207821–822 (female, 33.3, 36.1), 207823 (juvenile, 25.3), 207824–826 (females, 32.7, 33.4, 31.0), 207827 (female?, 26.9), 207828 (female, 35.9). *Arthroleptis wahlbergii*.—SOUTH AFRICA: MCZ A-22259 (female, 34.6); TMP 21316 (female?, 24.1), 21345 (female, 24.1), 21347 (female, 25.1), 22945 (female, 21.3), 23947 (female?, 25.6), 27871 (female, 22.4), 62729 (female, 23.5), 62730 (male, 18.4), 63540 (female, 20.9), 79048 (unknown, 18.8), 79403 (female, 18.4). *Arthroleptis zim-meri*.—GHANA: ZMB 8389, 27806 (syntypes; unknown, 19.2, 18.3).