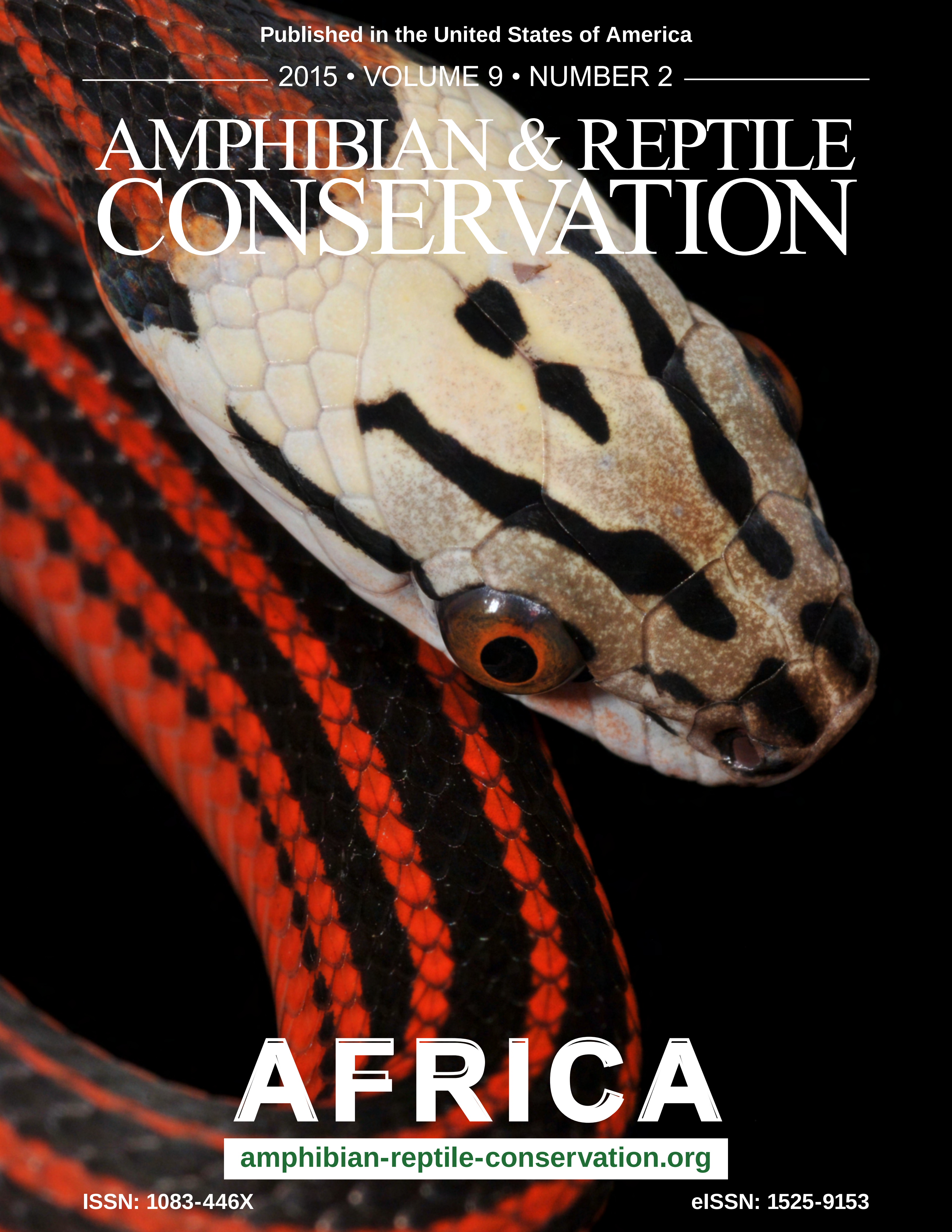

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The anuran fauna of a West African urban area

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***Abstract.*—Reported are the results of an amphibian survey in the district of Daloa and surroundings, in central-western Ivory Coast. Spanning a three year period, we investigated two general areas, each during the rainy and dry seasons. During 62 days of field work 30 anuran species were recorded. The urban environment mainly contained widespread anuran species with preferences for savannah-dominated landscapes and farmbush habitats. The recorded total anuran species richness in the urban area exceeded the diversity in the savannah islands/forest mosaic bordering the Daloa district. This indicates many savannah species may do well in urban situations. However, this higher species richness was only due to one site that possessed particularly diverse amphibian breeding sites, thus illustrating the necessity of maintaining suitable habitats for a wide-range of species. One of the most surprising findings was *Kassina schioetzi*, a species usually difficult to find in its natural habitat. In Daloa it seems to have successfully adapted to the urban conditions. Although the anuran richness in the Daloa area was relatively low compared to other Ivorian humid savannah areas, it supported an important part of the countries amphibian diversity. Nevertheless the forest habitats, and specifically the forest islands bordering the Daloa district, should be considered sensitive conservation areas.**

Key words. Amphibians, conservation status, Côte d'Ivoire, Upper Guinea, urban ecology

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West Africa has been experiencing intensive urbanization to such a point that human modified landscapes are gradually taking over the majority of natural landscapes, in particular native forests (Deikumah and Kudom 2010; Bible 2013). Whereas various Ghanaian forests are protected and/or sustainably managed (Adum et al. 2013; Ofori-Boateng et al. 2013), only very few Ivorian forest remnants receive sufficient protection and sustainable management (e.g., see Mayaux et al. 2004). The Ivorian population has exploded over the past four decades, tripling from 6.7 million in the early 1970s to approximately 22 million people today (Bible 2013), has largely accelerated an urbanization process causing massive environmental damage. The gradual disruption of forests, has worsened in several forested areas of the Ivory Coast during the prolonged political crisis in the first decade of the 21st century, has mainly stemmed from increase land demand for agriculture and urbanization (Bible 2013; Hansen et al. 2013).

The Haut-Sassandra region is traditionally an important trading center, particularly for cocoa production in the Ivory Coast, has attracted 44.8% of national and 23.4% of foreign farmers (Assiri et al. 2009). During the country's 2010–2011 post election violence, Daloa, the third largest city of the country and the regional capital of the Haut-Sassandra region, became a refuge for people from the northern, central, and western Ivory Coast, resulting in a rapid urbanization process. As one result, forests surrounding the city are increasingly fragmented. To enhance the protection of biological diversity, the Ivorian Ministry of Scientific Research has therefore recently recommended the collection of scientific information to update the biodiversity data of the Haut-Sassandra region. As data for amphibians were still lacking, we sur-

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veyed the amphibian fauna within the district of Daloa and its surroundings, and herein report for the first time an assessment of the species richness and composition of the anuran fauna in a West African urban area.

Methods

Study area. Daloa is the third largest city in the Ivory Coast and the regional capital of the Haut-Sassandra region. It is situated in central-western Ivory Coast (06°53’01.8”–06°94’97.8” N; 006°25’65.3”–006°68′89.0” W), in the transition zone between semi-deciduous forest and humid Guinea savannah. The town is an important trading center, particularly for cocoa. The region has a mean annual temperature of 26.3 °C; the annual precipitation ranges from 1,200 to 1,700 mm. The climate includes a long rainy season (April to June) with the highest precipitation peak in June, a short dry season (July to August) alternating with a short rainy season (September to October), and a long dry season (November to March). The relative mean humidity is 75% (Eldin 1971).

Description of the survey areas (Fig. 1). Our definition of an urban area follows McDonnell and Pickett (1993) and Demographia (2008), i.e., taking into consideration a minimum density of 400 humans/km^2 and other factors such as density of buildings, roads and other infrastructure. We surveyed two general areas: 1) the district of Daloa (urban area), and 2) the savannah islands/forest mosaic bordering the Daloa district (non-urban aspect). Our surveys were covering a three year period (see Appendix 1 for further details). We investigated four sites inside the urban area namely: Balouzon (Bal: 45 ha), Eveché (Eve: 50 ha), Gbokora (Gbo: 80 ha), and Tazibouo (Taz: 100 ha). As a comparison, we surveyed Sapia (Sap: 150 ha) and Zaibo (Zai: 190 ha), two non-urban sites in the savannah islands/forest mosaic adjacent to urban Daloa (see Appendix 1). The Balouzon and Eveché areas were mainly characterized by unpaved roads, a swampy area used for vegetable cultivation, and a concentration of buildings. A large stream, bordered by coconut trees and grasses, was used for fishing activities. The vegetation in Gbokora was dominated by grasses and a semi-deciduous forest interspersed by a highway. Some swampy areas surveyed in this site were being used for vegetable cultivation. This area was noisy due to heavy traffic. A concentration of buildings and streetlights were characteristic of the Gbokora site. The Tazibouo site mainly consisted of unpaved roads, buildings, semi-deciduous forest adjacent the Daloa Jean Lorougnon Guédé University, and some construction sites. This site also comprised the Theological and Pastoral Institute of Daloa whose garden was dominated by bamboo, other grasses, and several stands of different or-

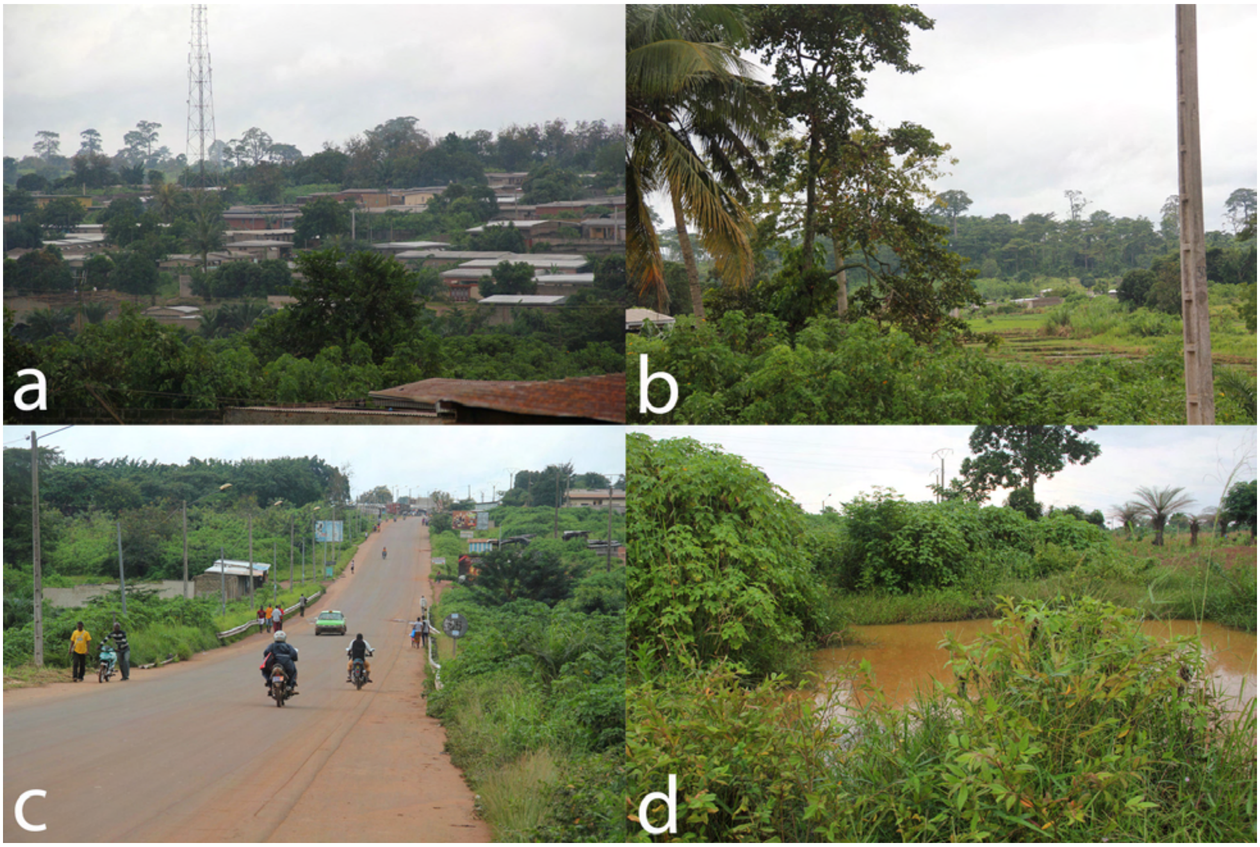

Fig. 1. Typical aspects of habitats of the urban Daloa; a = concentration of houses in a high population zone; b = degraded forest on the periphery of the urban area; c = highway crossing degraded forest and farmbush; d = amphibian breeding pond in the urban environment.

namental plants. Some water bodies, i.e., two large permanent ponds situated near a roadside and bordered by grasses, were encountered. The ponds served as a water point for cattle. A few termite mounds were also present. A swampy area investigated was used for rice and vegetable cultivations. Some parts of this area were lightened by streetlights at night. The sites Sapia and Zaibo, adjacent to the district of Daloa represented non-urban conditions. However, they had lost the majority of their natural forest cover, resulting in an overall change from a forest to a savannah-dominated landscape. Both sites mainly consisted of farmbush, small farms, coffee, and cocoa plantations. Some swamps that were part of these two sites had been converted to rice fields. Small forest islands were still encountered at Zaibo, but fewer forest islands were left at the Sapia site.

Field work, sampling effort and vouchers. Amphibians were mainly located opportunistically, during visual and acoustic surveys of all available habitats by NGK. Surveys were undertaken daily between 07:00–11:00 and 18:00–22:00 GMT over a total of 62 days (see Appendix 2) at all general survey areas. A hand-held GPS receiver (Garmin 12XL) was used to record the geographical positions of all study sites. The searching techniques used included acoustic surveying, visual scanning of terrain and refuge examination (e.g., lifting logs and rocks, peeling away barks, scraping through leaf litter, looking around or within burrows, and termite mounds). Amphibians encountered were not marked and repeated sightings thus cannot be excluded. As we only include presence/absence data and not abundances in our analyses this seem to be of negligible importance.

Below we comment only on a few species being remarkable concerning their distribution, taxonomy, biology or threats, or being particularly typical for the urban amphibian fauna. The nomenclature used herein follows the taxonomy by Frost (2015). After capture, frogs were identified to species level, measured, sexed, and if not kept as vouchers, released in their respective habitats. Snout-urostyle-length (SUL) was taken with a dial caliper (accuracy ± 0.5 mm). Records of *Xenopus muelleri* were based on visual observations only. For all other species we deposited vouchers at the Jean Lorougnon Guédé University, Daloa, Ivory Coast (see Appendix 3). Frog vouchers were euthanized humanly in a 1,1,1-Trichloro-2-methyl-2-propanol hemihydrate (MS222) solution and thereafter preserved in 70% ethanol.

Statistics. We used the daily species lists to calculate the sampling efficiency. We calculated the estimated species richness with the Chao2 and Jack-knife1 estimators (software: EstimateS, Colwell 2006). These estimators are incidence based, calculating with the presence/absence data of the daily species lists (62 days of survey work) for 30 anuran species. To avoid order effects we accomplished 500 random runs of the daily species lists. The Sørensen's Similarity Index (β) was used to determine the extent of similarity between the two main surveyed areas (herein the district of Daloa and the savannah islands/forest mosaic bordering the Daloa district; β may vary from 0 to 1 (Sørensen 1948; Wolda 1981).

Results

Species richness and faunal similarities

In total we recorded 30 anuran species (Table 1). Acoustics indicated more than one *Arthroleptis* species live in our area. So far, it is not possible to separate taxa from

Table 1. Anuran species recorded in the urban and non-urban areas of Daloa, with sites (see Appendices 1–3), general habitat preference and distribution range. S = savannah, FB = farmbush (degraded forest and farmland), F = forest, A = Africa (occur also outside West Africa), WA = West Africa (defined as the area west of the Cross River in Nigeria), UG = Upper Guinea (forest zone west of the Dahomey Gap), E = endemic to Ivory Coast and eastern Guinea, * = taxon comprise complex of several species, ** = records on this survey comprise several species (according to acoustics).

Family / Species	Site	Habitat			Distribution			
		S	FB	F	A	WA	UG	E
Arthroleptidae								
Arthroleptis spp.**	Bal, Eve, Gbo, Sap, Taz, Zai	—	X	X	—	—	X	(?)
Leptopelis spiritusnoctis	Zai		X	X	—	X	—	—
L. viridis	Bal, Eve, Gbo, Taz	X	—	—	X	—	—	—
Bufonidae								
Amietophrynus maculatus	Gbo, Sap, Taz, Zai	X	X	—	X	—	—	—
A. regularis	Taz	X	X	—	X	—	—	—
Dicroglossidae								
Hoplobatrachus occipitalis	Bal, Eve, Gbo, Sap, Taz, Zai	X	X	—	X	—	—	—
Hemisotidae								
Hemisus marmoratus	Taz, Zai	X	X	—	X	—	—	—
Hyperoliidae								
Afrixalus dorsalis	Bal, Eve, Gbo, Sap, Taz, Zai	X	X	—	X	—	—	—

Table 1 (continued). Anuran species recorded in the urban and non-urban areas of Daloa, with sites (see Appendices 1–3), general habitat preference and distribution range. S = savannah, FB = farmbush (degraded forest and farmland), F = forest, A = Africa (occur also outside West Africa), WA = West Africa (defined as the area west of the Cross River in Nigeria), UG = Upper Guinea (forest zone west of the Dahomey Gap), E = endemic to Ivory Coast and eastern Guinea, * = taxon comprise complex of several species, ** = records on this survey comprise several species (according to acoustics).

Family / Species	**Site**	**Habitat**			**Distribution**			
Hyperoliidae (cont.)		S	FB	F	A	WA	UG	E
Hyperolius concolor concolor	Bal, Eve, Gbo, Sap, Taz, Zai	X	X	—	—	—	X	—
H. fusciventris fusciventris	Sap		X	X	—	—	X	—
H. guttulatus	Zai	X	X	—	X	—	—	—
H. nitidulus	Bal, Eve, Gbo, Sap, Taz	X	—	—	—	X	—	—
H. picturatus	Gbo, Sap, Taz, Zai	—	X	X	—	—	X	—
H. sp.	Taz	—	X	X	—	—	X	—
Kassina schioetzi	Taz	X	X	—	—	—	X	—
K. senegalensis	Sap, Taz	X	—	—	X	—	—	—
Phrynobatrachidae								
*Phrynobatrachus calcaratus**	Sap	—	X	X	X	—	—	—
P. francisci	Bal, Taz	X	—	—	—	X	—	—
*P. gutturosus**	Sap, Taz, Zai	X	X	X	—	—	X	—
P. latifrons	Bal, Eve, Gbo, Sap, Taz, Zai	X	X	—	X	—	—	—
Phrynomeridae								
Phrynomantis microps	Taz	X	—	—	X	—	—	—
Pipidae								
Xenopus muelleri	Taz	X	—	—	X	—	—	—
Ptychadenidae								
Ptychadena bibroni	Bal, Eve, Gbo, Sap, Taz, Zai	X	X	—	X	—	—	—
*Ptychadena mascareniensis**	Bal, Eve, Gbo, Sap, Taz, Zai	X	X	—	X	—	—	—
Ptychadena oxyrhynchus	Sap, Taz, Zai	X	X	—	X	—	—	—
Ptychadena tournieri	Sap, Taz	X	—	—	—	X	—	—
Ptychadena pumilio	Bal, Eve, Gbo, Sap, Taz, Zai	X	X	—	X	—	—	—
Ptychadena tellinii	Taz	X	—	—	X	—	—	—
Ranidae								
Amnirana albolabris	Sap, Zai	—	X	X	X	—	—	—
A. galamensis	Taz	X	—	—	X	—	—	—

the *Arthroleptis poecilonotus*-complex based on morphology. They can be distinguished by advertisement call and genetic characters. However, assigning populations, based on these characters, to available names (indistinguishable museum types without molecular data) is not possible (for a short review of the taxonomic situation in West African *Arthroleptis* spp. see Rödel and Bangoura 2004). We thus provisionally lumped all records of this genus as *Arthroleptis* spp. A list of recorded anurans with site records, known habitat preference and their distribution ranges is given in Table 1.

Based on the daily species lists we calculated our sampling efficiency. The Jack-knife 1 estimator calculated 33 anuran species, the Chao 2 estimator estimated 31 species for the study area. We hence recorded almost the entire (94% and 99%, respectively) estimated species richness. More than one fifth of the encountered species (seven spp., 23%; Table 1) depend on forest but tolerate farmbush habitats (degraded forest). Nine species (30%) are very closely associated with savannah habitats. Thirteen species (43%) exhibit a strong preference for savannah and farmbush habitats and are normally not found in forest. Four species (13%) do not occur outside West Africa [defined as the area west of the Cross River in Nigeria; see Penner et al. (2011)], and are often restricted to smaller parts of West Africa. Seven of all recorded species (23%) occur only in the Upper Guinea forest zone (forests west of the Dahomey Gap). The total number of species recorded in the district of Daloa was 25, while the species richness in the adjacent savannah/forest mosaic was 21. However, the high species number for Daloa was mainly due to one site (Tazibouo). When excluding this

Table 2. Sørensen's similarity values for pairwise comparisons of the anuran community between the six surveyed sites (see text and Appendix 1).

Sites	Eve	Gbo	Taz	Sap	Zai
Bal	0.95	0.87	0.61	0.62	0.59
Eve	–	0.91	0.57	0.64	0.61
Gbo	–	–	0.65	0.67	0.71
Taz	–	–	–	0.65	0.63
Sap	–	–	–	–	0.71

site diversity was higher in the savannah/forest mosaic. The number of species common to both areas was 16 (Sørensen's Similarity Index β: 0.70). Within the district of Daloa we recorded 11 species in Balouzon, 10 species in Eveché, 12 in Gbokora, and 25 in Tazibouo. Within the savannah/forest mosaic we recorded 18 and 16 species in Sapia and Zaibo, respectively.

The results of the Sørensen's similarity for pairwise comparisons in the six surveyed sites are presented in Table 2. At least more than 50% of the recorded species were similar between sites. The anuran fauna of Daloa urban area was most similar to that of the Comoé National Park, a savannah area in northern Ivory Coast (β: 0.72). With 68% and 66% faunal similarity the Lamto Faunal Reserve and the Marahoué National Park, which are situated in the same vegetation zone as Daloa, were very similar to the Daloa fauna. Other Ivorian protected areas such as the Mont Péko and Mont Sangbé National Parks comprise savannah and real rainforest zones and thus consequently differed in their faunal composition, compared to Daloa (Table 3).

Species accounts

Amietophrynus regularis (Reuss, 1833) – The genus *Amietophrynus* currently encompasses 40 species of true African toads [Frost 2015; although this list also contains non-vaild taxa such as *Amietophrynus chudeaui* (Chabanaud, 1919) see Rödel (2000)]. *Amietophrynus regularis* has a wide distribution in Africa and inhabits a broad range of habitats from moist and dry savannahs, montane grassland, forest margins, and agricultural habitats, as well as human settlements, often in association with rivers (Rödel 2000; Channing and Howell 2006). In our urban sites *A. regularis* (Fig. 2) seemed to reach its highest abundances directly around human settlements. At night, it was found in gardens, around houses, parking areas, buildings, or below streetlights, preying mostly on insects. During the day, it was found under rocks or logs. The most imminent threat to the toad's survival in the city of Daloa is its exploitation for scientific courses at the university. Every year several hundred individuals are collected by students and subsequently killed and dissected in anatomy courses. This exploitation seems to have reached a point where the species is becoming rare in the city. However, concerning the entire range of the species, it is very common and of Least Concern (IUCN 2015).

Hoplobatrachus occipitalis (Günther, 1859) is the most commonly consumed frog species in West Africa. The frog trade varies regionally from e.g., local scale in Burkina Faso, to intensive cross-border trade in northern Benin and Nigeria (Mohneke et al. 2009, 2010). The consumption of *H. occipitalis* (Fig. 3a) has recently increased to a considerable extent in the Ivory Coast where this species is an important component of animal protein in some local populations (NGK, unpubl. obs.). In Daloa, the trade of *H. occipitalis* mainly took place on a local scale at the different markets of the district. Usually a batch of five adult specimens was sold for 500.00 FCFA (app. 0.84 USD). Frog meat are sold fresh (Figs. 3b, c) or dried (Fig. 3d). It is used in soups, stews, or sauces by the local populations. The local price in Daloa markets was mean to low compared to prices recorded in Burkina Faso and Nigeria, respectively. According to Mohneke et al. (2010), in Burkina Faso, the price for one frog depended on its size and varied between 25.00 FCFA for a small frog, up to 250.00 FCFA (0.05 USD and 0.50 USD) for a large one. In Nigeria, they reported one bag containing at least 1,000 frogs cost 26.94–40.40 USD on purchase and 40.40–67.34 USD at sale. In the urban area of Daloa hard data on harvested frog numbers and respective consequences for the local populations are lacking. The local trade of *H. occipitalis* hence needs more attention and detailed investigation.

Hyperolius concolor concolor (Hallowell, 1844)(Fig. 4) is a typical West African farmbush species living in degraded forest of the forest zone and gallery forests in the savannah zone (Schiøtz 1967; Rödel 2000). It seemed to do very well under urban condition and was hence among the most widespread species recorded in the ur-

Table 3. Sørensen's similarity value (β) between the anuran fauna of the Daloa urban area and other Ivorian areas, and respective species richness; twenty-five species were recorded in urban Daloa (this study); NP= national park; FR= faunal reserve.

Area	Species richness	Number of species common with the Daloa urban area	β-value (Sørensen)	Source
Comoé NP	33	21	0.72	Rödel and Spieler (2000)
Lamto FR	40	22	0.68	Adeba et al. (2010)
Marahoué NP	33	19	0.66	Rödel and Ernst (2003)
Mont Péko NP	33	11	0.38	Rödel and Ernst (2003)
Mont Sangbé NP	45	20	0.57	Rödel (2003)

Fig. 2. *Amietophrynus regularis* female recorded in the garden of the Theological and Pastoral Institute of Daloa.

ban sites of Daloa (Table 1); it was particularly abundant among grasses near ponds. In the rainy season we recorded some, presumably migrating, individuals on windows, balconies, and in houses.

Hyperolius sp. – The genus *Hyperolius* Rapp, 1842 is one of the most diverse African anuran genera with currently approximately 28 species occurring in West Africa (Schiøtz 1967, 1999; Frost 2015). A major taxonomic problem is many species of this genus are highly variable (e.g., Schiøtz 1999). On 15 September 2013, at around 07h00 GMT, we found a *Hyperolius* on humid ground in the Tazibouo site, within the garden of the Theological and Pastoral Institute, after it had rained heavily the night before. Our individual lacked a vocal sac and gland and hence is either female or juvenile (Fig. 5). It resembles either a juvenile *H. picturatus* or a newly metamorphosed individual phase J of *H. sylvaticus ivorensis*, which is normally brownish to green with paired undelimited dorsolateral stripes, and an hourglass pattern (Schiøtz 1999). The size of our reed frog was 20 SUL, thus exceeding the size of freshly metamorphosed *Hyperolius* of most species (compare e.g., Schiøtz 1967; Rödel 2000). Its dorsal surface was beige with a greenish grey hourglass pattern. The iris was golden, the anterior and posterior sides of pupil were red. The ventral surface was whitish. Without having male specimens and advertisement calls available it cannot be decided if this frog represents an undescribed species or only an atypical, but known *Hyperolius* species.

Kassina schioetzi Rödel, Grafe, Rudolf, and Ernst, 2002 was known so far from the Mont Péko National Park, the Marahoué and Comoé National Parks, and the Lamto Faunal Reserve, all situated in the Ivory Coast (Rödel et al. 2002; Rödel and Ernst 2003; Adeba et al. 2010). It lives along the savannah forest edge, reaching into the savannah zone along rivers. The species may also occur in Bia National Park, western Ghana, but a voucher from there exhibited a mixture of characters with *K. cochranae* (Hillers et al. 2009). *Kassina schioetzi* is usually hard to find in all localities so far investigated (see above and own experience of the authors). In the district of Daloa (Tazibouo), some males were observed calling at night from more exposed sites (Fig. 6). We also encountered a small number of other males calling in a bamboo patch within the Theological and Pastoral Institute, and at a grassy roadside in the vicinity of a large pond. Our recorded males measured 32.1 ± 1.6 (SUL, *n* = 4), thus being within the known range of *K. schioetzi* (Rödel et al. 2002).

Leptopelis viridis (Günther, 1868) (Fig. 7) is one of the most characteristic species inhabiting the West African savannahs and the degraded areas of the former rainforest belt. As a synanthropic species, it also lives in villages (Schiøtz 1967; Rödel 2000). It is one of the most widespread anurans in the urban sites of Daloa. *Leptopelis viridis* was found around houses, and in gardens. The majority of the recorded males were found at night calling exposed on the ground between short grasses, which is in contrast to the calling sites in natural habitats. There the species calls, often from high perch sites, in bushes and trees (Grafe et al. 2000; Rödel 2000).

Phrynomantis microps Peters, 1875 is a medium-sized microhylid frog inhabiting the savannah regions of West Africa (Hirschfeld and Rödel 2011) where it hides in burrows or empty termite mounds during the day and the dry season. The frog was also observed to occupy and live essentially unharmed in the nest of the highly aggressive ant species – *Paltothyreus tarsatus* (e.g., Rödel and Braun 1999; Rödel et al. 2013). In Daloa, *P. microps* was heard calling at night in tufts of grass around houses after heavy rainfalls. In the garden of the Theological and Pastoral Institute, a calling male was observed in association with an Emperor Scorpion (*Pandinus imperator*) in a hole behind the wall of a building. The association of *P. microps* with scorpions has also been reported by Rödel and Braun (1999) and Rödel (2000). We captured another male (Fig. 8) on 08 September 2013 around 22h00 GMT at the edges of a wide roadside pond beside the Theological and Pastoral Institute.

Xenopus muelleri (Peters, 1844) is an aquatic species inhabiting the West African savannah ponds of highly variable size during the rainy season and the edges of rivers during the dry season (Rödel 2000). In the urban site Tazibouo, the frog was observed to live in holes drilled in the ground by the national company of water distribution. The depths of these holes varied from 0.7–1.20 m.

Discussion

Despite their importance to ecosystem functions (Mohneke and Rödel 2009; Hocking and Babbitt 2014), amphibians are still among the least studied vertebrates particularly in urban and suburban areas in the tropics (Hamer and McDonnell 2008; Pickett et al. 2001). Almost 85% of amphibian species threatened by urbanization are encountered in the tropics (IUCN, Conservation International and NatureServe 2006). Many factors are known to negatively influence the herpetofauna inhabiting big cities. Among these factors are habitat loss, habitat fragmentation, isolation, pollution, over harvesting, and road traffic (Hammer and McDonnell 2008; Perry et al. 2008; Stuart et al. 2008; Deikumah and Kudom 2010; Tonini et al. 2011). However, many species are able to adapt to urban conditions and sometimes urban areas may even surprise with the discovery of scientifically new species (Newman et al. 2012; Feinberg et al. 2014; Howlader et al. 2015). This also concerns the Ivorian city of Abidjan where a monotypic genus *Morerella cyanophthalma* and a night-frog *Astylosternus laticephalus* have recently been discovered and described (Rödel et al. 2009, 2012).

With its geographic position in a transition zone between the semi-deciduous forest and humid savannah, we expected the urban landscape of Daloa region to promote a diverse amphibian fauna. However, the overall species richness (30 spp.) was lower compared to the species richness recorded in western, central, and northern Ivorian savannah areas, for instance the Mont Sangbé National Park (45 species, Rödel 2003), Lamto Faunal Reserve (40 species, Adeba et al. 2010), Marahoué and Mont Péko National Parks (33 species for each park, Rödel and Ernst 2003), or the Comoé National Park (33

Fig. 3. *Hoplobatrachus occipitalis* from the district of Daloa (a) and a woman trading this species on a local market (b); batches of five adult specimens, fresh (b and c) or dried (d), were sold for 500.00 FCFA (app. 0.84 USD).

Fig. 4. A calling *Hyperolius concolor concolor* male recorded at the garden of the Theological and Pastoral Institute of Daloa.

Fig. 5. Dorsolateral view of a juvenile *Hyperolius* sp. with uncertain taxonomic status from the urban Daloa.

species, Rödel and Spieler 2000). Compared to these and other West African savannah areas with known amphibian assemblages such as north-western Benin (Nago et al. 2006), east-central Guinea (Greenbaum and Carr 2005), central-northern Guinea (Hillers et al. 2008a), or eastern Ghana (Leaché et al. 2006), the urban landscape of Daloa ranks among the West African areas of medium to low amphibian species richness. While we recorded few forest related species e.g., *Amnirana albolabris*, *Leptopelis spiritusnoctis*, *Phrynobatrachus calcaratus*, and *P. guttturosus* (Rödel and Branch 2002; Assemian et al. 2006; Kouamé et al. 2014; Kpan et al. 2014; the latter two species comprising out of cryptic species with savannah and forest specialists), most of the recorded frogs were widespread species with preferences for savannah-dominated landscape and farmbush habitats. The six surveyed sites all shared at least half of their species with all other sites. We observed the highest species richness at the Tazibouo site (25 spp.) which was the only urban site comprising various suitable breeding habitats. For instance in the

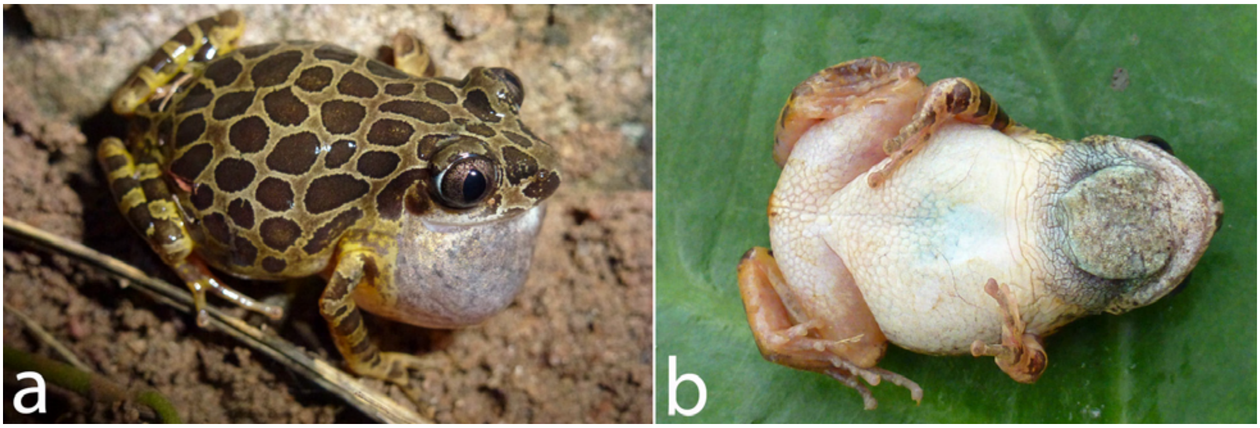

Fig. 6. *Kassina schioetzi* from Daloa urban area; shown is a male calling from the ground (a), and its whitish venter and almost circular gular gland (b) characteristic for the species.

garden of the Theological and Pastoral Institute, ephemeral and perennial wetlands, well-suited for the co-existence of species with different reproductive strategies were present: e.g., very small temporary breeding sites (*Phrynobatrachus* spp.), larger, almost permanent breeding sites (*Afrixalus dorsalis*, *Hyperolius concolor*, *Kassina schioetzi*, *K. senegalensis*, *Phrynomantis microps*), and humid places for species with terrestrial direct development (*Arthroleptis poecilonotus*-group). This garden also played an important role in providing refuge for several other species in particular during the heat of the day and the dry season.

In addition to the fact that many amphibian species depend on different but complementary habitats (e.g., aquatic sites for the tadpoles, terrestrial site of the metamorphosed individuals), their populations are usually structured as meta-populations (Pope et al. 2000; Marsh and Trenham 2001). Urbanization and in particular fragmentation and isolation of habitats by roads and other urban infrastructure is reducing the connectivity of population networks (Vos and Chardon 1998). Hence, we expected to record lower amphibian diversity in the district of Daloa than in the savannah-forest mosaic adjacent to this district. Surprisingly, the total anuran richness in the urban environment was higher than in the adjacent savannah-forest mosaic. This result indicates many amphibian species may survive under urban situations, such as in the district of Daloa. However, this high total species richness was due to only one of four urban sites, i.e., the Theological and Pastoral Institute, comprising many different habitat types and particularly diverse breeding sites. The other urban sites actually had slightly lower species richness than the non-urban sites. This illustrates a high amphibian diversity in urban areas may be maintained and even exceed such as of nearby non-urban areas; however, this can only be achieved by offering a wide range of different habitats suitable for various amphibian species.

Apart from roads potentially reducing or ceasing gene flow, amphibians further face direct threats in urban areas, in the form of the collection of anurans for anatomy and food consumption. Compared to European towns (e.g., Mollov 2005), however, there are still plenty of habitats available to amphibians, the traffic is usually less intense as many of the roads remain unpaved allowing frogs to cross. In fact our non-urban sites were all within a matrix of agricultural land and thus most likely prone to a variety of pesticides which could be a higher threat than the threats experienced in towns. The adaptability of amphibians within the urban development seemed to be species-specific and was highly variable even between sites. For example some species such as *Hyperolius guttulatus*, *H. fusciventris fusciventris*, *Amnirana albolabris*, *Leptopelis spiritusnoctis*, and *Phrynobatrachus calcaratus*, encountered in the savannah-forest mosaic outside of Daloa were never found in the urban sites. This is most likely due to the fact that their specific habitats are no longer present. For instance *Hyperolius guttulatus* breeds almost exclusively in very large and deeper ponds (Rödel 2000; Schiøtz 1967, 1999); and *Phrynobatrachus calcaratus* typically lives at rain forest edges or in gallery forests in the savannah zone (Rödel 2000). Respective habitat types for both latter species were not found in the urban environment. It is known that in forested areas the alteration of the microclimate, due to degradation of the vegetation structure, causes a shift in species composition (Ernst and Rödel 2005, 2006; Hillers et al. 2008b; Ofori-Boateng et al. 2013). Such effects might be even worse in the usually more open habitats of urban areas.

Conclusion

The study is indicating that an unexpected high number of anuran species seem to be able to survive in a current African city. However, this is not the case for all species. For those species the protection of natural forest and savannah ecosystems is very important. The forest habitats, and specifically the forest ‘‘islands” bordering the Daloa district, should thus be considered sensitive areas and dispersal corridors need to be maintained. Within the

Fig. 7. Dorsolateral view of *Leptopelis viridis*, one of the most widespread anurans from the Daloa urban area.

Fig. 8. Dorsolateral view of a male *Phrynomantis microps* from Daloa urban area.

urban areas, the availability of a diverse set of habitats is a prerequisite for the maintenance of high amphibian species richness.

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Appendix 1. Geographic position and short description of study sites in the Daloa study area.

Site	Latitude (N)	Longitude (W)	Elevation (m a.s.l.)	Habitat description
Bal	N06°53'64.5"	W006°25'65.3"	259	Highway; grassy habitats; heavy traffic; dense human population
Eve	N06°53'01.8"	W006°26'05.9"	261	Large stream bordered by coconut trees and grass; unpaved roads; concentration of buildings; swampy area used for vegetable cultivation; dense human population
Gbo 1	N06°54'15.8"	W006°27'15.3"	265	Semi-deciduous forest patch; swampy area dominated by grassy vegetation; buildings; highway, heavy traffic; streetlight; swampy area partly used for vegetable cultivation; dense human population
Gbo 2	N06°54'03.4"	W006°27'09.6"	275	Buildings; shrubby vegetation; unpaved roads; highway; dense human population
Sap 1	N06°87'20.8"	W006°37'83.8"	239	Subsistence farming; rice field in a swampy area; high grassy vegetation
Sap 2	N06°87'22.8"	W006°37'93.7"	260	Forests islands; cocoa plantation at edge of a rice field; high grassy vegetation
Sap3	N06°87'37.1"	W006°38'09.7"	276	Stream crossing cocoa plantation; palm tree at edge of the water body; plantain and coffee plantations
Sap 4	N06°86'83.8"	W006°38'99.3"	244	Swampy area; high grassy vegetation; rice field; humid savanna; tracks
Sap 5	N06°86'83.8"	W006°37'61.5"	229	Rice field in a swampy area; coconut trees at edge
Taz 1	N06°90'42.8"	W006°43'97.4"	274	Semi deciduous forest patch close to the Jean Lorougnon Guédé University; garden of the Theological and Pastoral Institute, dominated by bamboo, grasses and stands of different ornamental plants; two large wide ponds surrounded by vegetation (Asteraceae); streetlight; unpaved roads, concentration of buildings; dense human population
Taz 2	N06°90'33.7"	W006°43'78.9"	268	Swampy area; buildings; rice field; vegetable cultivation; many constructions of houses underway
Zai 1	N06°94'97.8"	W006°67'35.7"	223	Swamps within a semi deciduous forest; stream; ponds; grassy vegetation; clearing; rice field; cocoa plantation
Zai 2	N06°94'33.6"	W006°68'89.0"	222	Very large rice field; high grasses; edge of coffee and cocoa plantations; forest patch
Zai 3	N06°94'65.9"	W006°66'58.7"	209	Rice field crossed by a stream: coffee plantation; tracks; forest patch

Appendix 2. Amphibian survey periods in the urban and non-urban areas of Daloa (compare Appendix 1).

Site	Surveyed periods						
	10–21 Aug. 2011	27 Aug.–1 Sep. 2011	27 Sep.–1 Nov. 2012	16–25 Aug. 2013	18–27 Oct. 2013	18–27 Jun. 2014	16–24 Aug. 2014
Urban area	**6 days**	**2 days**	**1 day**	**6 days**	**2 days**	**6 days**	**3 days**
Bal	6	2	1	6	2	6	3
Eve	6	2	1	6	2	6	3
Gbo	6	2	1	6	2	6	3
Taz	6	2	1	6	2	6	3
Non-urban area	**6 days**	**4 days**	**4 days**	**4 days**	**8 days**	**4 days**	**6 days**
Sap	3	2	2	2	4	2	3
Zai	3	2	2	2	4	2	3
Total days	**12**	**6**	**5**	**10**	**10**	**10**	**9**

Appendix 3. List of amphibian voucher specimens from the district of Daloa and surroundings. Given are field and collection numbers (NG), collection site (compare Appendix 1) and collection date.

Arthroleptidae: *Arthroleptis* spp.: NG001 (Taz, 08 Nov. 2011); NG002 (Sap, 16 Oct. 2013); NG003 (Zai, 23 Oct. 2013); *Leptopelis spiritusnoctis*: NG004 (Zai, 23 Oct. 2013); *L. viridis*: NG005 (Taz, 24 Oct. 2011); NG006 (Taz, 30 Oct. 2013); **Bufonidae**: *Amietophrynus maculatus*: NG007 (Zai, 25 Oct. 2013); *A. regularis*: NG008 (Taz, 19 Oct. 2011); **Dicroglossidae**: *Hoplobatrachus occipitalis*: NG009 (Taz, 25 Oct. 2011); **Hemisotidae**: *Hemisus marmoratus*: NG010 (Taz, 08 Sep. 2010); NG011 (Sap, 25 Oct. 2013); **Hyperoliidae**: *Afrixalus dorsalis*: NG012 (Taz, 18 Aug. 2011); *Hyperolius concolor concolor*: NG013 (Taz, 18 Aug. 2011); NG014 (Sap, 18 Oct. 2013); *H. fusciventris fusciventris*: NG015 (Sap, 19 Oct. 2013); *H. guttulatus*: NG016 (Zai, 23 Oct. 2013); NG017 (Zai, 25 Oct. 2013); *H. nitidilus*: NG018 (Taz, 25 Aug. 2011); NG019 (Sap, 16 Oct. 2013); *H. picturatus*: NG020 (Taz, 01 Sep. 2011); NG021 (Sap, 18 Oct. 2013); NG022 (Taz, 23 Oct. 2013); *H.* sp.: NG023 (Taz, 15 Sep. 2013); *Kassina schioetzi*: NG024–027 (Taz, 08 Sep. 2013); *K. senegalensis*: NG028 (Taz, 17 Aug. 2011); NG029 (Taz, 30 Aug. 2013); **Microhylidae**: *Phrynomantis microps*: NG030 (Taz, 08 Sep. 2013); **Phrynobatrachidae**: *Phrynobatrachus calcaratus*: NG031–036 (Sap, 19–20 Oct. 2013); *P. francisci*: NG037–038 (Taz, 01 Sep. 2011); NG039 (Taz, 17 Aug. 2013); *P. gutturosus*: NG040 (Taz, 19 Aug. 2013); NG041 (Sap, 20 Oct. 2013); *P. latifrons*: NG042 (Taz, 20 Aug. 2011); NG043 (Taz, 25 Aug. 2011); NG044 (Sap, 19 Oct. 2010); NG045 (Zai, 23 Oct. 2013); **Ptychadenidae**: *Ptychadena bibroni*: NG046 (Taz, 09 Sep. 2012); NG047 (Zai, 24 Oct. 2013); *P. tellinii*: NG048 (Taz, 01 Sep. 2013); *P. mascareniensis*: NG049 (Taz, 16 Sep. 2013); NG050 (Zai, 24 Oct. 2013); *P. oxyrhynchus*: NG051–052 (Taz, 06 Sep. 2012); NG053 (Zai, 24 Oct. 2013); *P. pumilio*: NG054 (Taz, 16 Sep. 2013); NG055 (Sap, 19 Oct. 2013); *P. tournieri*: NG056 (Taz, 10 Sep. 2012); **Ranidae**: *Amnirana albolabris*: NG057 (Sap, 19 Oct. 2013); *A. galamensis*: NG058 (Taz, 24 Aug. 2014).

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The reptiles of the summits of Mont Oku and the Bamenda Highlands, Cameroon*

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***Abstract.*—The list of the non-avian reptiles occupying the summits above 1,400 m elevation of Mount Oku and the Bamenda Highlands in Cameroon comprise 50 species (one tortoise, 18 lizards, and 31 snakes) belonging to 12 families and 29 genera. This assemblage has a high biogeographic interest because it harbors species with a large altitudinal spectrum and several high elevation endemic forms (submontane). Those species are currently severely threatened by human expansion in the area. Human impacts include direct collections of several endemic species with a high commercial value for the international pet trade, but most importantly deforestation and the growing encroachment of people, cattle, and agriculture. Efficient actions are urgently needed to preserve this unique heritage for future generations.**

Key words. Biogeography, conservation, biodiversity, afro-montane herpetofauna

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Introduction

African mountain formations clearly show an island-like distribution pattern, which explains their high biogeographical disposition and the importance of those mountain ranges for the conservation of their distinctive fauna (Gartshore 1986; Fjeldsa and Lovett 1997). The Cameroon Volcanic Dorsal extends in its southern part for 800 km, and is represented by a succession of insular-like reliefs (true or continental islands). It begins with the island of Annobón (elevation 655 m; Equatorial Guinea), located more than 360 km from the African mainland, and extends through the islands of Sao Tomé (2,024 m), Principe (948 m) and Bioko (formerly called Fernando Poo; 3,106 m). It continues on to the mainland, including the highest volcanic summit of Western Africa, Mount (Mt.) Cameroon, which rises to 4,085 m. North of Mt. Cameroon, emerge Mt. Nlonako (1,822 m), the important volcanic range of Manengouba (2,411 m), and the reliefs of the Bakossi Highlands. North of those first reliefs stands an imposing orographic set which includes most of the Highlands generally called the Bamenda Highlands (BH). Towards the south it starts with a large and elevated volcanic edifice, the Bamboutos Mountains (2,740 m). Through the Santa Range (Mt. Léfo or Peak of Santa, 2,550 m elevation), the Bamboutos Mountains connect to the main peak, Mt. Oku, at 3,011 m. Elevations then decrease relatively quickly before joining the northern part of the Cameroon Volcanic Dorsal that ends with the Tchabal Mbabo (2,460 m). The relief then undergoes an eastern shift in their orientation, to fit the septentine border of the Adamaoua, with the smaller peaks of Mt. Alantika (1,885 m) and Mt. Mandara (1,442 m) separated by the depression of the Benoue valley, which does not exceed 150 m elevation.

The central axis of the Cameroon Volcanic Dorsal has lateral extensions including more or less important bastions, including on the western flank, Mts. Rumpi (1,764

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*This paper was written in homage to our late colleague and friend Dr. Odile Bain (CNRS, MNHN).

m) and in Nigeria, Sonkwala (also called Obudu Plateau) and Gotel (2,418 m). In the east stand Mts. Bana (2,097 m), Mbapit (1,989 m), Nkogam (2,263 m), and Mbam (2,335 m). The majority of these mountains truly function like islands for orophilous species because their elevation is substantially higher than surrounding territories of low elevation (at most 100 m), thus usually prohibiting the faunal exchange of climatically demanding, orophilous species between neighboring mountain ranges.

To the northeast of the Cameroon Volcanic Dorsal rests the largely tabular area of the Adamaoua, a vast middle mountain barrier extending from east to west. Mean elevation of that central Cameroon relief stays relatively low (about 1,100 m), but is contiguous with the high western ranges and functions as a faunistic exchange corridor, creating a zone of biogeographical interest. It is indeed increasingly recognized that under the colder climate of the Plio-Pleistocene climatic oscillations, the Adamaoua represent a refugia, an efficient "hyphen" between the Cameroon Volcanic Dorsal and the mountains scattered across the eastern edge of the Congo Basin in Eastern Africa (Wagner et al. 2008; Barej et al. 2011). Some imposing volcanic relief is strewed on the Adamaoua Plateau, especially towards its septentine rim. The most important, about 40 km east of the city of Ngaoundere, is the Hossere Nganha, which reaches 1,923 m elevation and is a location where some endemic species of reptile and amphibians are encountered (Amiet 1971; Ineich and Chirio 2004).

In Cameroon, the highest peaks (above 2,000 m) are located at Mt. Cameroon, Mts. Bamboutos, Mt. Oku, and at Tchabal Mbabo. With the exception of Mt. Cameroon, those formations have been significantly degraded by man and most often comprise only forest remnants within montane grasslands grazed by the abundant cattle of the Fulani herdsmen (Fig. 1).

Mt. Oku (rarely called Mt. Kilum: 6.12°N and 10.28°E, elevation 3,011 m) is located in the most septentine part of the BH, not far from the transition zone between mountain forest and savanna. Summits above 2,800 m are covered with an afro-alpine grassy lawn (Fig. 1), devoid of trees, in which there is even a bog. The north side is home to one of the best-preserved mountain forest fragments in the region (Figs. 2, 3). An associated vegetation is also found there including wet mountain forests, which are well developed around Lake Oku (6°12'N and 10°27'E), and a crater lake located about 2,300 m above sea level. Another lake, Lake Bambili (5°56'N and 10°15'E), is present in the region. Cattle herds are common around the massif and even into the montane forest protected areas. These forests are important elements in the economy and local culture as they allow the production of a wide range of forest products essential to the survival of local populations (wood, honey, and medicinal plants, e.g., *Prunus africanus* used in the treatment of prostate cancer and subjected to strict control by the Washington Convention on International Trade of Endangered Species) (Figs. 4, 5). Scared and felled trees are visible even in the forest reserves, and caused by the overflow of human activity along the many forest paths and trails that allow easy access (Macleod 1987) (Fig. 2).

This report provides a critical inventory of the reptile species recorded from the summit area (above 1,400 m elevation) of the BH, demarcated by the valley that separates it from Manengouba/Mt. Cameroon (less than 700 m) and the Tikar Plain that separates it from Tchabal Mbabo (Fig. 6). We also discuss the biogeographic affinities of the study region. Many of the reptiles found there are

Fig. 1. The beautiful cattle of the Fulani herdsmen observed on pastures high in the region of Mt. Oku are fat and healthy. 6.21°N and 10.44°E. *Picture: I. Ineich, May 8, 2007.*

Fig. 2. The path leading from Oku Elak village to the summit of Mt. Oku is very popular and easy to access. *Picture: I. Ineich, May 6, 2007.*

Fig. 3. Just before the summit of Mt. Oku, the vegetation is covered with dense epiphytic altitude plants. *Picture: I. Ineich, May 6, 2007.*

Fig. 4. Villagers apply strong pressure on the fauna and flora of Mt. Oku forests. It is common to find traps to catch bush meat, here a brush-tailed porcupine (a forest porcupine species). *Picture: I. Ineich, May 6, 2007.*

Fig. 5. Hives, placed high in the trees almost to the top of Mt. Oku (here), produce a thick, white honey of excellent quality, highly sought after. *Picture: I. Ineich, May 7, 2007.*

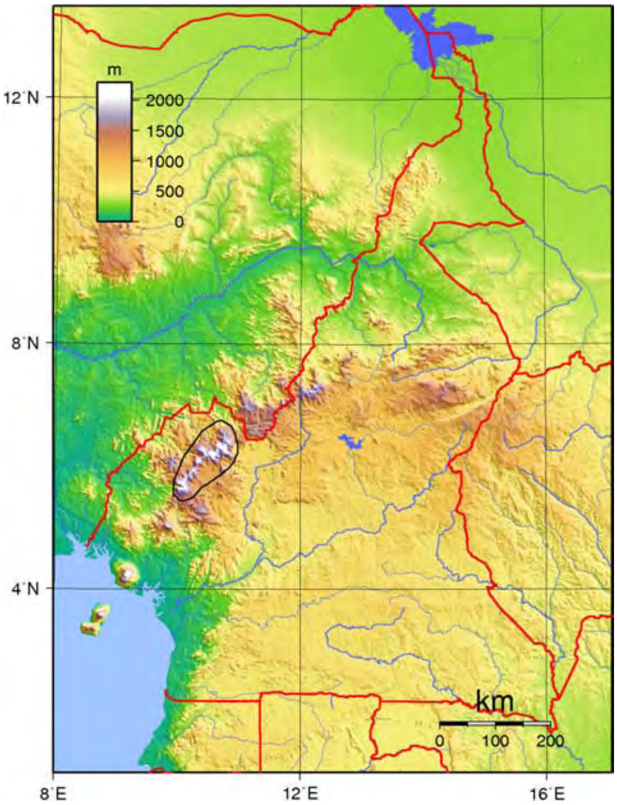

Fig. 6. Map of Cameroon with the geographical area of the mountain range (circled in black) retained as part of this study. Country boundaries are shown in red.

endemic mountain species whose distribution is restricted and unfortunately now highly fragmented. Our knowledge of this herpetofauna has been greatly improved by field work undertaken under the CamHerp project which ultimately resulted in the publication of a complete Atlas of the reptiles of the country (Chirio and LeBreton 2007). The BH, as defined above, hosts 50 non avian reptile species among which 16 are endemic to our study area. Others overflow very locally into neighboring Nigeria (Obudu plateau and Mts. Gotel), the Central African Republic (eastern borders of the Adamaoua), or Equatorial Guinea (Bioko Island). Only one snake species, *Dipsadoboa unicolor*, is also present in Eastern Africa. The mountain biodiversity is thus relatively low but the level of endemicity is quite high. All of the area undoubtedly represents significant challenges to preserve the richness and originality of the endemic afro-montane herpetofauna. The regions studied here represent a much drier area than the larger mountains such as Mt. Cameroon located southwest on the Cameroon Volcanic Dorsal. The herpetofauna includes common species, in addition to taxa more restricted to these formations and their climate. Other studies on the altitude mountains of the Cameroon Volcanic Dorsal ridge have produced impressive species lists, but unlike our study (only 50 species found above 1,400 m), they also include herpetofauna from the base of the mountain ranges (Herrmann et al. 2005, 2006).

Inventory of Taxa Present in the Study Area

Below we discuss all species of non-avian reptiles reported from the BH above 1,400 m (Fig. 6) from our collection (total 374 specimens), including our observations and/or data available in the literature. We include chelonians (one specimen available), lizards (266 specimens), and snakes (107 specimens). In each of these groups we deal with the species alphabetically, by family, and by taxa in families, in alphabetical order. We indicate the list of available specimen(s) in the MNHN-RA collections (Muséum national d'Histoire naturelle, Reptiles and Amphibians collections, Paris), that originate mainly from collections made during the CamHerp project. Note, however, that only a subset of CamHerp lizards have been entered into MNHN collections, while most snakes have not been accessioned in to the MNHN-RA yet and only field tag details (CamHerp xxx) are given.

CHELONIANS

Testudinidae Gray, 1825

Kinixys homeana Bell, 1827 (One specimen)

Material: CamHerp 121 (Mboh village, 6.327°N and 10.348°E, elev. 1,800 m, coll. CamHerp M. LeBreton, July 8, 2002).

This tortoise prefers relatively humid spots, where it seems to feed on mushrooms. It is found in all the western part of Cameroon, from the plain to 1,800 m at Mboh in the BH. The main threat is its frequent use as bushmeat by local people as well as collection for sale in the country's major markets (Lawson 2001; Luiselli and Diagne 2014).

LIZARDS

Agamidae Spix, 1825

Agama agama (Linnaeus, 1758) (Two specimens)

Material: CamHerp 4483I (Boyui village, 6.242°N and 10.311°E, elev. 1400 m, coll. CamHerp M. LeBreton and L. Chirio, April 19, 2000) – CamHerp 168 (Mbiame, 6.190°N and 10.849°E, elev. 1955 m, coll. CamHerp, December 14, 2002).

This agama is undoubtedly the most anthropophilic species in its group; it occupies almost all the villages in its range but is also common in savanna outcrops and degraded forests. It is present in Bafoussam (elev. 1,500 m), and found from sea level to over 2,000 m on Mts. Bana.

Agama sp. 2 (in: Chirio and LeBreton 2007) (four specimens)

Material: CamHerp 3576X-3579X (4 specimens, Dzindong waterfall, 5.622°N and 10.106°E, elev. 2,350 m, coll. CamHerp M. LeBreton and L. Chirio, May 5, 2001).

This rare and endemic species of Cameroon has not been described yet. It occurs from the Bamboutos and Mbapit Mountains in the BH to Tchabal Mbabo in Adamaoua at altitudes located between 1,900 and 2,350 m at Dzindong waterfall (Chirio and LeBreton 2007).

Agama sp. 4 (in: Chirio and LeBreton 2007) (Nine specimens)

Material: MNHN-RA 1998.0277-0285 (Nine specimens, Mt. Oku, five km north of Oku village, on rocky outcrops, elev. 2,200 m, coll. L. Chirio, June 25, 1998).

This endemic species of Cameroon, identified by Chirio and LeBreton (2007: 172–173), is still not described; it is only known from two mountain stations. It is a large agama living mainly on the rocky outcrops of altitude savannas. It occurs only between 1,900 and 2,000 m above sea level like at the localities of Fungoï and Tabenken.

Chamaeleonidae Gray, 1825

It is only recently that the molecular work of Tilbury and Tolley (2009) demonstrated that the two subgenera of the genus *Chamaeleo* auct., *Chamaeleo* Laurenti, 1768 sensu stricto, and *Trioceros* Swainson, 1839 should be considered as two valid genera. Other studies have subsequently confirmed this (Tolley et al. 2013). Cameroon has great species richness of chameleons (14 species) compared to its neighboring countries. This diversity is mainly located in mountainous areas and is characterized by a high level of endemism. The family is represented by three genera: *Chamaeleo* (five species), *Rhampholeon* Günther, 1874 (at least one species), and *Trioceros* (eight species and three subspecies; Barej et al. 2010). Within *Trioceros*, the most common to occur at elevation include *Trioceros oweni*, the most basal taxon of the genus in Cameroon, *T. camerunensis*, *T. cristatus*, *T. montium*, *T. perreti*, *T. wiedersheimi*, *T. serratus*, *T. quadricornis eisentrauti*, *T. q. quadricornis*, and *T. q. gracilior*. The genus *Rhampholeon* occurs over 1,700 m in Mt. Cameroun but it is curiously absent in the BH. Six species are very clear mountain endemics occupying restricted areas in the Cameroon Volcanic Dorsal mountain ridge. Half of Cameroon chamaeleons are mountain endemics with restricted ranges. A molecular phylogeny of the genus *Trioceros* in Cameroon was established by Pook and Wild (1997) and completed by Barej et al. (2010). Three altitudinal groups in Cameroon can be recognized within the genus *Trioceros*: a plains group (*Trioceros oweni*), a plains and submontane group (*Trioceros camerunensis*, *T. cristatus*, and *T. montium*), and a submontane and mountain group (*Trioceros pfefferi*, *T. perreti*, *T. serratus*, *T. wiedersheimi*, and *T. quadricornis*). Only species of the last group are present in our study area.

Chamaeleo gracilis Hallowell, 1844 (three specimens)

Material: MNHN-RA 2005.3191-3192 (two specimens, Bamessing, 6.004°N and 10.352°E, elev. 1,200 m, coll. CamHerp L. Chirio, October 26, 2000) – MNHN-RA 2005.3590 (Balengu, 5.114°N and 10.450°E, elev. 1,480 m, coll. CamHerp L. Chirio, April 6, 2000).

This species is found in the Ethiopian Rift Valley from 200–1,900 m (Largen and Spawls 2010), whereas in Cameroon it is reported between 5 and 1,775 m above sea level (Chirio and LeBreton 2007). It was observed but not collected at Bafoussam by one of us (LC, June 22, 2000).

Chamaeleo laevigatus Gray, 1863 (seven specimens)

Material: MNHN-RA 2005.2721 (Fundong, 6.249°N and 10.315°E, elev. 1,500 m, coll. CamHerp, July 8, 2002) – MNHN-RA 2005.3301-3305 (five specimens, Jakiri village along the road from Bamenda to Nkambe, 6.055°N and 10.658°E, elev. 1,550 m, coll. CamHerp M. LeBreton, July 8, 2002) – MNHN-RA 2005.3398 (Awing village (Benjom), 5.867°N and 10.266°E, elev. 1,747 m, coll. CamHerp, M. LeBreton, July 8, 2002).

This species, presently known to occur in Cameroon, was initially mistaken with *Chamaeleo senegalensis* Daudin, 1802 by Chirio and LeBreton (2007), a taxon whose distribution is more western. In East Africa, *C. laevigatus* occurs in moist savanna between 1,000–1,500 m but can fall to 300 m elsewhere (Spawls et al. 2002; Largen and Spawls 2010). It is reported from 350–1,550 m altitude in Cameroon (Chirio and LeBreton 2007).

Trioceros pfefferi (Tornier, 1900) (three specimens)

Material: MNHN-RA 2005.3396 (Mboh village, 6.327°N and 10.348°E, elev. 1,900 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002) – MNHN-RA 2007.1499 (male; Mt. Oku, Afua, Ijim Forest, western side of Mt. Oku, 6.15°N and 10.40°E, elev. 2,000 m, coll. CamHerp L. Chirio, June 1st, 2000) – MNHN-RA 2007.1500 (female; Bali Ngemba Forest Reserve, 5.825°N and 10.087°E, elev. 1,400 m, coll. CamHerp L. Chirio, June 6, 2000).

This endemic species of the Cameroon Volcanic Dorsal is a typical inhabitant of the wet stations of the western sub-montane forest in the country. It is rare throughout its distribution and was only known from its original description from Nyassosso at Mt. Kupe for nearly a century (Wild 1993). It is found at Mt. Manengouba, and in the BH and Mt. Oku where it reaches almost 2,000 m above sea level. Densities seem higher in populations at Mt. Kupe (Hofer et al. 2003). Altitudinal distribution of the species ranges from 1,200–1,500 m (Schuetze 1998) and 1,100–1,900 m according to Tilbury (2010); the species is reported between 1,100 and 1,900 m from Mt. Kupe by Anderson and Van Heygen (2013). Captive females lay between six and nine eggs (Schuetze 1998).

The species is also present at Mt. Nlonako, very close to Mt. Manengouba. *T. pfefferi* has horns (males only), but its phylogenetic affinities are closer to the hornless species of the *T. wiedersheimi* group than to other Cameroon species (*T. montium* and *T. quadricornis*), indicating that the presence of horns has evolved several times within the genus *Trioceros*.

Its distribution is comparable to that of the *T. perreti* / *T. serratus* / *T. wiedersheimi* group and the *T. quadricornis* group (*T. q. quadricornis*, *T. q. gracilior*, and *T. q. eisentrauti*). These two groups of related taxa each have an endemic taxon in the Manengouba area, another in the BH and a third endemic in a peripheral region (to the north and west respectively). The populations of *T. pfefferi* recently discovered at Mbulu Hills and Ediango to the north (Gonwouo et al. 2006) should therefore be carefully compared with the more southern populations to assess their taxonomic status. Like other submontane and montane species from Cameroon, *T. pfefferi* occupies only medium and high mountain areas with wet, mainly pristine evergreen forests, often near streams (Jakubowicz and Van Tiggel 1998). It perches at heights between 1.6 m and 2.1 m (Herrmann et al. 2005), 7 m at Mt. Kupe, and 3.5 to 5.0 m at Manengouba (Anderson and Van Heygen 2013). The species is threatened on Mt. Manengouba by both logging and collecting for the pet trade.

Trioceros quadricornis gracilior Böhme and Klaver, 1981 (17 specimens)

Material: MNHN-RA 1998.0434-0435 (two specimens, Mt. Oku, above Oku village, elev. 2,200 m, coll. CamHerp L. Chirio, June 25, 1998) – MNHN-RA 2005.2715-2720 (six specimens, Mt. Oku, Elak Oku village, 6.202°N and 10.505°E, elev. 2,000 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002) – MNHN-RA 2005.2722 (Oku Manchok, 6.241°N and 10.524°E, elev. 2,130 m, coll. CamHerp M. LeBreton and L. Chirio, December 14, 2002) – MNHN-RA 2005.2723 (Mt. Oku, Lake Oku, 6.20°N and 10.45°E, elev. 2,250 m, coll. CamHerp M. LeBreton and L. Chirio, April 19, 2000) – MNHN-RA 2005.2724, 2005.2726-2727 (three specimens, Mt. Oku, Oku village, 6.202°N and 10.505°E, elev. 2,000 m, coll. CamHerp M. LeBreton and L. Chirio, April 19, 2000) – MNHN-RA 2005.2725 (Mt. Oku, Simonkuh village, 6.234°N and 10.572°E, elev. 2,109 m, coll. CamHerp M. LeBreton, July 8, 2002) – MNHN-RA 2007.1423 (male; Mt. Oku, Oku village, 6.202°N and 10.505°E, elev. 2,000 m, coll. I. Ineich and N. Lhermitte-Vallarino, May 8, 2007) - MNHN-RA 2007.1424 (male; Mt. Oku, Oku village, 6.202°N and 10.505°E, elev. 2,000 m, coll. I. Ineich and N. Lhermitte-Vallarino, May 8, 2007) - MNHN-RA 2007.1426 (male; Mt. Oku, Oku village, 6.202°N and 10.505°E, elev. 2,000 m, coll. I. Ineich and N. Lhermitte-Vallarino, May 7, 2007).

Barej et al. (2010) revised the *T. quadricornis* complex with additional materials and molecular data. The morphological differences between the populations of the south (Mt. Kupe and Mt. Manengouba) and north (BH to Obudu Plateau in Nigeria) were supported by genetics, thus confirming the subspecific status of *T. q. quadricornis* (Tornier, 1899) and *T. q. gracilior* Böhme and Klaver, 1981. *T. q. gracilior* is present at Mts. Bamboutos, Mbulu Hills (Gonwouo et al. 2006), Mt. Lefo, Mt. Oku and onto the Obudu Plateau in Nigeria, while *T. q. quadricornis* occupies the forests of Mt. Manengouba and Mt. Kupe. This study also relegated *Chamaeleo eisentrauti*, once considered a valid species, to subspecific status as *T. q. eisentrauti* (Mertens, 1968). This form is endemic to Rumpi Hills in western Cameroon. All these taxa occupy primary mountain forests, and *T. q. gracilior* occurs up to 2,700 m in altitude. Tilbury (2010) reported the taxon between 1,600–2,500 m. The separation between these three subspecific taxa, attested by their low genetic divergence, is thus probably recent and associated with the altitudinal shifting of cool forests to the mountain peaks after the end of Pleistocene glacial periods.

Trioceros q. gracilior (Fig. 7) is an endemic subspecies of Cameroon and neighboring Nigeria (Plateau Obudu). This is an arboreal montane forest lizard (mostly met at the interface forest/grassland) that is still relatively abundant locally, such as around the village of Elak Oku (6.244°N, 10.508°E, elev. 1,970 m). Its altitudinal distribution reaches 2,400 m above sea level at Mt. Oku (Ijim Ridge; Wild 1994) and 2,700 m at Mt. Mekua in the Bamboutos (Gonwouo et al. 2006; Barej et al. 2010). Its perch height is much greater than that of *T. serratus* (see below) and averages around 1.9 m at Mt. Oku (Gonwouo et al. 2006). Wild (1994) found the chameleon from one m above the ground to the top of the canopy at Mt. Oku, with a preference for branches near streams. The minimum night temperature recorded in its habitat at 2,400 m is 4.7 °C in December 1993 (Wild 1994). The female lays from 6 to 24 eggs that are partially incubated before being laid (Abate 1994).

This species is particularly threatened by trade in exotic pets, and especially by rampant habitat destruction (deforestation, cultures, bush fires, grazing). Eucalyptus, an alien tree widely introduced in the region creates unfavorable habitat. However, the species seems able to persist in fragmented forest remnants and transitional habitats (Fig. 8). Its densities are estimated at four times higher at Mt. Oku compared to populations in Mbulu Hills (Gonwouo et al. 2006), and almost twice as high as at Mt. Manengouba (*T. q. quadricornis*). The conservation status of the species remains nevertheless very fragile and sensitive to environmental degradation. The threat of commercial harvesting is now better regulated by effective measures implemented mostly via European Union CITES regulation.

Trioceros serratus (Mertens, 1922) (101 specimens) (Figs. 9–14)

Material: MNHN-RA 1997.3642 (male; Mt. Oku, Oku village, coll. CamHerp L. Chirio, May 1997) – MNHN-RA 1998.0415 (female; Mt. Oku, Lake Oku, elev. 2,200 m, coll. CamHerp L. Chirio, July 6, 1998) – MNHN-RA 1998.0416-0430 (15 specimens, Mt. Oku, elev. 2,000-2,500 m, coll. CamHerp L. Chirio, June 25, 1998) – MNHN-RA 2005.2728-2732 (five specimens, Mt. Oku area, Anyajua village, above Bello, 6.236°N and 10.394°E, elev. 2,100 m, coll. CamHerp M. LeBreton and L. Chirio, April 19, 2000) – MNHN-RA 2005.2733-2734, 2005.2736 (three specimens, Awing village (Benjom), 5.867°N and 10.266°E, elev. 1,747 m, coll. CamHerp M. LeBreton and L. Chirio, December 14, 2002) – MNHN-RA 2005.2735 (Awing village (Benjom), 5.867°N and 10.266°E, elev. 1,747 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002 – MNHN-RA 2005.2737 (Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton and L. Chirio, December 14, 2002) – MNHN-RA 2005.2738-2744 (seven specimens, Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002 [MNHN-RA 2005.2739, .2741 and .2743: December 14, 2002]) – MNHN-RA 2005.2745 (Bamboutos, Mt. Mekua, 5.688°N and 10.095°E, elev. 2,700 m, coll. CamHerp L. Chirio, March 30, 2000) – MNHN-RA 2005.2748 (Bingo village, 6.166°N and 10.290°E, elev. 1,435 m, coll. CamHerp M. LeBreton and L. Chirio, December 14, 2002) – MNHN-RA 2005.2749-2752 (four specimens, Mt. Oku, Elak Oku village, 6.202°N and 10.505°E, elev. 2,000 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002) – MNHN-RA 2005.2755-2759 (five specimens, Mbiame, 6.190°N and 10.849°E, elev. 1,955 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002 [MNHN-RA 2005.2758-2759: December 14, 2002]) – MNHN-RA 2005.2760-2761 (two specimens, Mbockghas, elev. 2,092 m, coll. CamHerp M.

Fig. 7. Despite its specific name, individuals of *T. q. gracilior* may have two to six horns. Adult male, Elak Oku village, Mt. Oku. Note the presence of concentric rings on the horns, a characteristic feature (synapomorphy) of the genus *Trioceros*. MNHN-RA 2007.1424. *Picture: I. Ineich, May 13, 2007.*

Fig. 8. Associated crops (beans, coffee, bananas, corn) encountered near villages (here around Elak Oku village) are not completely adverse to chameleons when a large plant and shrub cover is maintained. *Picture: I. Ineich, May 8, 2007.*

LeBreton and L. Chirio, December 14, 2002) – MNHN-RA 2005.2762-2771 (10 specimens, Mboh village, 6.327°N and 10.348°E, elev. 1,900 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002) – MNHN-RA 2005.2774-2775, MNHN-RA 2005.2777, MNHN-RA 2005.3381 (four specimens, Mufe village, 6.30°N and 10.35°E, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002) – MNHN-RA 2005.2776, 2005.2778-2780 (four specimens, Njinkfuin, 6.187°N and 10.375°E, elev. 1,500 m, coll. CamHerp M. LeBreton and L. Chirio, April 19, 2000) - MNHN-RA 2005.2781-2787, 2005.2900 (five males and three females; Mt. Oku, Simonkuh, 6.234°N and 10.572°E, elev. 2,109 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002) – MNHN-RA 2005.2788 (male; Mt. Oku, Oku village, 10.505°E and 6.202°N, elev. 2,000 m, coll. CamHerp M. LeBreton and L. Chirio, April 19, 2000) – MNHN-RA 2005.2812-2815 (four specimens, Tefo village, 6.30°N and 10.37°E, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002) – MNHN-RA 2005.2816-2824 (nine specimens, Veko village, 6.139°N and 10.578°E, elev. 2,044 m, coll. CamHerp M. LeBreton and L. Chirio, December 14, 2002 [MNHN-RA 2005.2817, .2819-2824: coll. July 8, 2002]) – MNHN-RA 2005.2900 (Mt. Oku, Simonkuh, 6.234°N and 10.572°E, elev. 2,109 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002) – MNHN-RA 2005.3382 (Babadjou, 5.699°N and 10.187°E, elev. 1,580 m, coll. CamHerp L. Chirio, no date) – MNHN-RA 2005.3383 (Mbiame, 6.190°N and 10.849°E, elev. 1,955 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002) - MNHN-RA 2007.0461-0464 (two males and two females; Mt. Oku area, around Elak Oku village, 6.244°N and 10.507°E, elev. 1,973 m, coll. I. Ineich and N. Lhermitte-Vallarino, May 6, 2007) – MNHN-RA[1] 2007.1461 (Mt. Oku, Oku village, elev. 2,000 m, coll. I. Ineich and N. Lhermitte-Vallarino, May 7, 2007) – MNHN-RA 2007.1462 (Mt. Oku, Oku village, elev. 2,000 m, coll. I. Ineich and N. Lhermitte-Vallarino, May 8, 2007) – MNHN-RA 2007.1463-1464, 2007.1472 (three specimens, Mt. Oku, Oku village, elev. 2,000 m, coll. I. Ineich and N. Lhermitte-Vallarino, May 8, 2007) – MNHN-RA 2007.1465 (male; Mt. Oku area, Lake Oku, 6.202°N and 10.461°E, elev. 2,272 m, coll. I. Ineich and N. Lhermitte-Vallarino, May 8, 2007) – MNHN-RA 2007.1494 (male, neotype of *T. serratus*; Mt. Oku, on the side along the road from Anyajua to Belo, not far from Belo, coll. I. Ineich, May 9, 2007).

Fig. 9. *Trioceros serratus* male observed near a house in the village of Elak Oku at Mt. Oku. MNHN-RA 2007.1463. *Picture: I. Ineich, May 8, 2007.*

Fig. 10. The neotype of *Trioceros serratus*, MNHN-RA 2007.1494, photographed several days after his capture (see also other photographs below). *Picture: I. Ineich, May 13, 2007.*

Klaver and Böhme (1992) described the subspecies *T. wiedersheimi perreti* from Mt. Manengouba. Later molecular studies of Barej et al. (2010) highlighted the possible specific status of this taxon. This same study showed that the nominal subspecies *T. w. wiedersheimi* comprises two distinct genetic clades, separated geographically. Previously *T. w. wiedersheimi* was considered to occupy savanna and altitude grasslands from 1,400 to 2,450 m in Mts. Bamboutos, Mbulu Hills, Mt. Lefo, Mt. Mbam, Mt. Oku, and Mt. Tchabal Mbabo, and westwards into Nigeria at Mts. Gotel and Mambilla and the Obudu Plateaus. The original description of *T. wiedersheimi* was based on two syntypes, a female from Tchabal Mbabo and a subadult male from the BH. The female was designated as the lectotype of *T. w. wiedersheimi* by Klaver and Böhme (1992), thus restricting the type locality to Tchabal Mbabo. This restricted its distribution to the northern part of that previously accepted (Tchabal Mbabo and Tchabal Gangdaba). The southern populations (BH, Mt. Mbam and Mt. Oku) represent a distinct taxon that may also include the populations of the Koano, Mt. Lefo and Mbulu Hills, and Plateau of southern Nigeria, but this has to be verified. An available name, *Chamaeleo serratus* Mertens, 1922, was revalidated to accommodate these southern populations as *Trioceros serratus* (Mertens, 1922), although its name-bearing type was unfortunately destroyed during the Second World War. A neotype was designated by Barej et al. (2010) in recent MNHN collections (MNHN-RA 2007.1494, Figs. 10, 11). Its type locality is thus well attached to the area just above the city of Belo on the western flank of Mt. Oku.

Trioceros serratus occupies high savannas of the BH, Mt. Mbam and Obudu Plateau (Nigeria). Note, however, that the reports of Gotel Mountains in Nigeria should be attributed to *T. wiedersheimi*. In the BH region, the species is cited from Bafoussam (Bangwa), Big Babanki (= Kedjom Keku), the Bamileke region of Dschang, Kishong, Mezam (Bafout), and Tsch’a Bekom (Barej et al.

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[1] Note that specimens MNHN-RA 2007.461-464 reported by Barej et al. (2010) refers to MNHN-RA 2007.1461-1464.

Fig. 11. Neotype of *T. serratus* (MNHN-RA 2007.1494) *in situ* before collection at the edge of the road down from the summit of Mt. Oku (Anyajua village), just a little over Belo (6.175°N and 10.352°E). The chameleon was perched nearly 3 m up in a palm tree. *Picture: I. Ineich, May 9, 2007.*

Fig. 12. *Trioceros serratus* widely used the herb layer where it was comfortable. Here an individual seeking to hide on a blade of grass by stiffening its tail to make it look like an herbaceous branching. Not collected. *Picture: I. Ineich, May 8, 2007.*

2010). Our study allows addition of the following locations in the BH: Awing (Benjom), Baba II, Bali Ngemba, Bingo, Mbiame, Mbockghas, Mboh, Mufe, Njinkfuin, Tefo, and Veko. It was reported from Bafut (elev. 1,200 m, 6.08°N and 10.10°E) by Joger (1982) as *Chamaeleo wiedersheimi*.

Fig. 13. Individuals assigned to *T. serratus* altitude populations (top, Elak Oku village; MNHN-RA 2007.1463) differ from those from lower altitudes like here (bottom) the neotype of *T. serratus* (MNHN-RA 2007.1494) by some important scalation and coloring characters. *Picture: I. Ineich, May 2007.*

Gonwouo et al. (2006) consider the taxon (named *T. w. wiedersheimi*) to occur from 1,500 m to 2,450 m altitude, often in sympatry with *T. quadricornis gracilior* on Bamboutos Mts. at Foto, Dschang, and Mts. Lefo, Mt. Oku, and Obudu Plateau in Nigeria, and 2,700 m in Mt. Mekua. Wild (1994) reported the species between 2,200 m and 2,500 m at Mt. Oku (Ijim Ridge). Tilbury (2010) cited the species from 2,600 m above sea level at Mt. Oku. Perch height average is 90 cm at Mt. Oku, the lowest value found for different stations of its range (over two m at Tchabal Mbabo). Wild (1994) reported a mean perch height of 53 cm at Mt. Oku and a maximum height of 157 cm. However, we collected the neotype of the species in a palm tree at three m height near the edge of a main road (Fig. 11)! The low perch height observed in altitude at Mt. Oku could be attributed to the scarcity of livestock and predators that cause little disruption for chameleons, or to a still unknown interaction between climate and vegetation (Fig. 12). The species tolerates some degree of habitat degradation and does not hesitate to venture into cultivated areas retaining some original vegetation. Yet it is a sensitive species, recently threatened by the exotic pet trade and especially the destruction of its habitat (culture, fires, deforestation). The population at Mt. Oku, however, is still abundant. The species is common around the village of Elak Oku, including gardens and plantations. This is the most abundant Cameroon mountain chameleon. The species occupies relatively open habitats but does not hesitate to venture into closed canopy forest. A minimum night temperature of 2.9 °C was recorded in its habitat at 2,500 m altitude in December 1993 (Wild 1994). *Trioceros serratus* mostly occupies herbaceous and shrub layer below two m, while *T. q. gracilior* occupies bushy and shrub layers above one meter, which generates a syntopy area in the stratum located between one and two m (Wild 1994). Habitat separation in syntopy should be possible through the important size differences between both taxa, probably preventing dietary overlap.

The systematics of this species complex is not satisfactory, despite the revision of Barej et al. (2010). In fact, besides the obvious differences in size and coloration, the lowland form (larger) collected near Belo also differs from the altitude form (smaller) of the summit of Mt. Oku by the number of small scales around the large granules on the flanks (Figs. 13, 14). Also one of us (II) collected the neotype of *T. serratus* up in a palm tree and this form seems much more arboreal than the altitude Mt. Oku form. It is very unlikely that these two morphotypes belong to the same taxon and further studies are required.

Gekkonidae Gray, 1825

Hemidactylus angulatus Hallowell, 1852 (nine specimens)

Material: MNHN-RA 2005.1602-1603 (two specimens, Mt. Oku, Anyajua village above Bello, 6.236°N and 10.394°E, elev. 2,100 m, coll. CamHerp, respectively April 14, 2001, and April 19, 2001) – MNHN-RA 2005.1616 (Bingo village, between Ijim and Bamenda, 6.162°N and 10.319°E, elev. 1,600 m, coll. CamHerp, April 19, 2000) – MNHN-RA 2005.1692-1693 (two specimens, Bingo village, 6.166°N and 10.290°E, elev. 1,435 m, coll. CamHerp M. LeBreton, respectively December 14, 2002, and July 8, 2002) – MNHN-RA 2005.1761 (Idjim, Birdlife Project, 6.226°N and 10.433°E, elev. 1,600 m, coll. CamHerp L. Chirio, April 19, 2000) – MNHN-RA 2005.1927-1928 (two specimens, Njinkfuin, 6.187°N and 10.375°E, elev. 1,500 m, coll. CamHerp L. Chirio, April 19, 2000) – MNHN-RA 2005.2496 (Boyui village, 6.242°N and 10.311°E, elev. 1,400 m, coll. CamHerp L. Chirio, April 19, 2000).

This house gecko is probably one of the most anthropophilous species in the country, where it has a wide distribution throughout the northern region. The species is abundant in homes but does not hesitate to shelter also in rocks and trees in remote areas. It is found from sea level to above 2,000 m at Tabenken and Nkambe.

Hemidactylus kamdemtohami Bauer and Pauwels, 2002 (one specimen)

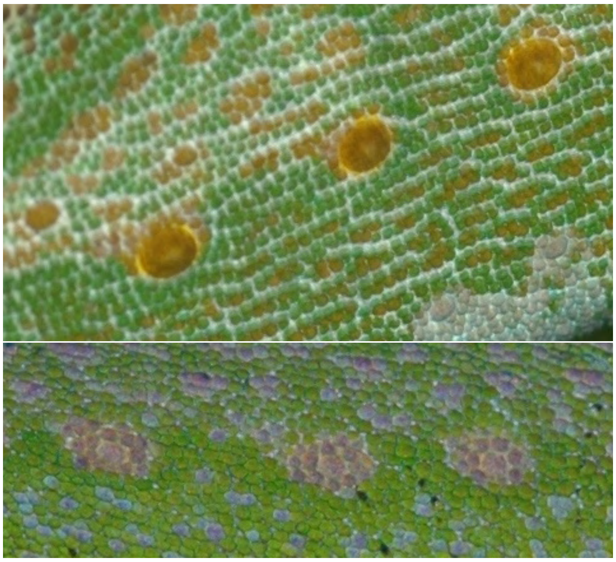

Fig. 14. Individuals assigned to altitude *T. serratus* populations (on top, Elak Oku village; MNHN-RA 2007.1463) are very different from those from lower altitudes like here (on botom) the neotype of *T. serratus* (MNHN- RA 2007.1494) by the conformation of the large granules arranged on the flanks and also by the number and arrangement of small scales placed around these large granules. *Pictures: I. Ineich, May 2007.*

Material: MNHN-RA 2002.0739 (Balengou, elev. 1,480 m, 5.114°N and 10.450°E, coll. CamHerp, June 29, 2001).

Balengou remains the only known Cameroon location for this gecko, which elsewhere is known from Equatorial Guinea (Mt. Allen) and Gabon (Mt. Iboundji). *H. kamdemtohami* is without any doubt a submontane species. Its occurrence at lower elevations in Gabon may be because Mt. Iboundji, covered with evergreen forests, is wetter than the BH and thus the altitudinal limit of the species is reduced.

Scincidae Gray, 1825

Lacertaspis chriswildi (Böhme and Schmitz, 1996) (seven specimens)

Material: MNHN-RA 1997.3649 (Mt. Oku, in a garden of Oku village, elev. 2,000 m, coll. CamHerp L. Chirio, June 8, 1997) – MNHN-RA 1997.3650 (Mt. Oku, in the forest, elev. 2,350 m, coll. CamHerp L. Chirio, March 22, 1997) – MNHN-RA 1998.0286-0288 (three specimens, Mt. Oku forest, elev. 2,200 m, coll. CamHerp L. Chirio, June 25, 1998) – MNHN-RA 2005.2600-2601 (two specimens, Mt. Oku, Oku forest, 6.250°N and 10.507°E, elev. 2,350 m, coll. CamHerp M. LeBreton and L. Chirio, respectively May 5, 2000, and May 11, 2000).

This little lizard is endemic to the montane forests of West Cameroon (Schmitz 2004; Schmitz et al. 2005; Herrmann et al. 2006). It is found at Mt. Kupe in the Takamanda forest, Mt. Oku, and the Tchabal Mbabo Massif. It occurs up to 2,800 m altitude at Mt. Oku but does not seem to fall below 1,000 m.

Lacertaspis lepesmei (Angel, 1940) (35 specimens)

Material: MNHN-RA 1998.0295-0300, 1999.0401-0404, 1999.8418-8436 (29 specimens, without any precise location, coll. CamHerp) – MNHN-RA 2004.0061 (Bamboutos, Fulbe house, 5.637°N and 10.106°E, elev. 2,450 m, coll. CamHerp, May 5, 2001) – MNHN-RA 2005.2597-2599 (Bamboutos, Mt. Mekua, 5.688°N and 10.095°E, elev. 2,700 m, coll. CamHerp, respectively May 8, 2000, April 18, 2000, and April 19, 2000) – MNHN-RA 2005.2602-2603 (two specimens, without precise location, coll. CamHerp).

This small, submontane endemic skink is only known from the rocky slopes of Bamboutos Mountains, between 2,350 and 2,700 m altitude (Fig. 15). It is not present in the Mt. Oku region. Its classification in the IUCN Red List and the measures to undertake for the conservation of its habitat should be a priority.

Lepidothyris fernandi (Burton, 1836) [formerly *Mochlus fernandi*] (one specimen)

Material: MNHN-RA 2005.1265 (Tefo village, 6.30°N and 10.37°E, elev. 1,700 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002).

The genus was recently revised (Wagner et al. 2009). In Eastern Africa, the species occurs between 600 and 2,100 m (Spawls et al. 2002) whereas in Cameroon it is only reported from sea level to 1,200 m at Bafut. This skink was also observed on the eastern sides of the BH at Kenshi, at an elevation of 1,080 m on April 17, 2004 (6.107°N and 9.713°E).

Leptosiaphos ianthinoxantha (Böhme, 1975) (25 specimens)

Material: MNHN-RA 2002.0798, 2002.0800, 2002.0928-0930, 2002.0934 (six specimens, Mbockghas, 6.222°N and 10.582°E, elev. 2,092 m, coll. CamHerp M. LeBreton, December 14, 2002) – MNHN-RA 2002.0942, 2005.2617-2620 (five specimens, Mbockghas, 6.222°N and 10.582°E, elev. 2,092 m, coll. CamHerp M. LeBreton and L. Chirio, December 14, 2002) – MNHN-RA 2005.2607 (Bamboutos, Fulbe house, 5.637°N and 10.106°E, elev. 2,450 m, coll. CamHerp, May 5, 2001) – MNHN-RA 2005.2613-2616 (four specimens, Bamboutos, Mt. Mekua, 5.688°N and 10.095°E, elev. 2,700 m, coll. CamHerp, March 30, 2000, May 5, 2000 [.2615], and May 8, 2000 [.2616]) – MNHN-RA 2005.2621-2627, 2005.2629 (eight specimens, Mt. Oku, Simonkuh, 6.234°N and 10.572°E, elev. 2,109 m, coll. CamHerp M. LeBreton, July 8, 2002, December 14, 2002 [.2625], and January 16, 2003 [.2622, .2626]) – MNHN-RA 2005.2628 (Bamboutos, slopes of Mt. Mekua, 5.698°N and 10.101°E, elev. 2,300 m, coll. CamHerp, March 19, 2002).

Fig. 15. *Lacertaspis lepesmei*. MNHN-RA 2004.0061 (see above). *Picture: M. LeBreton.*

Fig. 16. *Leptosiaphos ianthinoxantha*. Cameroon, Mt. Oku, Oku Simonkou village. *Picture: M. LeBreton, November 2002.*

This small skink is endemic to montane grasslands of the Western Highlands of Cameroon (Schmitz et al. 2005) (Fig. 16). It is found at Mt. Lefo (Forest Reserve of Bafut-Ngemba) and in the Bamboutos Mountains. Its occurrence at Mt. Oku had been suspected by Wild in 1994. It is a semi-burrowing species living in open montane grasslands, and is oviparous. The species occurs up to 2,700 m altitude at Mt. Mekua in the Bamboutos where its populations are highly localized but occur in high densities.

Leptosiaphos pauliani (Angel, 1940) (one specimen)

Material: MNHN-RA 1939.0082 (holotype; Bamboutos, coll. J.-L. Perret).

This small endemic lizard was recorded by Perret (1973) from Nyassosso on the slopes of Mt. Kupe at 1,100 m above sea level (holotype of *Riopa erythropleuron* Mertens, 1968) and from Mts. Bamboutos at 2,300 m above sea level (holotype of *Lygosoma* (*Liolepisma*) *pauliani* Angel, 1940). It was not found during the CamHerp project work; its presence in the BH is questionable. This strictly submontane species may be limited to the area of submontane forests located between 1,100 and 2,000 m above sea level in the Mts. Kupe and Bamboutos.

Leptosiaphos vigintiserierum (Sjöstedt, 1897) (two specimens)

Material: MNHN-RA 1998.0294 (Mt. Oku, elev. 2,000 m, coll. CamHerp L. Chirio, September 1st, 1997) – MNHN-RA 2004.0062 (Bamboutos, waterfall and sacred forest, 5.622°N and 10.106°E, elev. 2,350 m, coll. CamHerp, May 5, 2001) – Bamboutos, slopes of Mt. Mekua, 5.698°N and 10.101°E, elev. 2,300 m, coll. CamHerp, March 19, 2002).

This species is endemic to the Cameroon Volcanic Dorsal (Schmitz et al. 2005) (Fig. 17). It is found from Bioko Island (Equatorial Guinea), Mt. Cameroon, and Mt. Oku (Mt. Nkolodou, Mt. Kala, Mt. Kupe, and Mt. Nlonako). It mainly occurs in the high meadows of the peaks above the evergreen forest areas. It reaches 2,450 m at Mts. Bamboutos and can be relatively abundant locally.

Trachylepis maculilabris (Gray, 1845) (33 specimens)

Material: MNHN-RA 1997.3643 (pass on the Bafoussam road, elev. 1,850 m, coll. CamHerp L. Chirio, April 1997) – MNHN-RA 1998.0289-0293 (five specimens, Mt. Oku, five km north of Oku village, elev. 2,000 m, coll. CamHerp L. Chirio, June 25, 1998) – MNHN-RA 2005.1610-1611 (two specimens, Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton and L. Chirio, respectively July 8, 2002, and December 14, 2002) – MNHN-RA 2005.1616 (Bingo village, between Ijim and Bamenda, 6.162°N and 10.319°E, elev. 1,600 m, coll. CamHerp M. LeBreton and L. Chirio, April 19, 2000) – MNHN-RA 2005.1617 (Bali Ngemba village, 5.833°N and 10.077°E, elev. 1,398 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002) – MNHN-RA 2005.1623 (Bamboutos, waterfall and sacred forest, 5.622°N and 10.106°E, elev. 2,350 m, coll. CamHerp, May 5, 2001) – MNHN-RA 2005.1692-1693 (Bingo village, 6.166°N and 10.290°E, elev. 1,435 m, coll. CamHerp M. LeBreton and L. Chirio, December 14, 2002) – MNHN-RA 2005.1761 (Idjim village, Birdlife Project, 6.226°N and 10.433°E, elev. 1,600 m, coll. CamHerp M. LeBreton and L. Chirio, April 19, 2000) – MNHN-RA 2005.1762 (Jakiri village, road from Bamenda to Nkambe, 6.055°N and 10.658°E, elev. 1,550 m, coll. CamHerp M. LeBreton and L. Chirio, December 14, 2002) – MNHN-RA 2005.1847-1848 (two specimens, Mbiame village, 6.190°N and 10.849°E, elev. 1,955 m, coll. CamHerp M. LeBreton and L. Chirio, December 14, 2002) – MNHN-RA 2005.1852 (Mbockghas, 6.222°N and 10.582°E, elev. 2,092 m, coll. CamHerp M. LeBreton and L. Chirio, December 14, 2002) – MNHN-RA 2005.1853-1858 (six specimens, Mboh village, 6.327°N and 10.348°E, elev. 1,900 m, coll. CamHerp M. LeBreton and L. Chirio, December 14, 2002 [.1853], and July 8, 2002 [.1854-1858]) – MNHN-RA 2005.1897 (Mufe village, 6.30°N and 10.35°E, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002) – MNHN-RA 2005.1935-1938 (four specimens, Mt. Oku, Simonkuh village, 6.234°N and 10.572°E, elev. 2,109 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002, and December 14, 2002 [.1938]) – MNHN-RA 2005.1944 (Veko village, 6.139°N and 10.578°E, elev. 2,044 m, coll. CamHerp M. LeBreton and L. Chirio, December 14, 2002) – MNHN-RA 2005.1958-1959 (two specimens, Sarkong Hill, west of Jakiri, 6.054°N and 10.598°E, elev. 1,600 m, coll. CamHerp, March 19, 2002) – MNHN-RA 2005.2484 (Tefo village, 6.30°N and 10.37°E, elev. 1,700 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002).

Fig. 17. *Leptosiaphos vigintiserierum.* Cameroon, Mt. Mekua, Bamboutos. Specimen CamHerp 3643I. *Picture: M. LeBreton, March 12, 2002.*

This skink has a wide distribution in Africa and in Cameroon it is found in a variety of habitats from lowland forests to altitude grasslands. The species is also anthropophilic and can be abundant in gardens and villages in the southern half of the country. This lizard occurs from sea level to above 2,550 m at Mt. Lefo or on the top of Mt. Nlonako around 1,825 m (Herrmann et al. 2005). In East Africa *T. maculilabris* is reported from the seaside to above 2,300 m (Spawls et al. 2002; Largen and Spawls 2010). Note, however, that its taxonomy is not clearly established (Mausfeld et al. 2004) and that it currently represents a species complex containing several cryptic taxa.

Trachylepis mekuana (Chirio and Ineich, 2000) (six specimens)

Material: MNHN-RA 2001.0109 (Bamboutos, Mt. Mekua, 5.688°N and 10.095°E, elev. 2,700 m, coll. CamHerp, April 19, 2000) – MNHN-RA 2002.0922 (Bali Ngemba village, on rocks above the valley, 5.830°N and 10.066°E, elev. 1,640 m, coll. CamHerp M. LeBreton, July 8, 2002) – MNHN-RA 2005.1289-1291 (three specimens, Bamboutos, slopes of Mt. Mekua, 5.698°N and 10.086°E, elev. 2,600 m, coll. CamHerp, March 19, 2002) – MNHN-RA 2005.2606 (Bamboutos, 5.637°N and 10.106°E, elev. 2,450 m, coll. CamHerp L. Chirio, March 30, 2000).

This endemic mountain lizard of the BH in Cameroon occupies only the top of Bamboutos Mountains (Mt. Mekua) and the Massif of Bali-Ngemba at elevations located between 2,400 and 2,700 m (Fig. 18). The increasing use of its habitat for grazing and planting food crops seriously threatens the survival of this species. Its classification on

Fig. 18. *Trachylepis mekuana.* Mt. Mekua, Bamboutos. March 18, 2002. *Picture: L. Chirio.*

Fig. 19. *Atractaspis i. irregularis* – Cameroon, Yaounde. *Picture: M. LeBreton, January 4, 2011.*

the IUCN Red List and habitat conservation measures should be a priority.

SNAKES

Atractaspididae Günther, 1858

Atractaspis irregularis irregularis (Reinhardt, 1843) (six specimens)

Material: CamHerp 0627C, 0423C (two specimens, Abu village, NE of Fundong, 6.297°N and 10.331°E, elev. 1,750 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 3501I (Awing village (Benjom), 5.867°N and 10.266°E, elev. 1,747 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 1269C, 1495I (two specimens, Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 0158C (Mbiame, 6.190°N and 10.849°E, elev. 1,955 m, coll. CamHerp, December 14, 2002).

This burrowing and venomous snake (Barrière et al. 2006) exhibits an extensive African distribution (Fig. 19). It occupies dense evergreen forests and degraded semi-deciduous forests, forest-savanna mosaics (moist savanna), the Western Highlands, and the extreme south of the Adamaoua. It is found in altitude from 500 m to 2,000 m at Tabenken. This snake was mentioned in Wum (elev. 1,023 m) by Böhme (1975). In East Africa, the species is reported from 600 m to 2,000 m above sea level (Spawls et al. 2002; Largen and Spawls 2010).

Polemon collaris (W. Peters, 1881) (four specimens)

Material: CamHerp 3468I, 3707I (two specimens, Bingo village, 6.166°N and 10.290°E, elev. 1,435 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 3738I (Mbiame, 6.190°N and 10.849°E, elev. 1,955 m, coll. CamHerp M. LeBreton, July 8, 2002) – CamHerp 3664I (Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton, December 14, 2002).

This small forest burrowing snake is found at altitudes between 5 and 1,955 m in Cameroon. Joger (1982) mentions the species from Wum (elev. 1,023 m).

Colubridae Oppel, 1811

Crotaphopeltis hotamboeia (Laurenti, 1768) (four specimens)

Material: CamHerp 0141, 2488I (two specimens, Jakiri village on the road of Nkambe to Bamenda, 6.055°N and 10.658°E, elev. 1,550 m, coll. CamHerp M. LeBreton, July 8, 2002, and December 14, 2002) – CamHerp 2483I (Veko village, 6.139°N and 10.578°E, elev. 2,044 m, coll. CamHerp M. LeBreton, July 8, 2002) – CamHerp 0159C (Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton, December 14, 2002).

This widely distributed snake occurs at elevations from 400–2,500 m in East Africa (Largen and Spawls 2010). In Cameroon, it is found at altitudes between 160 and 2,044 m. Mountain populations in Cameroon show a particular coloration, with a typical dark spotted belly; they could belong to a distinct taxon (see below). The relationship of individuals from Veko and Baba II villages to the submontane species listed below should be reviewed.

Crotaphopeltis sp. (three specimens)

Material: CamHerp 4469, 4470 (two specimens, Mt. Oku, Bello village, 6.170°N and 10.344°E, elev. 1,450 m, coll. CamHerp, April 19, 2000) – CamHerp 0349I (City of Bamenda, 5.958°N and 10.165°E, elev. 1,300 m, coll. CamHerp, March 20, 2001).

This “species” has not been described yet but its validity, which remains to be confirmed, was indicated by Chirio and LeBreton (2007: 400–401). It is considered endemic to the mountains of Cameroon and occurs between 1,050 m and 1,500 m.

Dasypeltis confusa Trape and Mané, 2006 (three specimens)

Material: CamHerp 2436I (Veko village, 6.139°N and 10.578°E, elev. 2,044 m, coll. CamHerp M. LeBreton, July 8, 2002) – CamHerp 0097 (Awing village (Benjom), 5.867°N and 10.266°E, elev. 1,747 m, coll. CamHerp M. LeBreton, July 8, 2002) – CamHerp 1367C (Bali Ngemba village, 5.833°N and 10.077°E, elev. 1,398 m, coll. CamHerp M. LeBreton, July 8, 2002).

This snake is a typical inhabitant of the humid savanna of Cameroon where it occurs at altitudes between 510 m and 2,044 m.

Dasypeltis fasciata A. Smith, 1849 (three specimens)

Material: CamHerp 0218C (Jakiri village on the road from Bamenda to Nkambe, 6.055°N and 10.658°E, elev. 1,550 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 2272I (Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 2436I (Veko village, 6.139°N and 10.578°E, elev. 2,044 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002).

This semi-arboreal snake is found at altitudes between 4 and 1,380 m. It is reported from Bafut (elev. 1,200 m, 6.08°N and 10.10°E) by Joger (1982).

Dipsadoboa unicolor Günther, 1858 (two specimens)

Material: MNHN-RA 1998.0438-0439 (two specimens, Mt. Oku, Oku village, elev. 2,000 m, coll. CamHerp L. Chirio, end 1997).

This nocturnal and semi-arboreal snake has a wide African distribution from Guinea (Conakry) to Burundi. In Cameroon, it occupies not only the altitude forest of the west of the country but also evergreen degraded forests. It occurs from around sea level up to 2,000 m at Mt. Oku and up to 2,044 m in Veko, a village in the southeast of Mt. Oku. At Mt. Nlonako, the species does not reach the higher elevations of the massif (Herrmann et al. 2005).

This snake is still present over 1,600 m at Mt. Nimba (Ineich 2003), but can occur elsewhere up to 3,000 m and also can withstand low temperatures while remaining active at night and hunting amphibians on which it feeds. In East Africa, it is only reported between 1,500 m and 3,000 m elevation. The conspecificity of West African populations (Mt. Nimba, Cameroon Volcanic Dorsal) with those of the East African mountains has not been confirmed.

Dipsadoboa weileri (Lindholm, 1905) (seven specimens)

Material: CamHerp 0835, 0101M, 0043C (three specimens, Mboh village, 6.327°N and 10.348°E, elev. 1,900 m, coll. CamHerp M. LeBreton, July 8, 2002 (two specimens), and December 14, 2002 (one specimen)) – CamHerp 0606C (Fundong, 6.249°N and 10.315°E, elev. 1,500 m, coll. CamHerp M. LeBreton, July 8, 2002) – CamHerp 0248C (Veko village, 6.139°N and 10.578°E, elev. 2,044 m, coll. CamHerp M. LeBreton, July 8, 2002) – CamHerp 1437C (Mbiame village, 6.190°N and 10.849°E, elev. 1,955 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 119 (Awing village (Benjom), 5.867°N and 10.266°E, elev. 1,747 m, coll. CamHerp M. LeBreton, December 14, 2002).

This nocturnal forest semi-arboreal snake occurs in Cameroon at altitudes from 10 m to above 2,000 m. The species is more likely a central African species which was erroneously reported from West Africa (Trape and Baldé 2014).

Dispholidus typus (A. Smith, 1828) (one specimen)

Material: CamHerp 3197I (Baba II village, elev. 1,772 m, 5.857°N and 10.102°E, coll. CamHerp M. LeBreton, December 14, 2002).

This diurnal semi-arboreal snake has a wide pan-African distribution in the savannas. The subspecies *Dispholidus typus occidentalis* Perret, 1961 described from Cameroon remains doubtful but requires a thorough revision before its validity can be evaluated (Broadley and Wallach 2002). Perret (1961: 138) recognized *D. t. occidentalis* based on its color with green males, strongly streaked with black, red and brown females, as well as the presence of two elliptical black spots, slightly oblique, situated laterally on each side of the neck in both sexes. The species occupies forest-savanna mosaic, the western Highlands and the high savannas. Its altitude record on its whole range is 2,400 m (Spawls et al. 2002; Wagner and Böhme 2007; Largen and Spawls 2010).

Grayia tholloni Mocquard, 1897 (one specimen)

Material: CamHerp 2050C (Jakiri village, on the road from Bamenda to Nkambe, 6.055°N and 10.658°E, elev. 1,550 m, coll. CamHerp M. LeBreton, July 8, 2002).

This water snake is found up to 1,400 m above sea level in East Africa (Largen and Spawls 2010) and between 510 and 1,550 m in Cameroon.

Philothamnus angolensis Bocage, 1882 (two specimens)

Material: MNHN-RA 1998.0410 (Mt. Oku, above the village, elev. 2,200 m – tail broken – formerly identified as *Philothamnus bequaerti*, coll. CamHerp L. Chirio, June 25, 1998) – CamHerp 3749I (Mbiame, 6.190°N and 10.849°E, elev. 1,955 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002).

This arboreal snake of wet savanna occupies degraded forests, forest-savanna mosaics, the western Highlands, and altitude savannas like the Sudan savanna in the plains. Herrmann et al. (2006) reported the species up to 2,450 m at Mt. Meletan in the Bamboutos, as well as at Tchabal Mbabo Range. A snake reported from the area as *Philo-*

thamnus irregularis by Joger (1982) refers to this species (Hughes 1985: 518; Böhme and Schneider 1987). In East Africa, it occupies various habitats from the sea border up to 2,000 m elevation (Spawls et al. 2002). This species from Central and Eastern Africa only extends very little west beyond the Cameroon border.

The Mt. Oku specimen deposited in the collections (MNHN-RA 1998.0410) is a female formerly identified as *Philothamnus bequaerti* but here conservatively considered to correspond to *P. angolensis*. It measures 565 mm SVL and stubby tail measurement is 201+ mm. There are 15 dorsal scale rows in the middle of the body, 1+164 unkeeled ventral plates, and 79+ subcaudals, also unkeeled. Anal plate is divided. The supralabials (right/left) are 9 (4–6 touching the eye)/9 (4–6), infralabials 9/9, temporals 1 + 1/1 + 1, preoculars 1/1 and postoculars 2/2. The inside of the mouth is white. Its assignment to *P. angolensis* is not entirely compatible with the species' description, however.

Philothamnus hughesi Trape and Roux-Estève, 1990 (one specimen)

Material: CamHerp 880 (Veko village, 6.139°N and 10.578°E, elev. 2,044 m, coll. CamHerp M. LeBreton, December 14, 2002).

This tree snake of wet savannas occurs at an altitudinal range between 740 and 2,100 m.

Thrasops flavigularis (Hallowell, 1852) (one specimen)

Material: MNHN-RA 1998.0436 (skin, head and neck only; Mt. Oku, Oku village, elev. 2,050 m, coll. CamHerp L. Chirio, November 8, 1997).

This snake is a typical inhabitant of the dense forests of Central Africa, from Cameroon to the Democratic Republic of Congo. It is common to find in the villages and plantations. *Thrasops flavigularis* occupies the Highlands up to 2,000 m at Mt. Oku. Gonwouo et al. (2007) recognize it as an inhabitant of submontane forests in Cameroon. This snake, once considered non-venomous, is capable of inflicting serious envenomations (Ineich et al. 2006) and should be handled with caution.

Our specimen, MNHN-RA 1998.0436, only consists of the head, neck [in good condition], and the skin of an individual eaten by the local population. It has 15 dorsal scale rows in the middle of the body, which seems rare according to Chippaux (2006), because there are more often only 13 – however 15 dorsal scales seems more typical of grass field populations (Stucki-Stirn 1979). Preoculars are 2/2 and the upper is the largest (>2 times the size of the lower). The upper preoculars are widely separated from the frontal. The first post-ocular prevents contact of the supralabial 6 with the eye. Postoculars 3/3 and the lower is much larger and elongated (>4 times) than the other two substantially equal in size. The lower postocular contacts two supralabials (5–6). There are only 7(4–5)/7(4–5) supralabials and 10/11 infralabials. Temporals 1+1/1+1. This specimen slightly differs from the diagnosis given by Chippaux (2006: 108–109) and Stucki-Stirn (1979: 320–328) for the species.

According to Chippaux (2006), our specimen differs from *Thrasops jacksoni* because it has 2 preoculars (versus 3), its much larger lower postocular (vs. sup. and inf. larger) and 7 supralabials (vs. 10–12) and from *Thrasops occidentalis* because the large postocular is in contact with 2 supralabials (vs. postocular in contact with 3 supralabials). We refer that damaged specimen to *Thrasops flavigularis* and consider some of the characters indicated in the diagnosis of the species given by Chippaux (2006) as incomplete.

Elapidae Boie, 1827

Dendroaspis jamesoni jamesoni (Traill, 1843) (eight specimens)

Material: MNHN-RA 2000.4360, 2000.4376, 2002.0385-0389 (seven specimens, Bamenda, gift Latoxan, coll. October 30, 2000) – CamHerp 3428I (Jakiri village on the road from Nkambe to Bamenda, 6.055°N and 10.658°E, elev. 1,550 m, coll. CamHerp M. LeBreton, December 14, 2002).

This venomous tree snake has a wide distribution range extending from Togo in West Africa to Angola in southern Africa. It occupies dense evergreen and semi-deciduous forests, forest-savanna mosaics, the Western Highlands, and high savannas of Adamaoua (681 m at Tchabal Mbabo; Herrmann et al. 2006). It often frequents plantations and gardens but is unaggressive. It occurs in altitude up to 2,000 m at Mts. Bana. Gonwouo et al. (2007) considered the species as an inhabitant of mountain forests located above 1,800 m. It seems to live up to 2,200 m elsewhere on its range. In East Africa this green mamba is reported from 600 m to 2,200 m above sea level (Spawls et al. 2002).

Naja melanoleuca Hallowell, 1857 (22 specimens)

Material: CamHerp 1488I, 3184I (two specimens, Abu village, northeast of Fundong, 6.297°N and 10.331°E, elev. 1,750 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 1222C, 3175C, 3736C (three specimens, Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton, July 8, 2002) – CamHerp 3140I, 3394I (two specimens, Bali Ngemba village, 5.833°N and 10.077°E, elev. 1,398 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 0880C, 3295I (two specimens, Bingo village, 6.166°N and 10.290°E, elev. 1,435 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 4496 (Fundong, 6.249°N and 10.315°E, elev. 1,500 m, coll. CamHerp L. Chirio, April 19, 2000) – CamHerp 3134I (Jakiri village along the road from Bamenda to Nkambe, 6.055°N and 10.658°E, elev. 1,550 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 1234I, 0557C (two specimens, Mbiame village, 6.190°N and 10.849°E, elev. 1,955 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 0856, 0014C, 0133C (three specimens, Mbockghas village, 6.222°N and 10.582°E, elev. 2,092 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 0392C, 1086C, 2356I, 3392I (four specimens, Mboh village, 6.327°N and 10.348°E, elev. 1,900 m, coll. CamHerp, July 8, 2002) – CamHerp 3291I (Sarkong Hill, west of Jakiri village, 6.054°N and 10.598°E, elev. 1,600 m, coll. CamHerp, March 19, 2002) – CamHerp 1452C (Veko village, 6.139°N and 10.578°E, elev. 2,044 m, coll. CamHerp M. LeBreton, July 8, 2002).

This species (Fig. 20) has a wide distribution and the systematics of the species complex remains problematic. The name *N. melanoleuca* has only to be applied to central African populations. It occupies dense evergreen and semi-deciduous forests, forest-savanna mosaics, and the Western Highlands. It is found from sea level up to 2,700 m at Mt. Meletan in the Bamboutos. Gonwouo et al. (2007) consider that this snake can occur in mountain forests between 1,800 m and 3,000 m above sea level in Cameroon. The cobra is quoted from Bafut (elev. 1,200 m, 6.08°N, 10.10°E) by Joger (1982). The species, as currently recognized (sensu lato), is reported up to 2,500 m altitude in Kenya (Spawls et al. 2002; Wagner and Böhme 2007; Largen and Spawls 2010).

Naja nigricollis Reinhardt, 1843 (one specimen)

Material: CamHerp 1500C (Jakiri village along the road from Bamenda to Nkambe, 6.055°N and 10.658°E, elev. 1,550 m, coll. CamHerp M. LeBreton, July 8, 2002).

This spitting cobra species seems not to exceed 1,000 m elevation in East Africa where another related species, *Naja ashei* Wüster and Broadley, 2007, can occur above 1,750 m (Largen and Spawls 2010). *Naja nigricollis* is found between 20 and 1,800 m elevation in Cameroon.

Lamprophiidae Fitzinger, 1843

The validity of this family was recently demonstrated by Kelly et al. (2011). This work showed that the genus *Lamprophis* was polyphyletic. A new genus was created and other species previously included in the genus *Lamprophis* were divided into three groups: (1) *virgatus* and *fuliginosus*, together with *lineatus* and *olivaceus* were transferred to the revalidated genus *Boaedon* A.M.C. Duméril, Bibron, and A.H.A. Duméril, 1854; (2) *Lycodonomorphus* was nestled within *Lamprophis* sensu lato and a sister taxon of *Lamprophis inornatus*–the latter species was therefore transferred to the genus *Lycodonomorphus*; (3) *Lamprophis* sensu stricto was restricted to a small clade of four species endemic to South Africa, with *Lamprophis aurora* as type species. We follow this revised taxonomy here.

Fig. 20. *Naja melanoleuca.* Cameroon, Bamessing, October 31, 2003. *Picture: M. LeBreton.*

Boaedon fuliginosus (Boie, 1827) [formerly *Lamprophis fuliginosus*] (two specimens)

Material: CamHerp 0992C (Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton, July 8, 2002) – CamHerp 1365C (Veko village, 6.139°N and 10.578°E, elev. 2,044 m, coll. CamHerp M. LeBreton, December 14, 2002).

Boaedon fuliginosus is a snake often encountered in and around houses. Nocturnal and terrestrial, it has a very wide African distribution, although populations in southern and eastern Africa were referred to *B. capensis* (Hughes 1997). It occupies a variety of habitats ranging from dense evergreen and semi-deciduous degraded forests, to forest-savanna mosaics through the Adamaoua high savannas and Sudanian savannas. It occurs up to 2,044 m at Veko village in the BH and up to 2,400 m in East Africa (Spawls et al. 2002; Largen and Spawls 2010).

Boaedon virgatus (Hallowell, 1854) (one specimen)

Material: CamHerp 3747I (Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton, December 14, 2002).

This terrestrial forest species is present between 10 m and 1,770 m elevation in Cameroon.

Bothrolycus ater Günther, 1874 (five specimens)

Material: CamHerp 0487C, 3403I, 0174, 0306 (four specimens, Mboh village, 6.327°N and 10.348°E, elev. 1,900 m, coll. CamHerp M. LeBreton, July 8, 2002 (two specimens) and December 14, 2002 (two specimens) – CamHerp 3238I (Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton, December 14, 2002).

This terrestrial forest snake is present at elevations between 10 m and 1,500 m in Cameroon.

Gonionotophis stenophthalmus (Mocquard, 1887) (one specimen)

Material: CamHerp 0897 (Jakiri village along the road from Bamenda to Nkambe, 6.055°N and 10.658°E, elev. 1,550 m, coll. CamHerp M. LeBreton, July 8, 2002).

This semi-arboreal, ophiophagous forest snake is present between 50 m and 1,500 m elevation in Cameroon.

Lycophidion multimaculatum Boettger, 1888 (two specimens)

Material: MNHN-RA 2002.0943 (Awing village (Benjom), 5°3’28’’N and 10°1’4’’E, elev. 1,747 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp – (Bamboutos, Fulbe house, elev. 2,450 m, coll. CamHerp P. Makolowodé, June 12, 1999).

The specimen MNHN-RA 2002.0943 is identified as *Lycophidion multimaculatum*. It measures 250 mm SVL and its tail is 28 mm. It has 17 dorsal rows at midbody. Its non-keeled ventrals are 2+186 and unkeeled subcaudals 30. Anal plate is entire. Supralabials (right/left) 8 (3–5 in contact with the eye)/8 (3–5), infralabials 8/8 (1–4 in contact with the first pair of gular), temporals 1+2+3/1+2+3, preocular 1/1, postoculars 2/2. An apical pit distinguished on dorsal scales and anterior gulars are of the same size as the posterior. That specimen is uniform grey bluish dorsally and ventrally, only slightly lighter ventrally; no marks, rings, or spots can be seen. Its diagnosis is not entirely consistent with that of the species to which we refer to tentatively. The species is found between 510 m and 2,450 m elevation (Mt. Meletan, Bamboutos) in Cameroon. So it is a partially submontane species in Cameroon (i.e., but not strictly submontane, much like *Dipsadoboa unicolor*).

Psammophiidae Boie, 1827

Psammophis cf. *phillipsii* (Hallowell, 1844) (three specimens)

Material: CamHerp 180, 601C, 844C (three specimens, Mbiame, 6.190°N and 10.849°E, elev. 1,955 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002).

This terrestrial snake is common in Cameroon and Central African Republic. It occupies a variety of habitats ranging from degraded forests to high savannas. It does not hesitate to frequent the villages and even large cities like Yaounde. The species is abundant in the whole southern half of the country, except in undisturbed forest areas, and is found up to 2,000 m at Tabenken. Species status was granted to this taxon by Kelly et al. (2008) as *Psammophis occidentalis* Werner, 1919, but that name does not apply to those populations of the *P. phillipsii* complex (entire anal plate). They are however distinct from *P. phillipsii* sensu stricto and their status is under revision (Trape, pers. comm. to LC). Those populations were previously recognized as *P. phillipsii* by Chirio and Ineich (2006) and Chirio and LeBreton (2007). They belong to a central African species whose distribution does not occur west of the Cameroon border. This snake (as *Psammophis sibilans*) was also reported from Bafut (elev. 1,200 m, 6.08°N, 10.10°E) by Böhme (1975).

Psammophis sp. 1 (in: Chirio and LeBreton 2007: 540–541) (one specimen)

Material: CamHerp 0645C (Oku Simokuh village, 6.234°N and 10.572°E, elev. 2,109 m, coll. CamHerp, July 8, 2002).

This undescribed terrestrial species is an inhabitant of the Cameroon mountains, and seems to share external morphological affinities with an Ethiopian specimen from MNHN-RA collections. It occupies the Western Highlands, but also the Adamaoua high savannas. Currently its distribution is limited to a few peaks of the Cameroon Volcanic Dorsal, where it ascends to 2,109 m altitude at Mt. Oku.

Typhlopidae Jan, 1863

Afrotyphlops cf. *punctatus* (Leach, 1819) (11 specimens; see below)

Material: CamHerp 0087C, 3237I (two specimens, Tefo village, 6.30°N and 10.37°E, coll. CamHerp M. LeBreton, and L. Chirio, July 8, 2002) – CamHerp 1412I (Mufe village, 6.30°N and 10.35°E, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002) – CamHerp 1018C 1208C (two specimens, Mboh village, 6.327°N and 10.348°E, elev. 1,900 m, coll. CamHerp L. Chirio, July 8, 2002); CamHerp 1253C, 3135I, (two specimens, Mboh village, 6.327°N and 10.348°E, elev. 1,900 m, coll. CamHerp L. Chirio, December 14, 2002); CamHerp 0176C, 1021C (two specimens, Abuh village, NE of Fundong, 6.297°N and 10.331°E, elev. 1,750 m, coll. CamHerp M. LeBreton, December 14, 2002) – CamHerp 0396C, 0180M (two specimens, Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton, December 14, 2002).

Specimens are only provisionally attributed to this species pending further study and occur in marbled and unmarbled forms. This burrowing snake is found at altitudes between 5 m and 1,800 m in Cameroon from Mboh village (1,800 m), Baba II village (1,770 m) and Idjim village (1,600 m)). *Afrotyphlops* cf. *punctatus* is found between 10 m and 1,800 m above sea level in Cameroon, and has been reported from Wum (elev. 1,023 m, 6.39°N and 10.07°E) by Böhme (1975).

Viperidae Oppel, 1811

Atheris broadleyi Lawson, 1999 (one specimen)

Material: CamHerp 0974C (Bali Ngemba village, 5.833°N and 10.077°E, elev. 1,398 m, coll. CamHerp M. LeBreton, July 8, 2002).

This small arboreal forest viper (Fig. 21) is found at altitudes between 332 m and 1,398 m in Cameroon (Chirio and LeBreton 2007). The species is also present in the Central African Republic. The geographic distribution of this small tree viper is still unclear (Phelps 2010), but it occurs with certainty in Cameroon and the Central African Republic (Chirio and Ineich 2006).

Atheris squamigera (Hallowell, 1854) (two specimens)

Material: CamHerp 0336, 1205C (two specimens, Forest Reserve of Bali Ngemba, 5.825°N and 10.087°E, elev. 1,400 m, coll. CamHerp, March 19, 2002).

This semi-arboreal viper is an inhabitant of the dense forests that occur from sea level up to 1,900 m (Broadley 1998). This is exceeded by *Atheris nitschei*, an East African species that occurs up to 2,700 m (Phelps 2010).

Bitis arietans arietans (Merrem, 1820) (two specimens)

Material: CamHerp 0694C (Veko village, 6.139°N and 10.578°E, elev. 2,044 m, coll. CamHerp M. LeBreton, July 8, 2002) – CamHerp 3523I (Jakiri village along the road from Bamenda to Nkambe, 6.055°N and 10.658°E, elev. 1,550 m, coll. CamHerp M. LeBreton, December 14, 2002).

This big and massive snake has a pan-African distribution, and is also found on the Arabian Peninsula. It frequents forest-savanna mosaics, the Western Highlands, and all types of savannas (high, Sudanese, and Sahelian). It lives at ground level and bites are frequent, making it a feared snake. It occupies elevation areas up to 2,044 m in the village of Veko in the BH. Its wide distribution in Africa was largely influenced by the occupation of climatic refuges during periods of glaciation (Barlow et al. 2013). Other altitude populations exist such as those of the East African Mountain Arc or of the Drakensberg mountains in South Africa (Phelps 2010; Barlow et al. 2013). The altitudinal record for the species is around 2,200 m but the species seems able to occur even higher, up to 2,400 m (Spawls et al. 2002; Largen and Spawls 2010).

Bitis gabonica (A.M.C. Duméril, Bibron and A.H.A. Duméril, 1854) (one observed specimen)

Material: One specimen was observed but not collected near Bangangte at 1,480 m elevation.

This big forest viper was reported from Bafut (elev. 1,200 m, 6.08°N and 10.10°E) by Stucky-Stirn (1979) and found at 1,500 m in the western extension of the BH, and also at Mende in the Takamanda. It was observed by one of us (LC) at almost 1,500 m near Bangangte. In Cameroon it is found at altitudes between 5 m and only 1,500 m, but occurs over 2,300 m in East Africa (Kucharzewski 2011).

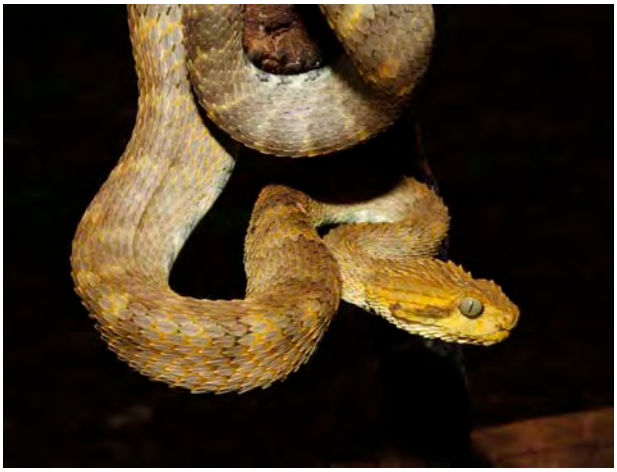

Fig. 21. *Atheris broadleyi.* Megangme, 4.598°N and 12.225°E, elev. 610 m, September 8, 2012. *Picture: M. LeBreton.*

Bitis nasicornis (Shaw, 1802) (no available specimen)

This bulky viper, characterized by its horn-shaped scales at the snout tip, shows a vast African distribution. It occupies dense evergreen and semi-deciduous forests, the Western Highlands, and the forest-savanna mosaics in well-preserved forest pockets. It prefers moist valley bottoms in the dense forests, and is considered a dangerous venomous snake. It occurs up to 2,000 m altitude at Lake Awing in the BH in Cameroon (specimen observed but not collected), and up to 2,400 m in East Africa (Spawls et al. 2002; Kucharzewski 2011). It was reported from Mbengwi, northwest of Bamenda (elev. 1,200 m) by Stucky-Stirn (1979).

Causus maculatus (Hallowell, 1842) (three specimens)

Material: CamHerp 1350C (Baba II village, 5.857°N and 10.102°E, elev. 1,772 m, coll. CamHerp M. LeBreton, July 8, 2002) – CamHerp 0147C (Bali Ngemba village, 5.833°N and 10.077°E, elev. 1,398 m, coll. CamHerp M. LeBreton, July 8, 2002) – CamHerp 0818I (Mbiame, 6.190°N and 10.849°E, elev. 1,955 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002).

This small nocturnal viper is very common in wet savanna and degraded forests areas. It does not hesitate to venture into the villages at night but its venom is only slightly harmful. Its distribution is broad and includes much of the African continent, from Mauritania to Uganda and Angola. It can be present up to 1,950 m altitude at Mbiame in the BH in Cameroon, which seems to be its altitude record all over its range (Kucharzewski 2011). Its presence in East Africa seems questionable and should probably refer to an undescribed high-elevation species close to the endemic species reported below. In Ethiopia it is only known from a few specimens collected between

500 and 1,000 m above sea level (Largen and Spawls 2010).

Causus sp. (in: Chirio and LeBreton 2007: 612–613) (four specimens)

Material: CamHerp 0964C (Mboh village, 6.327°N and 10.348°E, elev. 1,900 m, coll. CamHerp L. Chirio, July 9, 2002) – CamHerp 0196, 0695C, 0998C (three specimens, Mbiame, 6.190°N and 10.849°E, elev. 1,955 m, coll. CamHerp M. LeBreton and L. Chirio, July 8, 2002, and December 14, 2002 [0998C]).

This scarce montane species occupies both Cameroon and the Central African Republic (far west). It is not described yet but has numerous morphological affinities with the forms of the *Causus rhombeatus* (Lichtenstein, 1823) group from East and South Africa. In Cameroon, it occupies the Adamaoua high savannas and the Western Highlands where it looks for wet lowlands and the banks of mountain creeks. It is only found at altitude, from 700 m at Ngaouyanga (Adamaoua) up to 1,950 m at Mbiame (BH).

Biogeographic Affinities of the Reptiles of Mt. Oku and the Bamenda Highlands

The 50 reptile species in the study area are classified alphabetically below within each biogeographic region recognized.

Ubiquitous species (1): *Agama agama*.

Forest species from Western and Central Africa (9): *Bitis nasicornis – Boaedon virgatus – Dasypeltis fasciata – Dendroaspis j. jamesoni – Dipsadoboa unicolor – Dipsadoboa weileri – Goniocephalus stenophthalmus – Kinixys homeana – Trachylepis maculilabris*.

Central African forest species (8): *Atheris broadleyi – Atheris squamigera – Bitis gabonica – Bothrolycus ater – Lepidothyris fernandi – Naja melanoleuca – Polemon collaris – Thrasops flavigularis*.

African savanna species (12): *Afrotyphlops* cf. *punctatus – Atractaspis i. irregularis – Bitis a. arietans – Boaedon fuliginosus – Causus maculatus – Chamaeleo gracilis – Crotaphopeltis hotamboeia – Dasypeltis confusa – Dispholidus typus – Grayia tholloni – Hemidactylus angulatus – Naja nigricollis*.

Savanna species with eastern affinities (5): *Chamaeleo laevigatus – Lycophidion multimaculatum – Philothamnus angolensis – Philothamnus hughesi – Psammophis* cf. *phillipsii*.

Endemic Cameroon mountain species (13): *Agama* sp. 2 – *Agama* sp. 4 – *Causus* sp. – *Crotaphopeltis* sp. – *Lacertaspis chriswildi – Lacertaspis lepesmei – Leptosiaphos ianthinoxantha – Leptosiaphos pauliani – Leptosiaphos vigintiserierum – Trachylepis mekuana – Trioceros pfefferi – Trioceros quadricornis gracilior – Trioceros serratus*.

Montane species (2): *Hemidactylus kamdemtohami – Psammophis* sp. 1.

The species composition of our study area located on the Cameroon Volcanic Dorsal is characterized by the presence of a similar number of species in the three dominant elements: savanna forms, forest forms, and endemic montane forms.

Among the 50 reptile species in our study zone there are:

(1) two very anthropophilous species that rise high in elevation in the villages of the region: *Agama agama* and

Table 1. List of the 50 reptile species present in our study area at Mt. Oku and the Bamenda Highlands. For each species we indicate if it is a low elevation or montane species (submontane) (in bold characters) and its altitudinal limits known in Cameroon. For each family we indicate between brackets the number of species in our study area.

		Altitudinal limits in Cameroon (elevation indicated in meters)	
Families	**Species**	**Low elevation species**	**Submontane species**
Testudinidae (1)	*Kinixys homeana*	0–1800	
Agamidae (3)	*Agama agama*	0–2000	
	***Agama* sp. 2**		**1900–2350**
	***Agama* sp. 4**		**1900–2200**
Chamaeleonidae (5)	*Chamaeleo gracilis*	0–1500	
	Chamaeleo laevigatus	350–1550	
	Trioceros pfefferi		**1100–2000**
	Trioceros quadricornis gracilior		**1800–2700**
	Trioceros serratus		**1040–2700**

Table 1 (continued). List of the 50 reptile species present in our study area at Mt. Oku and the Bamenda Highlands. For each species we indicate if it is a low elevation or montane species (submontane) (in bold characters) and its altitudinal limits known in Cameroon. For each family we indicate between brackets the number of species in our study area.

		Altitudinal limits in Cameroon (elevation indicated in meters)	
Families	**Species**	**Low elevation species**	**Submontane species**
Gekkonidae (2)	*Hemidactylus angulatus*	0–2000	
	Hemidactylus kamdemtohami		**1450–1500**
Scincidae (8)	***Lacertaspis chriswildi***		**1000–2800**
	Lacertaspis lepesmei		**2350–2700**
	Lepidothyris fernandi	0–1700	
	Leptosiaphos ianthinoxantha		**1300–2700**
	Leptosiaphos pauliani		**1300–2000**
	Leptosiaphos vigintiserierum		**1000–2450**
	Trachylepis maculilabris	0–2100	
	Trachylepis mekuana		**2400–2700**
Atractaspididae (2)	*Atractaspis i. irregularis*	500–2000	
	Polemon collaris	0–1950	
Colubridae (11)	*Crotaphopeltis hotamboeia*	160–2044	
	***Crotaphopeltis* sp.**		**1050–1500**
	Dasypeltis confusa	500–1550	
	Dasypeltis fasciata	0–2050	
	Dipsadoboa unicolor		**80–2050**
	Dipsadoboa weileri	0–2050	
	Dispholidus typus	350–2150	
	Grayia tholloni	510–1550	
	Philothamnus angolensis	50–2450	
	Philothamnus hughesi	700–2100	
	Thrasops flavigularis	0–2050	
Elapidae (3)	*Dendroaspis j. jamesoni*	0–2000	
	Naja melanoleuca	0–2700	
	Naja nigricollis	0–1800	
Lamprophiidae (5)	*Boaedon fuliginosus*	250–2050	
	Boaedon virgatus	0–1800	
	Bothrolycus ater	0–1800	
	Gonionotophis stenophthalmus	50–1500	
	Lycophidion multimaculatum	500–2450	
Psammophiidae (2)	*Psammophis* cf. *phillipsii*	0–2000	
	***Psammophis* sp. 1**		**1450–2100**
Typhlopidae (1)	*Afrotyphlops* cf. *punctatus*	0–1800	
Viperidae (7)	*Atheris broadleyi*	300–1400	
	Atheris squamigera	0–1500	
	Bitis a. arietans	250–2000	
	Bitis gabonica	0–1500	
	Bitis nasicornis	0–2000	
	Causus maculatus	0–1950	
	***Causus* sp.**		**700–1950**

Trachylepis maculilabris. They both occur as well in West Africa, Central and Eastern Africa. However, note that *T. maculilabris* is an anthropophilic species that requires more moisture than *A. agama*, which only enters in the forest degraded by man;

(2) a mixed group of forest and savanna species that are ecologically tolerant; they are also found in the plains but they often reach 2,000 m in the BH and on the slopes of Mt. Oku. Most of them are also found in West Africa, except *Bothrolycus ater*, *Chamaeleo laevigatus*, *Dendroaspis j. jamesoni*, *Lycophidion multimaculatum*, *Naja melanoleuca* (sensu stricto), *Philothamnus hughesi*, *Polemon collaris*, and *Thrasops flavigularis*, which are limited to the large Central African forest block (and its surrounding areas);

(3) a group of mountain species, endemic or not to the study area: *Agama* sp. 2, *Agama* sp. 4, *Causus* sp., *Crotaphopeltis* sp., *Dipsadoboa unicolor*, *Hemidactylus kamdemtohami*, *Lacertaspis lepesmei*, *Lacertaspis chriswildi*, *Leptosiaphos ianthinoxantha*, *Leptosiaphos pauliani*, *Leptosiaphos vigintiserierum*, *Psammophis* sp. 1, *Trachylepis mekuana*, *Trioceros pfefferi*, *Trioceros quadricornis gracilior*, and *Trioceros serratus*.

Altitudinal Distribution

Among the mountain endemic species of the Cameroon Volcanic Dorsal, *T. quadricornis gracilior*, *T. serratus*, and *L. chriswildi* reach the highest elevations on Mt. Oku, although none occur beyond the treeline where subalpine meadows appear around 2,600 m above sea level (Fig. 22, Table 1). So far, no reptile species has been identified on the summit of Mt. Oku grasslands. However, as with Mt. Cameroon, specific searches for them have not been made, and amphibians are relatively well abundant as potential prey for batrachophagous snakes. It is however a harsh climate for reptiles, with cold nights and frequent frosts.

A clear nomenclature describing the altitudinal distribution patterns observed in Cameroon is difficult as differences between zoological groups are important. Amiet (1971) adopted the biogeographic classification of altitudinal distributions in Cameroon proposed by Letouzey (1968):

1,000 m/1,200 m = low and medium altitude rain forest strata;
1,000 m–1,200 m/1,600–1,800 m = submontane strata;
1,600 m–1,800 m/2,200–2,500 m = montane strata;
2,200 m–2,500 m/3,200–3,600 m = afro-subalpine strata;
above 3,200–3,600 m = afro-alpine strata.


Fig. 22. The altitude grassland of the summit at Mt. Oku no longer harbors any reptile. Chameleons can still be found in the forest on the edge of the meadows, up almost 2,600 m above sea level. However, one can observe there a tiny endemic viviparous toad under the stones on the ground. *Picture: I. Ineich, May 7, 2007.*

Later he (Amiet 1975) defined a "oro-cameroon faunistic element" of species with distributions above 1,000 m elevation. The term "orobiontes" (here replaced with submontane species) was used for these high altitude species. Montane species also present in lower areas around mountains were also distinguished as "monticolous species." Amiet (1987) estimated that the average annual temperature had lowered from 3.5 to 4.5 °C during the last glaciation in Cameroon, and showed that the altitudinal limit of 900 m to 1,000 m is an important ecological boundary, marking the exclusion of many lowland species and the appearance of true submontane species. This boundary in the BH, however was not at 1,000 m elevation but increased to 1,400 m, before a distinctive "submontane" herp assemblage occurs. The further mountain ranges are located from the sea the altitudinal limit for a species appears to increase. The separation of vicariant Cameroon "submontane" reptile assemblage is relatively recent and seems to mainly date from 25,000 to 15,000 BP (Amiet 1987).

Herrmann et al. (2005) presented a detailed study of herpetofauna of Mt. Nlonako, and identified only four of 89 species whose range exceeding 1,700 m altitude: *Trioceros pfefferi* (Chamaeleonidae), *Leptosiaphos vigin-*

tiserierum, *Trachylepis maculilabris* (Scincidae), and *Chamaelycus fasciatus* (Lamprophiidae). They noted that within the Cameroon Volcanic Dorsal a mountain range must exceed a certain altitude to allow the development of an endemic herpetofauna, otherwise faunal exchanges between ranges resulted in the presence of a shared submontane Cameroon biota.

Supraspecific Diversity

Although many reptile families in Cameroon, as in East African mountains, have endemic montane species, e.g., Agamidae, Chamaeleonidae, Scincidae, Psammophiidae, and Viperidae, there is a curious absence of montane Lacertidae in Cameroon. In Kenya, *Adolfus alleni* (Barbour, 1914) and *Adolfus masavaensis* (Wagner et al. 2014) occur in the summit grasslands of the Aberdares and Mt. Kenya, respectively, with ranges from 2,700 to 4,500 m (Spawls et al. 2002). In contrast, there are a number of skinks, particularly small, semifossorial members of the genera *Lacertaspis* and *Leptosiaphos*, that occur above 2,000 m, with *Trachylepis mekuana* and *Lacertaspis lepesmei* being high-altitude endemics.

Mountain dwelling taxa do not necessarily come from the same genera: inside Viperidae, the genera *Atheris* and *Bitis* often possess endemic montane forms sometimes encountered over 3,000 m in East Africa, with the monotypic *Montatheris hindii* being also endemic to montane heathlands. Only the genus *Causus* shows an endemic submontane species in Cameroon which does not even reach 2,000 m elevation. Note, however, that the genus *Atheris* holds endemic species in Cameroon or at least in the Cameroon region (*Atheris broadleyi*, *A. subocularis*), but curiously none of them are limited to the highlands, contrary to what can be observed in East Africa. The strongest affinities between East Africa and Cameroon seem to mainly concern two particularly diverse lizard families on the African continent, Chamaeleonidae and Scincidae (Ineich and Chirio 2004).

Endemism

Endemism at the Cameroon Volcanic Dorsal has a general pattern but with several exceptions. Speciation by vicariance clearly dominates with close but distinct taxa (except for *Trioceros pfefferi*; see our comments above) between separate massifs (e.g., Manengouba and BH-Mt. Oku). The highest peak of the Cameroon Volcanic Dorsal, Mt. Cameroon, an active volcano, is newer than the other summits located further north in the Dorsal. It has no endemic mountain reptiles, however, and this is certainly related to its geological age. However, no detailed study has been undertaken to estimate genetic divergences among disjunct populations of *Trioceros montium* which reaches 1,100–1,200 m at Mt Kupe, but 1,500 m at Manengouba (Anderson and Van Heygen 2013). This species is currently assigned to a single taxon, without subspecific distinction, but may well follow a similar evolutionary pathway like other mountain chameleons of Cameroon.

Threats and Conservation

The threats to this submontane herpetofauna are numerous (Euskirchen et al. 2000). The conservation status of all the endemic species is fragile, and their limited ranges are being rapidly degraded. However, they are characterized by locally high densities, which unfortunately also makes them all the more easy to collect. In fact, species of mountain chameleon from Cameroon are highly sought after for the international exotic pet trade. However, the most serious threat to their existence is the rapid human population growth in the region of Mt. Oku and the Western Highlands. It makes species preservation difficult because human pressure on land for agriculture and livestock, and consequent deforestation, is destructive and growing with little regard to the conservation of endangered species that are increasing in number.

Conclusions

Like most other highland areas, the highest reliefs of Mt. Oku and the BH have only a limited herpetofauna. However the species assemblage is original in its composition. First, it contains a ubiquitous fauna, able to occupy a wide range of habitats from sea level to almost 2,000 m elevation. It also includes typical mountain species unable to survive below 1,000 m, and climbing up to 2,800 m. The vast majority of these latter species, highly specialized at least climatically, are endemic to the Cameroon Volcanic Dorsal and often to a single mountain range. The only study on the herpetofauna of Mt. Oku mentioned only two lizards and seven amphibians, including a scolecomorphid caecilian (Wild 1994). Our work considerably increases this list but unfortunately five potential new species first signaled by Chirio and LeBreton (2007) have still to be described.

The unique herpetofauna of this region is seriously threatened by exponential human growth and its associated impacts. The fertile volcanic soil in the region has always attracted humans, whose expanding population and utilization of natural resources, inevitably encroaches on the fragile habitats of reptiles. Survival and preservation of these populations for future generations must be met with prompt protective actions that are both robust and effective. In addition it must gain the support of the local human population if these endemic species are not to face extinction in the near future.

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The snakes of Niger

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***Abstract.*—We present here the results of a study of 1,714 snakes from the Republic of Niger, West Africa, collected from 2004 to 2008 at 28 localities within the country. Based on this data, supplemented with additional museum specimens (23 selected specimens belonging to 10 species) and reliable literature reports, we present an annotated checklist of the 51 snake species known from Niger. *Psammophis sudanensis* is added to the snake fauna of Niger. Known localities for all species are presented and, where necessary, taxonomic and biogeographic issues discussed.**

Key words. Reptilia; Squamata; Ophidia; taxonomy; biogeography; species richness; venomous snakes; Niger Republic; West Africa

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Introduction

Few studies have been dedicated to the snake fauna of the Republic of Niger, the largest country of West Africa with 1,267,000 km^2 between latitudes 11° and 24°N, and longitudes 0° and 16°E (Fig. 1). The northern part of the country is Saharan (Fig. 2), the central and southeastern parts Sahelian (Fig. 3–4), and the southcentral and southwestern parts Soudanian (Fig. 5). Elevation is low in most parts of the country, ranging from 200 m to 700 m, the highest point reaching 2,022 m in Aïr Mountains, an area of special biogeographical interest in the Sahara desert (Fig. 6). Several snake specimens collected during various Saharan expeditions were reported by Pellegrin (1909), Angel (1932, 1936), Angel and Lhote (1938), Villiers (1950a, 1950b) and Joger (1981). The snake fauna of Aïr Mountains was investigated by Villiers (1950a) and Kriska (2001). Important snake collections were made in southwestern Niger by Roman (1974, 1984), and in W National Park by Chirio (2009). Snakes observed in the Termit Massif were reported by Ineich et al. (2014). These specimens and/or additional material from Niger were included in several revisions or regional studies, in particular by Papenfuss (1969), Leviton and Anderson (1970), Roman (1972, 1974, 1977, 1984), Roux-Estève (1974), Hughes (1976, 1983, 1998), Hahn and Roux-Estève (1979), Broadley (1984), Chirio and Ineich (1991), Hahn and Wallach (1998), Trape (2002), Broadley and Hughes (2000), Wüster and Broadley (2003), Trape and Mané (2006a, 2006b), Trape et al. (2006, 2009, 2012), Crochet et al. (2008), Chirio et al. (2011), and Sindaco et al. (2013).

Materials and Methods

In January 2004 and February–March 2005, we deposited cans or buckets half filled with formaldehyde or ethanol in 22 villages in Niger. Cans or buckets—one per village—were housed by the chief of the village. We asked the villagers to deposit in these containers the snakes they killed when they were occasionnaly encountered in the vicinity of their village. A modest award (300 CFA, i.e., approximately 0.6 US $) was given for each preserved specimen. In most parts of Niger—as in most parts of Africa—all species of snakes are feared and systematically killed when they are encountered. Thus, the objective of the award was to acknowledge the effort of carrying killed snakes from surrounding fields to the village, this without encouraging snake search and killing. Visits to the villages were organized in February–March

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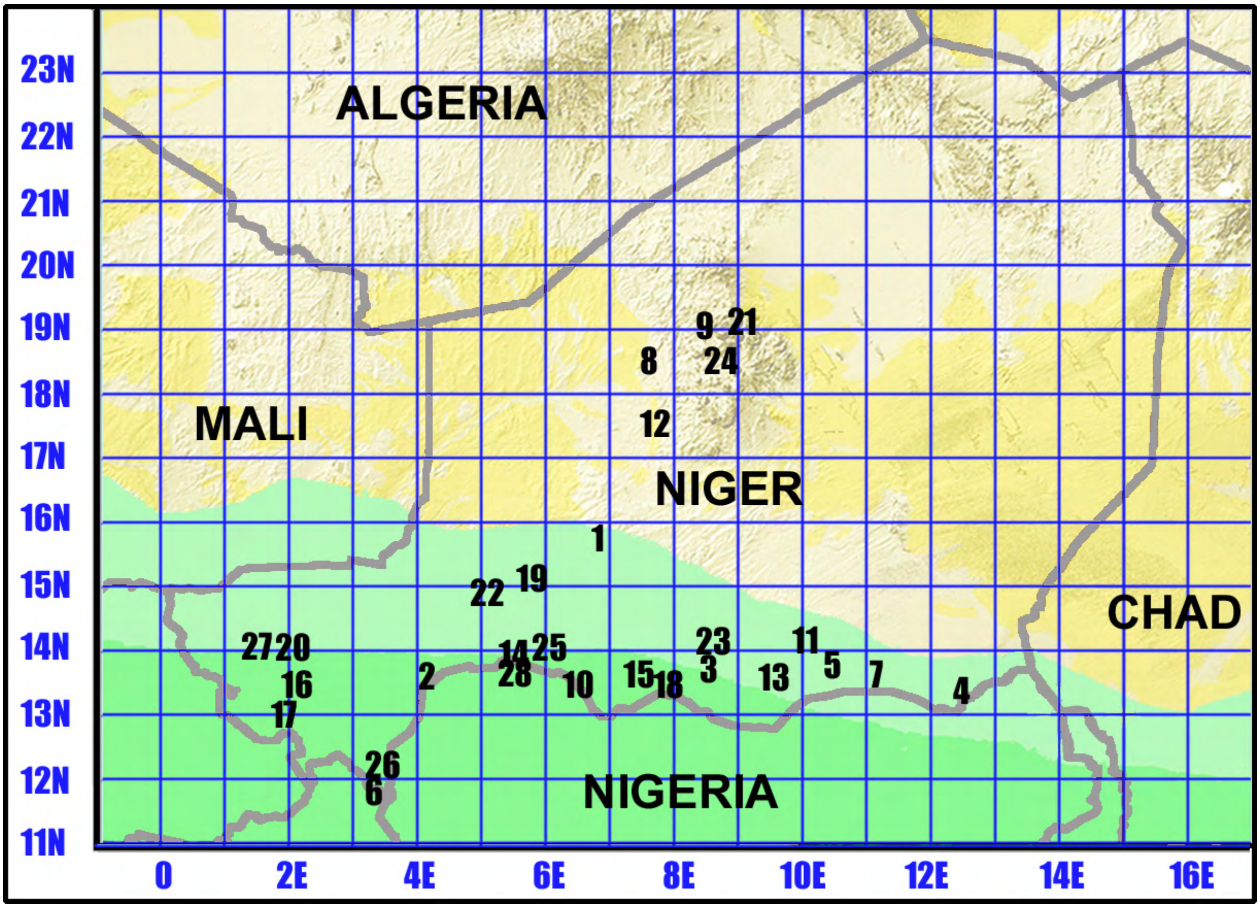

Fig. 1. Map of Niger with location of collection localities. See Table 1 for locality numbers. Colors for vegetation areas: Sudanian / Sahelo-Sudanian: green; Sahelian: light green; Saharan: yellow for sandy areas, white for stony areas, grey for rocky and mountainous areas.

2005, September–October 2005, and January 2008 to retrieve the specimens. During travels we also collected snakes at six additional localities. The 28 collecting localities (Table 1 and Fig. 1) were distributed either in the southern part of the country (11°52'N–14°52'N: 21 localities), where average annual rainfall ranges from 800 to 300 mm with a South-North gradient, or in the northern arid part of the country (15°06'N–19°07'N: 7 localities), including Aïr Mountains, where rains range from 250 to less than 50 mm (Mahé et al. 2012).

Most specimens were deposited at the Institut de Recherche pour le Développement (Dakar, Senegal; acronym: IRD), but some specimens—including those of *Rhagerhis moilensis* used for comparison with the type series of *Rhamphiophis maradiensis*—were donated to the Museum national d'Histoire naturelle (Paris, France; acronym: MNHN). We also examinated selected specimens from Niger from the Institut Fondamental d'Afrique Noire in Dakar (acronym: IFAN), the Laboratoire de Bioécologie des Vertébrés in Montpellier (acronym: BEV), MNHN and Laurent Chirio private collection.

Specimens were identified to species according to classical identification keys for West African snakes (Trape and Mané 2006b, Chippaux 2006), recent revisions of several genera (Trape et al. 2009, Trape et al. 2012) and further taxonomic analysis (Trape et al., unpublished). For recent changes in snake generic names, we usually follow those adopted in the reptile database of Uetz and Hošek (http://www.reptile-database.org/).

Results

We collected a total of 1,714 specimens and examined 23 selected additional specimens from IFAN (two specimens), MNHN (17 specimens), BEV (one specimens) or Chirio's private collection (three specimens). They belonged to 43 species. Eight additional species are known with certainty from Niger but were not represented among the specimens we examined.

Family Typhlopidae Gray, 1845

Afrotyphlops lineolatus (Jan, 1864)
Material: One specimen.
Locality: Téla (1).
Literature records: Gaya (Chirio 2009, in error).
Remark: Our Téla specimen, the first known from Niger, was quoted in error from Gaya by Chirio (2009).

Table 1. Collection localities of snakes in Niger (this study). *A: January 2004 – February 2005; B: March 2005 – October 2005; C: November 2005 – January 2008; D: occasional encounters during travels.

N°	Locality	Latitude	Longitude	Elevation	Region	No of specimens	No of species	Sampling period*
1	Aborah	15°53’N	06°53’E	510 m	Central	3	2	B
2	Aholé	13°33’N	04°01’E	225 m	South Central	150	9	A, B, C
3	Baboul	13°42’N	08°35’E	454 m	South Central	62	8	A, B
4	Chétimari	13°12’N	12°25’E	314 m	South East	60	6	A, B, C
5	Cissia	13°52’N	10°25’E	390 m	South East	80	13	A, B, C
6	Gaya	11°52’N	03°26’E	170 m	South West	1	1	D
7	Goudoumaria	13°42’N	11°11’E	348 m	South East	10	3	B
8	Gougaram	18°27’N	07’48’E	503 m	Aïr	1	1	A
9	Iférouane	19°03’N	08°25’E	660 m	Aïr	1	1	A
10	Karosofoua	13°37’N	06°37’E	316 m	South Central	91	10	A, B, C
11	Kéllé	14°16’N	10°06’E	456 m	South East	9	9	B, C
12	Korri Solomi	17°37’N	07°40’E	467 m	Aïr	2	2	A
13	Kusa	13°42’N	09°34’E	406 m	South Central	19	8	A, B
14	Malbaza	13°57’N	05°30’E	324 m	South Central	51	5	B, C
15	Maradi	13°47’N	07°26’N	411 m	South Central	1	1	D
16	Niamey (airport)	13°28’N	02°10’E	226 m	South West	1	1	D
17	Piliki	13°08’N	01°57’E	210 m	South West	159	15	B, C
18	Saboulayi	13°30’N	07°50’E	440 m	South Central	70	8	A, B, C
19	Saouna	15°07’N	05°42’E	401 m	Central	1	1	B
20	Simiri (vicinity)	14°02’N	02°05’E	244 m	South West	1	1	D
21	Taghmert (6 km N)	19°06’N	09°02’E	794 m	Aïr	1	1	D
22	Tahoua	14°52’N	05°16’E	387 m	South Central	2	1	D
23	Tarka Dakouara	14°12’N	08°49’E	465 m	South Central	315	10	A, B, C
24	Tchintoulous	18°34’N	08°47’E	826 m	Aïr	1	1	A
25	Tékhé	14°01’N	06°01’E	323 m	South Central	209	11	B, C
26	Téla	12°08’N	03°28’E	193 m	South Central	170	21	A, B, C
27	Toundi Farkia	14°02’N	01°32’E	208 m	South West	20	5	B, C
28	Tounga Yacouba	13°55’N	05°26’E	306 m	South Central	223	10	A, B, C

Afrotyphlops punctatus (Leach, 1819)
Material: One specimen.
Locality: Birni N’Konni (1, coll. MNHN).
Literature records: Birni N’Konni (Pellegrin 1909, Papenfuss 1969, Roux-Estève 1974); SW Niger (Roman 1974: One specimen).

Family Leptotyphlopidae Stejneger, 1892

Myriopholis adleri (Hahn and Wallach, 1998)
Material: Two specimens.
Locality: Gaya (2, coll. Chirio).
Literature records: Gaya (Chirio 2009).
Remarks: Despite the rarity of records, this species now appears to occupy the whole sudano-sahelian belt from Senegal to Chad but avoids the more sahelian areas contrary to *Myriopholis boueti* (Trape 2006b, Trape, in preparation).

Myriopholis algeriensis (Jacquet, 1895)
Material: One specimen.
Locality: Agadez (1, coll. MNHN).
Literature records: Agadez (Angel 1932, as *Leptotyphlops macrorhynchus*), Agadez (Angel and Lhote 1938, Villiers 1950a, as *Leptotyphlops macrorhynchus*); Aïr (Kriska 2001, as *Leptotyphlops macrorhynchus*); Agadez (Trape 2002, as *Leptotyphlops algeriensis*).

Myriopholis boueti (Chabanaud, 1917)
Material: Two specimens.
Locality: Kéllé (1), Gaya (1, coll. Chirio).
Literature records: Gaya (Chirio 2009).

Myriopholis cairi (Duméril and Bibron, 1844)
Material: Eight specimens.
Locality: Bilma (8, coll. MNHN).

Fig. 2. The Ténéré desert near Adrar Chiriet (19°17'N, 09°14'E).

Literature records: Bilma (Angel 1936, Angel and Lhote 1938, as *Leptotyphlops macrorhynchus bilmaensis*; Hahn and Roux-Estève 1979, Hahn and Wallach 1998, Trape 2002, as *Leptotyphlops cairi*); Téouar (Villiers 1950a, 1950b, as *Leptotyphlops macrorhynchus bilmaensis*).
Remarks: IFAN 47-4-38 from Téouar (Aïr Mountains) is apparently lost: we have been unable to find it in Dakar or Paris. However, data on this specimen provided by Villiers (1950b) exclude *Myriopholis algeriensis, Myriopholis boueti*, *Myriopholis adleri*, and *Myriopholis lanzai*, and fit well with *Myriopholis cairi*.

Tricheilostoma bicolor (Jan, 1860)
Material: One specimen.
Locality: Niamey Airport (1).
Literature records: Niamey, Tapoa (Hahn and Roux-Estève 1979, Hahn and Wallach 1998, as *Leptotyphlops bicolor*); Gaya, Campement Nigercar (Chirio 2009).

Family Boidae Gray, 1825

Eryx colubrinus (Linnæus, 1758)
Material: Three specimens.
Localities: Cissia (1), Tarka Dakouara (2).
Literature records: Agadez, Tabello (Villiers 1950a, 1950b, Papenfuss 1969); Aïr (Kriska 2001).
Remarks: In Niger this species was known from Aïr Mountains and Tamesna, i.e., 300 km north of Tarka Dakouara and Cissia, but not from the southern part of the country. Since Cissia is only 60 km from northeastern Nigeria and shares similar sahelian vegetation, our data suggest that this species may also reach this country where it has never been mentioned.

Eryx muelleri Boulenger, 1892
Material: 104 specimens.
Localities: Aborach (1), Aholé (17), Baboul (2), Chetimari (4), Cissia (2), Karosofoua (2), Kéllé (1), Kusa (1), Maradi (1), Saboulayi (8), Tarka Dakouara (30), Tékhé (9), Téla (17), Toundi Farkia (2), Tounga Yacouba (7).
Literature records: SW Niger (Roman 1974: 27 specimens); Aïr (Kriska 2001); Alambaré, Gaya, Gourgou, Kouré (Chirio 2009); Termit (Ineich et al. 2014).

Family Pythonidae Fitzinger, 1826

Python regius (Shaw, 1802)
Material: No specimen collected.
Literature records: SW Niger (Roman 1974: Two specimens); Alambaré (Chirio 2009).

Python sebae (Gmelin, 1788)
Material: No specimen collected.
Literature records: SW Niger (Roman 1974: Four specimens); 11 km NW of Niamey (Broadley 1984); Gaya, Mekrou-Direct (Chirio 2009).
Remarks: In Sahelo and Sahelo-Soudanian areas, this species is associated with perennial rivers, lakes, and marshlands. None of our study villages was located near the Niger River (Fig. 7), Lake Chad or other perennial waters.

Family Lamprophiidae Fitzinger, 1843

Subfamily Atractaspidinae Bourgeois, 1968

Atractaspis micropholis Günther, 1872
Material: 11 specimens.

Fig. 3. A typical view of the Sahel north of Niamey (14°05'N, 01°42'E).

Localities: Kusa (1), Maradi (1, coll. MNHN), Saboulayi (9).
Literature records: Kusa, Saboulayi, Maradi (Trape et al. 2006); Gaya (Chirio 2009).

Atractaspis watsoni Boulenger, 1908
Material: 33 specimens.
Localities: Birni N'Konni (1, coll. MNHN), Chetimari (2), Cissia (1), Karosofoua (5), Malbaza (1), Piliki (6), Saboulayi (1), Tékhé (16).
Literature records: Birni N'Konni (Pellegrin 1909, as *Atractaspis nigra* (holotype), see Trape et al. 2006); Birni N'Konni (Laurent 1950, Papenfuss 1969, as *Atractaspis microlepidota micropholis*); SW Niger (Roman 1974, as *Atractaspis microlepidota micropholis*); Karosofoua, Ader de Tahoua (Trape et al. 2006); Gourgou (Chirio 2009).

Subfamily Lamprophiinae Fitzinger, 1843

Boaedon fuliginosus (Boie, 1827)
Material: 16 specimens.
Localities: Chetimari (1), Cissia (2), Karosofoua (1), Piliki (2), Tékhé (8), Téla (2).
Literature records: SW Niger (Roman 1974: Nine specimens); Alambaré, Dagaraga, Tapoa (Chirio 2009).

Boaedon lineatus Duméril, Bibron and Duméril, 1854
Material: Three specimens.
Locality: Téla (3).
Literature records: SW Niger (Roman 1974: Four specimens); Gaya (Chirio 2009).

Gonionotophis granti (Günther, 1863)
Material: No specimen examined.
Literature records: Gourgou (Chirio 2009).

Lycophidion semicinctum (Duméril, Bibron and Duméril, 1854)
Material: One specimen.
Locality: Téla (1).
Literature records: Gayia (Chirio 2009).

Mehelya crossi (Boulenger, 1895)
Material: 11 specimens.
Locality: Téla (11).
Literature records: Gayia (Chirio 2009).
Remarks: The Téla records were plotted on the grid map in Trape and Mané (2006b). Recently, Kelly et al. (2011) dumped several file snakes into the genus *Gonionotophis*. However, on the basis of dentition and osteology there appear to be several genera involved (D.G. Broadley, in litt.) and thus we prefer to provisionally keep all the West African file snakes in the genus *Mehelya*.

Subfamily Prosymininae Kelly, Barker, Villet and Broadley, 2009

Prosymna greigerti collaris (Sternfeld, 1908)
Material: Five specimens.
Localities: Piliki (2), Téla (2), Tounga Yacouba (1).

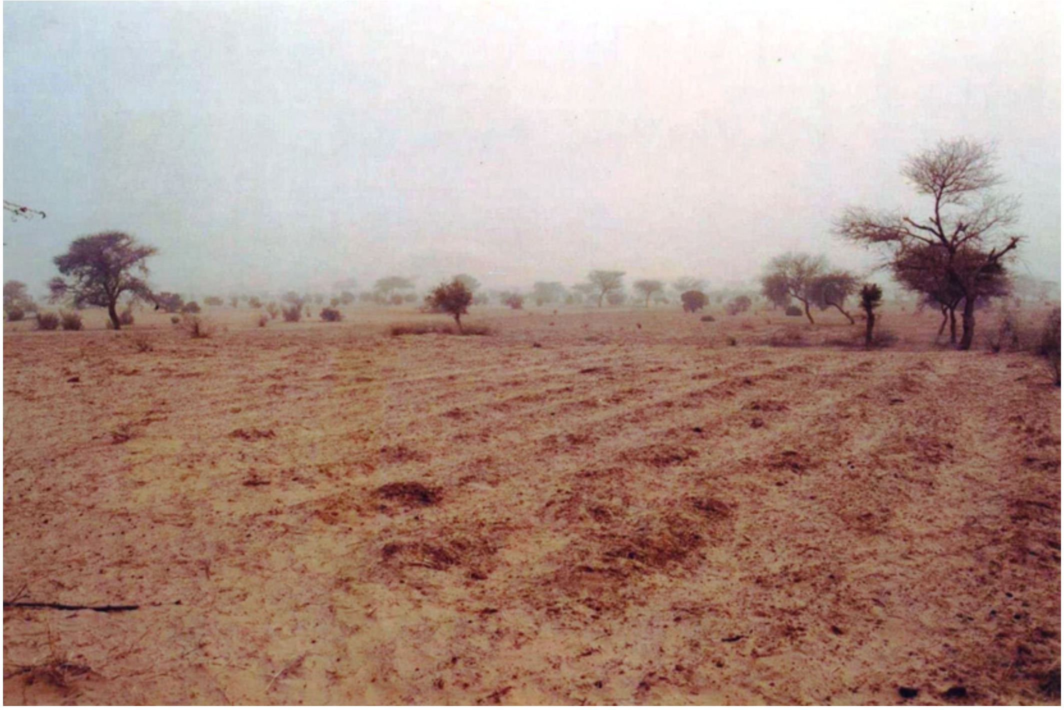

Fig. 4. Field in the Sahel near Chetimari in southwestern Niger during the dry season (13°15’N, 12°28’E).

Literature records: SW Niger (Roman 1974, as *Prosymna meleagris*: Two specimens); Alambaré, Gaya, La Tapoa (Chirio 2009); Alambaré, Kouré, La Tapoa, Malbaza (in error), Piliki, Tounga Yacouba, Téla (Chirio et al. 2011).

Subfamily Psammophiinae Dowling, 1967

Hemirhagerrhis nototaenia (Günther, 1864)
Material: One specimen.
Locality: Maradi (1, coll. MNHN).
Literature records: Maradi (Chirio and Ineich 1993, Broadley and Hughes 2000; picture of the Maradi specimen in Trape and Mané 2006b).

Psammophis aegyptius Marx, 1958
Material: Three specimens.
Localities: Korri Solomi (1), Adrar Bous (1, BEV coll.), Oued Er Roui (1, MNHN coll.).
Literature records: Agadez (Villiers 1950a, 1950b, Papenfuss 1969, as *Psammophis schokari*); cliff of Tiguidit (Dragesco-Joffé 1993, as *Psammophis schokari*), Termit (Ineich et al. 2014).
Remarks: It is unclear if *P. schokari* also occurs in Niger (see Dragesco-Joffé 1993), but all specimens we examined had the high number of ventrals of *P. aegyptius* (Trape and Mané 2006b).

Psammophis elegans (Shaw, 1802)
Psammophis elegans univittatus Perret, 1961
Material: 32 specimens, including four *univittatus*.
Localities: Baboul (3 + 1 *univittatus*), Cissia (3), Goudoumaria (6), Kellé (1), Kusa (1), Piliki (6 + 3 univittatus), Téla (8).
Literature records: SW Niger (Roman 1974); Gaya, La Tapoa (Chirio 2009).
Remarks: The satus of *univittatus* initially described from northern Cameroon is unclear. Hughes (circa 1998, unpublished document) reports specimens from Mali, Niger (La Tapoa, Garin, Maradi, Soku), Nigeria, Cameroon, and Central African Republic). This taxon is characterized by a single vertebral brown line, and lacking those usually present on the flanks in *elegans*. It appears sympatric with *elegans* in Niger and is also distributed in Burkina Faso where five specimens from Bam area (13°20’N, 01°30’W) of Roman’s collection are attributable to *univittatus* (J.-F. Trape, unpublished). Molecular studies are needed to clarify whether *univittatus* deserves taxonomic recognition or is simply intraspecific variation.

Psammophis lineatus (Duméril, Bibron, and Duméril, 1854)
Material: No specimen examined.
Literature records: SW Niger (Roman 1974, as *Dromophis lineatus*: 23 specimens); Point triple (Chirio 2009).

Psammophis praeornatus (Schlegel, 1837)
Material: Ten specimens.
Localities: Cissia (5), Késllé (1), Malbaza (1), Piliki (1), Tékhé (1), Téla (1).

Fig. 5. View of the Sudan savanna in W National Park in southwestern Niger during the dry season (12°25’N, 02°30’E).

Literature records: SW Niger (Roman 1974, as *Dromophis praeornatus*: 13 specimens); Gaya, La Tapoa (Chirio 2009).

Psammophis sibilans (Linnæus, 1758)
Material: 622 specimens.
Localities: Aholé (52), Baboul (22), Chetimari (42), Cissia (50), Goudoumaria (3), Karosofoua (64), Kéllé (1), Kusa (6), Malbaza (30), Piliki (28), Saboulayi (30), Saouna (1), Tarka Dakouara (100), Tékhé (80), Téla (20), Toundi Farkia (4), Tounga Yacouba (89).
Literature records: Azzel (Villiers 1950a, 1950b, Papenfuss 1969); SW Niger (Roman 1974: 101 specimens); Alambaré, Dagaraga, Gaya, Gourgou, Kouré, La Tapoa, Moli Haoussa, campement Nigercar (Chirio 2009).
Remarks: We attribute these specimens to *P. sibilans* (type locality: Egypt) pending a comprehensive molecular study that incorporates specimens from the full range of the *P. sibilans* complex. Such specimens are characterized by five infralabials in contact with the first pair of mentals, a divided anal, and a more-or-less striped dorsal pattern, with at least a black and white chain on the scales of the vertebral line (this chain is occasionally absent in the Sahel, but always present in Sudan and Guinea savanna areas).

Psammophis sudanensis Werner, 1919
Material: One specimen.
Locality: Tarka Dakouara (1).
Remarks: First record for Niger. This species is characterized by four infralabials in contact with the first pair of mentals and a typical head pattern, with a median yellow line starting from the back of the rostral and reaching the front of the parietals, i.e., crossing the median part of the frontal contrary to *P. sibilans*.

Rhagerhis moilensis (Reuss, 1834)
Material: 18 specimens.
Localities: Aholé (4), Baboul (1), Chetimari (1), Cissia (6), Gari’n Bakwai (3, MNHN coll.), Kellé (1), Kusa (1), Tarka Dakouara (3), Tounga Yacouba (1).
Literature records: Between Aïr and Adrar (Angel and Lhote 1938); Gari’n Bakwai (Chirio and Ineich 1991, as *Rhamphiophis maradiensis*); Termit (Dragesco-Joffé 1993); Aïr, Tamesna (Kriska 2001); Termit (Ineich et al. 2014).
Remarks: Chirio and Ineich (1991), when describing *Rhamphiophis maradiensis* on the basis of three specimens from Gari’n Bakwai near Maradi (Niger), unfortunately omitted to compare their new species with *Rhagerhis moilensis*. We have examined the types of *Rhamphiophis maradiensis* that are preserved in MNHN. We consider the two species to be synonymous as they have the same head shape, body color pattern, and meristic data. Ventral counts ranged from 166 to 172 in males and from 165 to 182 in females for our material from Niger. To facilitate further comparisons, our material is now deposited in MNHN.

Rhamphiophis oxyrhynchus (Reinhardt, 1843)
Material: 26 specimens.

Fig. 6. View of Aïr Mountains in northern Niger (19°06'N, 08°54'E).

Localities: Aholé (1), Karosofoua (1), Simiri (1), Tékhé (5), Téla (3), Tounga Yacouba (15).
Literature records: SW Niger (Roman 1974: three specimens); Dogondoutchi, Maradi, Sakabal, Gari'n Bakwai (Chirio and Ineich 1991).

Family Colubridae Oppel, 1811

Subfamily Colubrinae Oppel, 1811

Crotaphopeltis hotamboeia (Laurenti, 1768)
Material: 14 specimens.
Localities: Aholé (4), Piliki (1), Tarka Dakouara (1), Téla (5), Tounga Yacouba (5).
Literature records: Bebeye, Birni N'Konni (Pellegrin 1909, as *Leptodira hotamboeia*); Birni N'Konni (Papenfuss 1969); SW Niger (Roman 1974: 34 specimens); Alambaré, La Tapoa, Mekrou-Direct, Point triple (Chirio 2009).

Dasypeltis gansi Trape and Mané, 2006
Material: Three specimens.
Localities: Cissia (1), Piliki (1), Téla (1).
Literature records: Cissia, Piliki, Téla (Trape and Mané 2006a); Alambaré, Gaya, La Tapoa, Point triple (Chirio 2009).

Dasypeltis sahelensis Trape and Mané, 2006
Material: 70 specimens.
Localities: Aholé (2), Baboul (2), Cissia (3), Karosofoua (4), Piliki (15), Korri Solomi (1), Saboulayi (1), Tarka Dakouara (31), Tékhé (1), Téla (5), Tounga Yacouba (5).
Literature records: Aholé, Baboul, Karosofoua, Piliki, Korri Solomi, Saboulayi, Tarka Dakouara (Trape and Mané 2006a); Gaya (Chirio 2009).

Lytorhynchus diadema (Duméril, Bibron, and Duméril, 1854)
Material: No specimen examined.
Literature records: 39 miles N of Tanout (Leviton and Anderson 1970).

Meizodon coronatus (Schlegel, 1837)
Material: Two specimens.
Localities: Karosofoua (1), Téla (1).
Literature records: Gaya (Chirio 2009).
Remark: The Téla specimen, the first known from Niger, appeared in the distribution map of Trape and Mané (2006b).

Philothamnus irregularis (Leach, 1819)
Material: Nine specimens.
Locality: Téla (9).
Literature records: SW Niger (Roman 1974: seven specimens); Gaya, Gourgou (Chirio 2009).

Philothamnus semivariegatus smithi Bocage, 1882
Material: Four specimens.
Locality: Téla (4).
Remarks: Trape and Mané (2006b) attributed West African populations of *P. semivariegatus* to a distinct subspecies "*P. semivariegatus* ssp."—differing from the nominal subspecies by its dorsal coloration: almost uniformly green in West Africa, versus green with black crossbars

Fig. 7. The Niger River near Ayorou in eastern Niger (14°42’N, 00°55’E).

in southern, eastern, and central Africa. Trape and Baldé (2014) revived *smithi* Bocage, 1882, for this subspecies.
Literature records: Gourgou (Chirio 2009).
Remark: The Téla specimens, the first known from Niger, appeared in the distribution map of Trape and Mané (2006b).

Spalerosophis diadema cliffordi (Schlegel, 1837)
Material: 86 specimens.
Localities: Aholé (18), Tchintoulous (1), Baboul (8), Cissia (1), Karosofoua (3), Késllé (1), Kusa (3), Saboulayi (7), Tarka Dakouara (33), Tékhé (5), Tounga Yacouba (6).
Literature records: Vicinity of Agadez (Angel and Lhote 1938, as *Coluber diadema*); Agadez, Tabello (Villiers 1950a, 1950b, as *Coluber diadema*); Agadez, Tabello (Papenfuss 1969); SW Niger (Roman 1974: 18 specimens); Aïr (Kriska 2001).

Telescopus tripolitanus (Werner, 1909)
Material: 73 specimens.
Localities: Aholé (22), Baboul (1), Karosofoua (2), Késllé (1), Malbaza (5), Piliki (7), Saboulayi (1), Tarka Dakouara (5), Tékhé (18), Téla (2), Toundi Farkia (2), Tounga Yacouba (7).
Literature records: Tahoua (Angel and Lhote 1938, Papenfuss 1969, as *Taborphis variegatus*); Agadez, Tabello (Villiers 1950a, 1950b, Papenfuss 1969, as *Taborphis obtusus*); Niamey (Villiers 1951, Papenfuss 1969, as *Taborphis variegatus*); Agadez (Papenfuss 1969); SW Niger (Roman 1974, as *Telescopus obtusus*: 19 specimens); SW Niger (Roman 1977: six mapped localities); Aïr (Kriska 2001, as *Telescopus obtusus*); Agadez, Tabelot, Maradi, Piliki, Téla, Aholé, Tounga Yacouba, Malbaza, Tékhé, Karosofoua, Saboulayi, Baboul, Késllé, Tondi Farkia (Crochet et al. 2008); Gaya, Kouré (Chirio 2009).

Subfamily Grayiinae Kelly, Barker and Villet, 2003

Grayia smithi (Leach, 1818)
Material: One specimen.
Localities: Gaya (1).
Literature records: SW Niger (Roman 1974: 24 specimens).
Remarks: No specimen was collected by Chirio (2009) in W National Park, but Roman’s collection comprised 24 specimens from southwestern Niger, most of them probably collected along the Niger River or its perennial and semi-perennial tributaries.

Family Natricidae Boie, 1827

Natriciteres olivacea (Peters, 1854)
Material: No specimen examined.
Literature records: southwestern Niger, without locality (Roman 1984).
Remarks: Roman (1984) also reported *Natriciteres fuliginoides* (Günther, 1858) from Niger, but it was probably a misidentified *N. olivacea* since he confused the two species in Burkina Faso (see Trape 2005). The rare, confirmed records of *N. fuliginoides* in West Africa are all located close to rainforest areas (Trape, in preparation).

Family Elapidae Boie, 1827

Elapsoidea semiannulata moebiusi (Werner, 1897)
Material: One specimen.

Locality: Téla (1).
Literature records: SW Niger (Roman 1974: one specimen); Gayia, La Tapoa (Chirio 2009).

Naja haje (Linnæus, 1758)
Material: Eight specimens.
Localities: Cissia (3), Tahoua (2), Tékhé (3).
Literature records: Agadez (Villiers 1950a, Papenfuss 1969); SW Niger (Roman 1974: one specimen probably attributable to *Naja senegalensis*); Aïr, Tamesna (Kriska 2001); Cissia, Tékhé, Tahoua, Zinder (Trape et al. 2009); Gayia (Chirio 2009).

Naja melanoleuca Hallowell, 1857
Material: No specimen examined.
Literature records: SW Niger (Roman 1974: four specimens).

Naja nigricollis Reinhardt, 1843
Material: 66 specimens.
Localities: Goudoumaria (1), Kusa (4), Piliki (14), Téla (39), Toundi Farkia (8).
Literature records: SW Niger (Roman 1974: 19 specimens); Dagaraga, Gayia, La Tapoa, Moli Haoussa, Point triple (Chirio 2009).

Naja nubiae Wüster & Broadley, 2003
Material: Two specimens.
Locality: Irabellaben (2, coll. IFAN).
Literature records: Irabellaben (Villiers 1950a, 1950b, Papenfuss 1969, as *Naja nigricollis*, Wüster and Broadley 2003, Trape and Mané 2006b); Aïr (Kriska 2001, as *Naja nigricollis*).

Naja senegalensis Trape, Chirio, and Wüster, 2009
Material: Three specimens.
Localities: Karosofoua (2), Téla (1).
Literature records: Karosofoua, Téla (Trape et al. 2009); campement Nigercar (Chirio 2009).

Family Viperidae Oppel, 1811

Bitis arietans (Merrem, 1820)
Material: Four specimens.
Localities: Cissia (2), Kusa (2).
Literature records: Kimbouloua (Pellegrin 1909); Agadez, Azzel, Dabaga, Tassesset (Villiers 1950a, as Bitis lachesis); Tassenet (Villiers 1950b, as *Bitis lachesis*); Tassesset (Papenfuss 1969), SW Niger (Roman 1974: four specimens); Aïr (Kriska 2001); Gaya, Mekrou-Direct (Chirio 2009).

Causus maculatus (Hallowell, 1842)
Material: One specimen.
Locality: Piliki (1).
Literature records: SW Niger (Roman 1974: six specimens); Dagaraga, Gaya, La Tapoa, Moli Haoussa (Chirio 2009).

Cerastes cerastes (Linnæus, 1758)
Material: Three specimens.
Locality: Aborah (2), Iférouane (1).
Literature records: Dungas, Nguigmi (Pellegrin 1909, as *Cerastes cornutus*); Agadez, Kaouar, Chirfa, Djado (Angel and Lhote 1938); Agadez, Dabaga, Oued In Kakane near In Gall, Kori Tessouba (Villiers 1950a, Papenfuss 1969); Agadez (Villiers 1950b); 120 km SE of Arlit (Joger 1981); Aïr, Tamesna (Kriska 2001); Termit (Ineich et al. 2014). See also Trape and Mané (2006b) and Sindaco et al. (2013).
Remark: The Iférouane specimen had no "horns."

Cerastes vipera (Linnæus, 1758)
Material: One specimen.
Locality: Six km N of Taghmert (1).
Literature records: Erg of Bilma, erg of Ténéré, cliff of Tiguidit, Termit (Dragesco-Joffé 1993); Aïr (Kriska 2001); Termit (Ineich et al. 2014). See also Trape and Mané (2006b) and Sindaco et al. (2013).

Echis leucogaster Roman, 1972
Material: 446 specimens.
Localities: Aholé (29), Baboul (22), Chetimari (10), Karosofoua (6), Kéllé (1), Malbaza (14), Piliki (62), Saboulayi (13), Tarka Dakouara (110), Tékhé (64), Téla (19), Toundi Farkia (4), Tounga Yacouba (92).
Literature records: Tabello (Villiers 1950a, 1950b, as *Echis carinatus*); route de Dosso, Oualam, Boubon, Niamey, five km W of Niamey, 10 km N of Niamey, 15 km NW of Niamey, 27 km S of Niamey, Tondikouaré, Koutéré, Hamdallaye, Kouré, Sarandobéni, Tagabati, Saguia, Tiourridi, Sargadji, Doulgou, Malgorou, Kolo, Sokorbé (Roman 1972); SW Niger (Roman 1974: 82 specimens); Boubon, Lido (Roman 1976); Agadez, Tabello, Boubon, Doulgou, Kouré, Malgorou, Niamey, Sargadji, Tin Akof, Tiourdi (Hughes 1976); 10 km N of Dabnou, Dogon-Doutchi (Joger 1981); Gaya, Kouré (Chirio 2009); Termit (Ineich et al. 2014). See also Trape and Mané (2006b) and Sindaco et al. (2013, as *Echis pyramidum*).

Echis ocellatus Stemmler, 1970
Material: 25 specimens.
Localities: Piliki (9), Téla (17).
Literature records: Bebeye (Pellegrin 1909, as *Echis carinatus*); Boubon, Gaya, Tiouridi (Roman 1972); SW Niger (Roman 1974: seven specimens); Boubon, Lido (Roman 1976); Bebeye, Boubon, Gaya, Tiouridi (Hughes 1976); Alambaré, Gaya (Chirio 2009).

Table 2. Checklist of snake species of Niger.

Species	First documented report	Ecological zone in Niger
Afrotyphlops lineolatus	Trape and Mané 2015	Sudan savanna
Afrotyphlops punctatus	Pellegrin 1909	Sudan savanna
Atractaspis micropholis	Trape et al. 2006	Sudan savanna / Sahel
Atractaspis watsoni	Trape et al. 2006	Sudan savanna / Sahel
Bitis arietans	Pellegrin 1909	Sudan savanna / Sahel / Aïr
Boaedon fuliginosus	Roman 1974	Sudan savanna / Sahel
Boaedon lineatus	Roman 1974	Sudan savanna
Causus maculatus	Roman 1974	Sudan savanna / Sahel
Cerastes cerastes	Pellegrin 1909	Sahara / Aïr
Cerastes vipera	Dragesco-Joffé 1993	Sahara / Aïr
Crotaphopeltis hotamboeia	Pellegrin 1909	Sudan savanna / Sahel
Dasypeltis gansi	Trape and Mané 2006a	Sudan savanna
Dasypeltis sahelensis	Trape and Mané 2006a	Sudan savanna / Sahel / Aïr
Echis leucogaster	Roman 1972	Sudan savanna / Sahel / Sahara / Aïr
Echis ocellatus	Pellegrin 1909	Sudan savanna
Elapsoidea semiannulata	Roman 1974	Sudan savanna
Eryx colubrinus	Villiers 1950	Sahel / Aïr
Eryx muelleri	Roman 1974	Soudan savanna / Sahel / Aïr
Gonionotophis granti	Chirio 2009	Sudan savanna
Grayia smithi	Roman 1974	Sudan savanna
Hemirhagerrhis nototaenia	Chirio and Ineich 1993	Sudan savanna
Lycophidion semicinctum	Chirio 2009	Sudan savanna
Lytorhynchus diadema	Leviton and Anderson 1970	Sahara
Mehelya crossi	Trape and Mané 2006b	Sudan savanna
Meizodon coronatus	Trape and Mané 2006b	Sudan savanna
Myriopholis algeriensis	Trape 2002	Sahara / Aïr
Myriopholis adleri	Chirio 2009	Sudan savanna
Myriopholis boueti	Chirio 2009	Sudan savanna / Sahel
Myriopholis cairi	Hahn and Roux-Estève 1979	Sahara / Aïr
Naja haje	Villiers 1950a	Sahel / Aïr
Naja melanoleuca	Roman 1974	Sudan savanna
Naja nigricollis	Roman 1974	Sudan savanna / Sahel
Naja nubiae	Wüster and Broadley 2003	Aïr
Naja senegalensis	Trape et al. 2009	Sudan savanna
Natriciteres olivacea	Roman 1984	Sudan savanna
Philothamnus irregularis	Roman 1974	Sudan savanna
Philothamnus semivariegatus	Trape and Mané 2006b	Sudan savanna
Prosymna greigerti	Roman 1974	Sudan savanna
Psammophis aegyptius	Trape and Mane 2006b	Sahara / Aïr
Psammophis elegans	Roman 1974	Sudan savanna / Sahel
Psammophis lineatus	Roman 1974	Sudan savanna
Psammophis praeornatus	Roman 1974	Sudan savanna / Sahel
Psammophis sibilans	Villiers 1950a	Sudan savanna / Sahel / Aïr
Psammophis sudanensis	Trape and Mané 2015	Sudan savanna
Python regius	Roman 1974	Sudan savanna
Python sebae	Roman 1974	Sudan savanna, Sahel
Rhagerhis moilensis	Angel and Lhote 1938	Sahara / Sahel / Aïr
Rhamphiophis oxyrhynchus	Roman 1974	Sudan savanna
Spalerosophis diadema	Villiers 1950a	Sudan savanna / Sahel / Aïr
Telescopus tripolitanus	Roman 1977	Sudan savanna / Sahel / Aïr
Tricheilostoma bicolor	Hahn and Roux-Estève 1979	Sudan savanna

Discussion

Our collection of Nigerian snakes comprises 1,714 specimens belonging to 38 species. With additional museum material that we examined and accepting reliable literature reports the snake fauna of Niger comprises 51 species (Table 2), i.e., 19 species more than the previous checklist established by Roman (1984). The first checklist for Niger (Papenfuss 1969) comprised only 15 species. It is unclear whether *P. schokari* also occurs in Niger, or if only *P. aegyptius* is present. Data points probably in error for *Naja katiensis* and *Atractaspis dahomeyensis* in maps by Chippaux (2006) are not retained here, but these two species may still occur in southwestern Niger since close records exist for Burkina Faso (*Naja katiensis*) and Benin (*Atractaspis dahomeyensis*). As previously mentioned in Trape and Mane (2006b), *Rhamphiophis maradiensis* is a junior synonym of *Rhagheris moilensis*. The occurrence of *Psammophis sudanensis* in Niger, a rare species in West Africa (Trape and Mané 2006b, Trape and Baldé 2014), has not previously been noted.

North of 15°N, in the most arid part of the country (rains < 250 mm), the snake fauna comprises at least 17 species; with six typical Saharan species: *Myriopholis algeriensis*, *Myriopholis cairi*, *Lytorhynchus diadema*, *Psammophis aegyptius*, *Cerastes cerastes*, and *Cerastes vipera*; eight Sahelo-Saharan species: *Eryx colubrinus*, *Eryx muelleri*, *Dasypeltis sahelensis*, *Spalerosophis diadema cliffordi*, *Telescopus tripolitanus*, *Rhagerhis moilensis*, *Naja nubiae*, and *Echis leucogaster*; one Sahelo-Sudanian species: *Naja haje*; and two species widely distributed in West African savannas including the northern Sahel: *Psammophis sibilans* and *Bitis arietans*. In these areas, only nine specimens were collected during our study. Even if the duration of sampling was much lower than south of 15°N for most sites, this may reflect a lower density of snakes. However, it may also reflect more limited participation in the study by nomads contrary to settled agricultural workers. Some specific beliefs may also have played a role, e.g., for some northern populations killing a *Psammophis* is taboo. Our interviews of local populations suggested that at least *Cerastes cerastes* and *Psammophis aegyptius* are common in many areas of northern Niger.

Maximum diversity was observed in the southern part of the country, between 12°00'N and 14°00'N, where the snake fauna comprises at least 43 species, including either: Sahelo-Saharan: *Eryx colubrinus*, *Eryx muelleri*, *Dasypeltis sahelensis*, *Spalerosophis diadema cliffordi*, *Telescopus tripolitanus*, *Rhagerhis moilensis*, and *Echis leucogaster*; Sudanian and Sahelian: *Myriopholis adleri*, *Myriopholis boueti*, *Meizodon coronatus*, *Prosymna greigerti collaris*, *Psammophis praeornatus*, *Psammophis sudanensis*, *Rhamphiophis oxyrhynchus*, *Elapsoidea semiamnnulata moebiusi*, *Naja haje*, and *Naja senegalensis*; or species widely distributed in West African savannas: *Afrotyphlops lineolatus*, *Afrotyphlops punctatus*, *Tricheilostoma bicolor*, *Python regius*, *Python sebae*, *Boaedon fuliginosus*, *Boaedon lineatus*, *Crotaphopeltis hotamboeia*, *Dasypeltis gansi*, *Gonionotophis granti*, *Grayia smithi*, *Hemirhagerrhis nototaenia*, *Lycophidion semicinctum*, *Mehelya crossi*, *Natriciteres olivacea*, *Philothamnus irregularis*, *Philothamnus semivariegatus smithi*, *Psammophis elegans*, *Psammophis lineatus*, *Psammophis sibilans*, *Naja nigricollis*, *Naja melanoleuca*, *Bitis arietans*, *Causus maculatus*, and *Echis ocellatus*.

Despite the relatively high number of species recorded south of 14°N, many species were rarely collected and diversity was low in most areas. Two species represented together almost two-third of the 1,705 snakes that were collected south of 15°N: *Psammophis sibilans* (621 specimens, 36.4 %), and *Echis leucogaster* (446 specimens, 26.2 %). Five additional species represented at least 2% of the snakes that were collected: *Eryx muelleri* (104 specimens, 6.1 %), *Spalerosophis diadema cliffordi* (86 specimens, 5.0 %), *Telescopus tripolitanus* (72 specimens, 4.2%), *Dasypeltis sahelensis* (69 specimens, 4.0 %), and *Naja nigricollis* (66 specimens, 3.9 %). Two species were close to 2%: *Atractaspis watsoni* (33 specimens, 1.9%), and *Psammophis elegans* (32 specimens, 1.9%). In fact, except south of 13°N, snake diversity was low in almost all sampling sites, e.g., only 10 different species in Tarka Dakouara (14°12'N, 08°49'E) despite 315 specimens collected, but 21 species for 170 specimens collected in Téla (12°08'N, 03°28'E), our southernmost study area.

Regarding snakebite management, our data highlight the danger represented by *Echis leucogaster* and *Naja nigricollis*. These two highly venomous species are both abundant and widely distributed in the most populated areas of Niger, particularly *Echis leucogaster* which probably occurs throughout the whole country. Among the other dangerous species, *Cerastes cerastes*, *Cerastes vipera*, *Naja nubiae*, and *Naja haje* are essentially distributed in the most arid regions of the country, and *Echis ocellatus*, *Naja senegalensis*, *Naja melanoleuca*, *Atractaspis watsoni*, and *Atractaspis micropholis* in Sudan savanna areas.

The extensive collections made by Roman (1974, 1984) and Chirio (2009) in southwestern Niger, where rains, permanent surface waters, and biodiversity are the highest, combined with Aïr mountains records by Villiers (1950) have provided a relatively comprehensive overview of the snake fauna of Niger. However, among the species of our collection, five were new for Niger when collected (i.e., *Afrotyphlops lineolatus*, *Myriopholis boueti*, *Meizodon coronatus*, *Philothamnus semivariegatus smithi*, and *Psammophis sudanensis*), three belonged to new species that we described elsewhere (*Dasypeltis gansi*, *D. sahelensis* (Trape and Mané 2006a) and *Naja senegalensis* (Trape et al. 2009), and two belonged to species that we have revived from the synonymy of

Atractaspis microlepidota (i.e., *A. watsoni* and *A. micropholis*).

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Youssouph Mané is a Senegalese biologist and herpetologist born in 1961 in the Casamance Province of southern Senegal. His master dissertation at the University Cheikh Anta Diop of Dakar in 1992 investigated the snake fauna in the vicinity of Dielmo, a well preserved savanna area near the Sine-Saloum National Park in central Senegal. In 1997 Youssouph's doctorate thesis was on the ecology of bees in Casamance. After his thesis, he entered the Institut de Recherche pour le Développement at Dakar, participated in many herpetological field surveys in West Africa, and served as the curator of the IRD reptile collection. Youssouph has authored or co-authored 22 peer-reviewed papers and the book entitled "Guide des serpents d'Afrique occidentale. Savane et desert" (2006, with J-FT). Over his career to date, he has authored or co-authored the description of seven snake and two amphisbaenian species.

APPENDIX: list of specimens examined (IRD collection, Dakar).

***Afrotyphlops lineolatus*. Téla**: TR.4448.

***Atractaspis micropholis*. Kusa**: 5.N; **Saboulayi**: 34.N, 358.N, 375.N, 376.N, 377.N, 378.N, 379.N, 918.N, 930 N.

***Atractaspis watsoni*. Chetimari**: 845.N, 861.N; **Cissia**: 1069.N; **Karosofoua**: 297.N, 298.N, 299.N, 903.N; **Malbaza**: 464.N; **Piliki**: 301.N, 302.N, 352.N, 1407.N, 1444.N, 1450.N; **Saboulayi**: 357.N; **Tékhé**: 686.N, 757.N, 758.N, 762.N, 769.N, 775.N, 781.N, 787.N, 808.N, 815.N, 1274.N, 1282.N, 1290.N, 1303.N, 1336.N, 1353.N.

***Bitis arietans*. Cissia**: 1052.N, 1087.N; **Kusa**: 216.N, 227.N.

***Boaedon fuliginosus*. Chetimari**: 863.N; **Cissia**: 1065.N, 1066.N; **Karosofoua**: 827.N; **Piliki**: 1412.N, 1457.N; **Tékhé**: 1275.N, 1335.N, 1346.N, 1347.N, 1362.N, 1379.N, 1386.N, 698.N; **Téla**: 272.N, 720.N.

***Boaedon lineatus*. Téla**: 264.N, 711.N, 1564.N.

***Causus maculatus*. Piliki**: 349.N.

***Cerastes cerastes*. Aborah**: 356.N, TR.1513.

***Cerastes vipera*. Taghmert**: TR.1548.

***Crotaphopeltis hotamboeia*. Aholé**: 90.N, 91.N, 93.N, 580.N; **Piliki**: 345.N; **Tarka Dakouara**:125.N; **Téla**: 277.N, 286.N, 713.N, 714.N, 717.N; **Tounga Yacouba**: 33.N, 564.N, 1660.N.

***Dasypeltis gansi*. Cissia**: 252.N; Piliki: 331.N; Téla: 273.N.

***Dasypeltis sahelensis*. Aholé**: 1022.N, 587.N; **Baboul**: 394.N, 59.N; **Cissia**: 1051.N, 1071.N, 1083.N; **Karosofoua**: 820.N, 831.N, 899.N, 908.N; **Korri Solomi**: TR.1545; **Piliki**: 1405.N, 1418.N, 1434.N, 1437.N, 1445.N, 1452.N, 1466.N, 1467.N, 1468.N, 1470.N, 1473.N, 1491.N, 305.N, 309.N, 315.N; **Saboulayi**: 189.N; **Tarka Dakouara**: 10.N, 106.N, 115.N, 120.N, 130.N, 133.N, 163.N, 399.N, 400.N, 401.N, 402.N, 423.N, 431.N, 432.N, 433.N, 435.N, 444.N, 1106.N, 1112.N, 1149.N, 1195.N, 1206.N, 1240.N, 1262.N, 1269.N, 1273.N, 1703.N, 1704.N, 1705.N, 1706.N, 1707.N; Tékhé: 1363.N; Téla: 1543.N, 1552.N, 1561.N, 1569.N, 1579.N; **Tounga Yacouba**: 1662.N, 1686.N.

***Echis leucogaster*. Aholé**: 95.N, 570.N, 572.N, 574.N, 593.N, 603.N, 609.N, 611.N, 615.N, 617.N, 623.N, 627.N, 628.N, 972.N, 974.N, 980.N, 990.N, 992.N, 1002.N, 1004.N, 1005.N, 1016.N, 1023.N, 1024.N, 1025.N, 1026.N, 1027.N, 1028.N, 1034.N; **Baboul**: 45.N, 46.N, 52.N, 54.N, 62.N, 63.N, 65.N, 68.N, 69.N, 75.N, 76.N, 80.N, 81.N, 82.N, 83.N, 86.N, 386.N, 390.N, 391.N, 393.N, 395.N, 396.N; **Chetimari**: 233.N, 234.N, 235.N, 236.N, 240.N, 242.N, 243.N, 244.N, 656.N, 847.N; **Karosofoua**: 210.N, 212.N, 214.N, 215.N, 872.N, 878.N; **Kéllé**: 934.N; **Malbaza**: 469.N, 471.N, 472.N, 937.N, 939.N, 944.N, 945.N, 946.N, 949.N, 952.N, 956.N, 958.N, 964.N, 966.N; **Piliki**: 310.N, 311.N, 312.N, 313.N, 314.N, 317.N, 320.N, 321.N, 329.N, 333.N, 334.N, 335.N, 336.N, 337.N, 339.N, 341.N, 342.N, 343.N, 346.N, 700.N, 701.N, 702.N, 703.N, 705.N, 706.N, 707.N, 709.N, 825.N, 1398.N, 1399.N, 1400.N, 1402.N, 1411.N, 1415.N, 1416.N, 1417.N, 1420.N, 1421.N, 1423.N, 1425.N, 1428.N, 1429.N, 1433.N, 1435.N, 1441.N, 1442.N, 1448.N, 1449.N, 1453.N, 1455.N, 1458.N, 1459.N, 1464.N, 1465.N, 1469.N, 1474.N, 1476.N, 1478.N, 1482.N, 1485.N, 1487.N, 1489.N; **Saboulayi**: 179.N, 363.N, 364.N, 366.N, 916.N, 917.N, 922.N, 923.N, 924.N, 925.N, 927.N, 931.N, 932.N; **Tarka Dakouara**: 105.N, 109.N, 114.N, 119.N, 122.N, 132.N, 141.N, 149.N, 152.N, 153.N, 156.N, 161.N, 162.N, 403.N, 404.N, 405.N, 406.N, 415.N, 416.N, 417.N, 418.N, 419.N, 421.N, 424.N, 426.N, 428.N, 436.N, 437.N, 440.N, 441.N, 445.N, 446.N, 451.N, 452.N, 1107.N, 1108.N, 1110.N, 1111.N, 1113.N, 1114.N, 1115.N, 1116.N, 1118.N, 1121.N, 1123.N, 1125.N, 1127.N, 1133.N, 1136.N, 1137.N, 1141.N, 1142.N, 1143.N, 1146.N, 1147.N, 1148.N, 1150.N, 1152.N, 1153.N, 1154.N, 1155.N, 1156.N, 1157.N, 1164.N, 1165.N, 1167.N, 1171.N, 1173.N, 1178.N, 1180.N, 1181.N, 1182.N, 1183.N, 1185.N, 1187.N, 1199.N, 1201.N, 1203.N, 1204.N, 1207.N, 1209.N, 1210.N, 1211.N, 1212.N, 1215.N, 1217.N, 1220.N, 1223.N, 1226.N, 1228.N, 1229.N, 1233.N, 1234.N, 1236.N, 1237.N, 1239.N, 1244.N, 1248.N, 1251.N, 1252.N, 1253.N, 1254.N, 1258.N, 1259.N, 1261.N, 1263.N, 1265.N, 1266.N, 1267.N, 1268.N; **Tékhé**: 685.N, 759.N, 763.N, 764.N, 765.N, 766.N, 767.N, 772.N, 774.N, 782.N, 784.N, 785.N, 790.N, 792.N, 796.N, 799.N, 801.N, 802.N, 803.N, 813.N 1276.N, 1279.N, 1280.N, 1283.N, 1284.N, 1294.N, 1295.N, 1296.N, 1297.N, 1298.N, 1299.N, 1306.N, 1316.N, 1317.N, 1324.N, 1325.N, 1332.N, 1337.N, 1338.N, 1341.N, 1344.N, 1345.N, 1349.N, 1350.N, 1356.N, 1358.N, 1366.N, 1369.N, 1370.N, 1372.N, 1374.N, 1375.N, 1376.N, 1380.N, 1382.N, 1383.N, 1388.N, 1389.N, 1390.N, 1391.N, 1392.N, 1394.N, 1396.N, 1397.N; Téla: 4.N, 276.N, 287.N, 288.N, 292.N, 727.N, 734.N, 735.N, 740.N 1526.N, 1538.N, 1547.N, 1548.N, 1551.N, 1554.N, 1555.N, 1562.N, 1563.N, 1568.N; **Toundi Farkia**: 1044.N, 1045.N, 1047.N, 1049.N; **Tounga Yacouba**: 42.N, 43.N, 44.N, 473.N, 486.N, 487.N, 496.N, 497.N, 502.N, 503.N, 504.N, 505.N, 507.N, 508.N, 509.N, 510.N, 513.N, 520.N, 522.N, 524.N, 525.N, 526.N, 530.N, 531.N, 537.N, 539.N, 541.N, 546.N, 548.N, 549.N, 551.N, 552.N, 554.N, 555.N, 556.N, 557.N, 558.N, 559.N, 560.N, 561.N, 562.N, 563.N, 565.N, 566.N, 1583.N, 1586.N, 1587.N, 1589.N, 1590.N, 1592.N, 1594.N, 1595.N, 1599.N, 1600.N, 1602.N, 1606.N, 1608.N, 1614.N, 1616.N, 1618.N, 1620.N, 1624.N, 1625.N, 1632.N, 1634.N, 1635.N, 1637.N, 1641.N, 1648.N, 1650.N, 1653.N, 1654.N, 1661.N, 1665.N, 1666.N, 1667.N, 1670.N, 1671.N, 1673.N, 1675.N, 1676.N, 1677.N, 1679.N, 1680.N, 1683.N, 1685.N, 1690.N, 1691.N, 1692.N, 1694.N, 1699.N.

***Echis ocellatus*. Piliki**: 323.N, 324.N, 1451.N, 1475.N, 1479.N, 1480.N, 1481.N, 1483.N, 1484.N; **Téla**: 716.N, 729.N, 733.N, 744.N, 750.N 1502.N, 1516.N, 1525.N, 1529.N, 1539.N, 1541.N, 1542.N, 1553.N, 1558.N, 1577.N, 1580.N.

***Elapsoidea semiannulata moebiusi*. Téla**: 747.N.

***Eryx colubrinus*. Cissia**: 1089.N; **Tarka Dakouara**: 1190.N, 1224.N.

***Eryx muelleri*. Aborah**: 355.N; **Aholé**: 87.N, 94.N, 577.N, 578.N, 588.N, 590.N, 595.N, 610.N, 612.N, 616.N, 977.N, 998.N, 999.N, 1000.N, 1700.N, 1701.N, 1702.N; Baboul: 77.N, 392.N; **Chetimari**: 230.N, 231.N, 834.N, 854.N; **Cissia**: 1081.N, 1086.N; **Karosofoua**: 873.N, 890.N; **Késlé**; 642.N; **Kusa**: 226.N; **Maradi**: TR.4450; **Saboulayi**: 174.N, 362.N, 368.N, 369.N, 381.N, 914.N, 919.N, 920.N; **Tarka Dakouara**: 128.N, 129.N, 147.N, 407.N, 411.N, 414.N, 425.N, 427.N, 438.N, 448.N, 449.N, 453.N, 1124.N, 1126.N, 1132.N, 1144.N, 1168.N, 1179.N, 1191.N, 1200.N, 1205.N, 1208.N, 1214.N, 1216.N, 1218.N, 1242.N, 1250.N, 1255.N, 1257.N, 1272.N; **Tékhé**: 770.N, 783.N, 798.N, 1285.N, 1288.N, 1320.N, 1354.N, 1364.N, 1393.N; **Téla**: 294.N, 295.N, 715.N, 723.N, 724.N, 725.N, 726.N, 732.N, 736.N, 1505.N, 1506.N, 1513.N, 1528.N, 1550.N, 1557.N, 1560.N, 1575.N; **Toundi Farkia**: 372.N, 1050.N; **Tounga Yacouba**: 495.N, 499.N, 533.N, 1597.N, 1631.N, 1663.N, 1698.N.

***Lycophidion semicinctum*. Téla**: 1532.N.

***Mehelya crossi*. Téla**: 271.N, 282.N, 285.N, 293.N, 710.N, 730.N, 1495.N, 1500.N, 1507.N, 1511.N, 1535.N.

***Meizodon coronatus*. Karosofoua**: 882.N; **Téla**: 722.N.

***Myriopholis boueti*. Késlé**: 936.N.

***Naja haje*. Cissia**; 246.N, 248.N, 672.N; **Tahoua**: TR.4442, 832.N; **Tékhé**: 60.N, 690.N, 1395.N.

***Naja nigricollis*. Goudoumaria**: 661.N; **Kusa**: 218.N, 220.N, 221.N, 223.N; **Piliki**: 303.N, 306.N, 307.N, 326.N, 338.N, 340.N, 348.N, 351.N, 1408.N, 1409.N, 1431.N, 1439.N, 1446.N, 1447.N; **Téla**: 265.N, 266.N, 267.N, 268.N, 269.N, 270.N, 278.N, 289.N, 291.N, 737.N, 738.N, 739.N, 741.N, 742.N, 743.N, 745.N, 746.N, 751.N, 752.N, 753.N, 754.N 1496.N, 1497.N, 1498.N, 1499.N, 1501.N, 1503.N, 1508.N, 1519.N, 1520.N, 1521.N, 1524.N, 1534.N, 1549.N, 1571.N, 1574.N, 1576.N, 1578.N, 1581.N; **Toundi Farkia**: 1035.N, 1036.N1037.N, 1038.N, 1040.N, 1041.N, 1042.N, 1046.N.

***Naja senegalensis*. Karosofoua**: 201.N, 910.N; **Téla**: 1504.N.

***Philothamnus irregularis*. Téla**: 274.N, 275.N, 279.N, 280.N, 283.N, 290.N, 296.N, 712.N 1523.N.

***Philothamnus semivariegatus smithi*. Téla**: 755.N, 1527.N, 1537.N.

***Prosymna greigerti collaris*. Piliki**: 347.N, 1472.N; **Téla**: 1531.N, 1545.N; **Tounga Yacouba**: 536.N.

***Psammophis aegyptius*. Korri Solomi**: TR.4449.

***Psammophis elegans*. Baboul**: 73.N, 78.N, 85.N; **Cissia**: 262.N, 263.N, 674.N; **Goudoumaria**: 662.N, 663.N, 664.N, 665.N, 666.N, 669.N; **Késlé**: 935.N; **Kusa**: 648.N, **Piliki**: 308.N, 316.N, 318.N, 1422.N, 1443.N, 1454.N; **Téla**: 719.N, 1514.N, 1518.N, 1522.N, 1546.N, 1556.N, 1570.N, 1573.N.

***Psammophis elegans univittatus*. Baboul**: 388.N; **Piliki**: 1432.N, 1436.N, 1471.N.

***Psammophis praeornatus*. Cissia**: 253.N, 257.N, 260.N, 261.N, 675.N; **Késlé**: 641.N, **Malbaza**: 467.N; **Piliki**: 1490.N; **Tékhé**: 1378.N; **Téla**: 1572.N.

***Psammophis sibilans*. Aholé**. 88.N, 89.N, 92.N, 567.N, 568.N, 569.N, 571.N, 573.N, 576.N, 579.N, 581.N, 582.N, 583.N, 584.N, 586.N, 594.N, 596.N, 598.N, 599.N, 601.N, 602.N, 608.N, 613.N, 618.N, 619.N, 620.N, 622.N, 624.N, 630.N, 631.N, 632.N, 970.N, 973.N, 976.N, 981.N, 983.N, 984.N, 985.N, 986.N, 987.N, 988.N, 996.N, 997.N, 1001.N, 1008.N, 1014.N, 1017.N, 1018.N, 1020.N, 1029.N, 1031.N, 1032.N; Baboul: 47.N, 48.N, 49.N, 53.N, 56.N, 57.N, 58.N, 60.N, 61.N, 64.N, 66.N, 67.N, 70.N, 71.N, 72.N, 74.N, 79.N, 84.N, 385.N, 387.N, 397.N, 398.N; **Chetimari**: 229.N, 232.N, 237.N, 238.N, 239.N, 241.N, 649.N, 650.N, 651.N, 652.N, 653.N, 654.N, 655.N, 657.N, 658.N, 659.N, 660.N, 833.N, 835.N, 836.N, 837.N, 838.N, 839.N, 840.N, 841.N, 842.N, 843.N, 844.N, 846.N, 848.N, 849.N, 850.N, 851.N, 852.N, 853.N, 855.N, 856.N, 858.N, 859.N, 860.N, 862.N, 864.N; Cissia: 245.N, 247.N, 249.N, 250.N, 251.N, 254.N, 255.N, 256.N, 258.N, 259.N, 671.N, 673.N, 1053.N, 1054.N, 1055.N, 1056.N, 1057.N, 1058.N, 1059.N, 1060.N, 1061.N, 1062.N, 1063.N, 1064.N, 1067.N, 1068.N, 1072.N, 1073.N, 1074.N, 1075.N, 1076.N, 1077.N, 1078.N, 1082.N, 1084.N, 1085.N, 1088.N, 1090.N, 1091.N, 1092.N, 1095.N, 1096.N, 1097.N, 1098.N, 1099.N, 1100.N, 1101.N, 1102.N, 1103.N, 1104.N,; **Goudoumaria**: 667.N, 668.N, 670.N; **Karosofoua**: 190.N, 191.N, 192.N, 193.N, 194.N, 195.N, 196.N, 197.N, 198.N, 199.N, 200.N, 202.N, 203.N, 204.N, 205.N, 206.N, 207.N, 208.N, 211.N, 213.N, 817.N, 818.N, 819.N, 821.N, 822.N, 823.N, 824.N, 826.N, 828.N, 829.N, 830.N, 65.N, 866.N, 867.N, 868.N, 869.N, 870.N, 874.N, 875.N, 876.N, 877.N, 879.N, 880.N, 881.N, 883.N, 884.N, 885.N, 886.N, 888.N, 891.N, 892.N, 894.N, 895.N, 896.N, 897.N, 898.N, 901.N, 904.N, 905.N, 906.N, 907.N, 909.N, 911.N, 912.N; **Kéllé**: 640.N; **Kusa**: 217.N, 222.N, 224.N, 225.N, 644.N, 646.N; **Malbaza**: 454.N, 455.N, 456.N, 457.N, 458.N, 460.N, 461.N, 462.N, 463.N, 465.N, 466.N, 470.N, 938.N, 940.N, 941.N, 942.N, 943.N, 947.N, 948.N, 950.N, 954.N, 955.N, 957.N, 960.N, 961.N, 962.N, 963.N, 967.N, 968.N, 969.N; **Piliki**: 300.N, 304.N, 319.N, 322.N, 325.N, 327.N, 328.N, 330.N, 353.N, 704.N,1403.N, 1404.N, 1406.N, 1410.N, 1413.N, 1414.N, 1419.N, 1424.N, 1426.N, 1427.N, 1430.N, 1438.N, 1440.N, 1462.N, 1463.N, 1477.N, 1486.N, 1488.N; **Saboulayi**: 165.N, 166.N, 167.N, 169.N, 170.N, 171.N, 172.N, 173.N, 175.N, 176.N, 177.N, 178.N, 180.N, 182.N, 184.N, 185.N, 186.N, 187.N, 188.N, 359.N, 360.N, 365.N, 380.N, 384.N, 913.N, 915.N, 921.N, 928.N, 929.N, 933.N; **Saouna**: 354.N; **Tarka Dakouara**: 96.N, 97.N, 98.N, 99.N, 100.N, 101.N, 102.N, 103.N, 104.N, 107.N, 108.N, 110.N, 111.N, 112.N, 113.N, 116.N, 117.N, 118.N, 121.N, 124.N, 126.N, 127.N, 131.N, 134.N, 135.N, 136.N, 137.N, 138.N, 139.N, 140.N, 142.N, 143.N, 144.N, 145.N, 146.N, 148.N, 150.N, 151.N, 154.N, 155.N, 157.N, 158.N, 160.N, 164.N, 408.N, 410.N, 412.N, 434.N, 439.N, 442.N, 443.N, 447.N, 450.N, 1105.N, 1109.N, 1120.N, 1128.N, 1129.N, 1130.N, 1131.N, 1135.N, 1138.N, 1145.N, 1151.N, 1159.N, 1160.N, 1161.N, 1162.N, 1166.N, 1169.N, 1170.N, 1172.N, 1175.N, 1176.N, 1177.N, 1189.N, 1193.N, 1194.N, 1196.N, 1197.N, 1198.N, 1202.N, 1213.N, 1222.N, 1225.N, 1227.N, 123.N, 1230.N, 1232.N, 1235.N, 1238.N, 1241.N, 1243.N, 1245.N, 1247.N, 1249.N, 1256.N, 1260.N, 1270.N, 1271.N; **Tékhé**: 676.N, 677.N, 678.N, 679.N, 680.N, 681.N, 682.N, 683.N, 684.N, 687.N, 688.N, 689.N, 691.N, 692.N, 693.N, 694.N, 695.N, 696.N, 697.N, 699.N, 756.N, 761.N, 768.N, 771.N, 773.N, 776.N, 777.N, 780.N, 793.N, 797.N, 800.N, 809.N, 814.N, 816.N 1277.N, 1281.N, 1286.N, 1287.N, 1291.N, 1300.N, 1301.N, 1302.N, 1304.N, 1305.N, 1307.N, 1308.N, 1309.N, 1310.N, 1312.N, 1313.N, 1314.N, 1319.N, 1322.N, 1323.N, 1327.N, 1328.N, 1329.N, 1330.N, 1331.N, 1333.N, 1334.N, 1339.N, 1340.N, 1342.N, 1348.N, 1351.N, 1352.N, 1355.N, 1357.N, 1360.N, 1361.N, 1365.N, 1367.N, 1368.N, 1371.N, 1373.N, 1381.N, 1384.N, 1387.N; **Téla**: 718.N, 721.N, 728.N, 748.N, 1492.N, 1493.N, 1494.N, 1509.N, 1510.N, 1512.N, 1515.N, 1517.N, 1530.N, 1533.N, 1540.N, 1544.N, 1559.N, 1565.N, 1566.N, 1567.N; **Toundi Farkia**: 370.N, 373.N, 1039.N, 1043.N; **Tounga Yacouba**: 36.N, 37.N, 38.N, 39.N, 41.N, 374.N, 474.N, 475.N, 476.N, 477.N, 478.N, 479.N, 480.N, 481.N, 482.N, 485.N, 489.N, 490.N, 492.N, 500.N, 501.N, 506.N, 511.N, 512.N, 514.N, 515.N, 516.N, 517.N, 518.N, 519.N, 523.N, 527.N, 528.N, 529.N, 532.N, 534.N, 535.N, 542.N, 543.N, 544.N, 550.N, 553.N, 642.N, 1585.N, 1591.N, 1593.N, 1596.N, 1598.N, 1603.N, 1604.N, 1605.N, 1607.N, 1609.N, 1610.N, 1612.N, 1613.N, 1615.N, 1617.N, 1619.N, 1621.N, 1623.N, 1626.N, 1628.N, 1629.N, 1630.N, 1633.N, 1638.N, 1639.N, 1643.N, 1644.N, 1645.N, 1646.N, 1649.N, 1651.N, 1652.N, 1655.N, 1656.N, 1657.N, 1658.N, 1659.N, 1668.N, 1672.N, 1674.N, 1681.N, 1684.N, 1687.N, 1689.N, 1693.N, 1695.N.

***Psammophis sudanensis*. Tarka Dakouara**: 17.N.

***Rhagerhis moilensis*. Aholé**: 636.N, 1012.N, 1019.N, 1033.N; **Baboul**: 389.N; **Chetimari**: 857.N; **Cissia**: 1.N, 2.N, 3.N, 1080.N, 1093.N, 1094.N; **Kéllé**: 639.N; **Kusa**: 645.N, **Tarka Dakouara**: 409.N, 1158.N, 1174.N; **Tounga Yacouba**: 1588.N.

***Rhamphiophis oxyrhynchus*. Aholé**: 1013.N; **Karosofoua**: 209.N; **Simiri**: TR.270: **Tékhé**: 811.N 1315.N, 1318.N, 1321.N, 1343.N; **Téla**: 281.N, 284.N, 731.N; **Tounga Yacouba**: 40.N, 484.N, 488.N, 491.N, 498.N, 1582.N, 1584.N, 1601.N, 1622.N, 1627.N, 1640.N, 1647.N, 1664.N, 1669.N, 1678.N.

***Spalerosophis diadema cliffordi*. Aholé**: 6.N, 7.N, 575.N, 591.N, 597.N, 600.N, 605.N, 606.N, 607.N, 621.N, 625.N, 635.N, 637.N, 979.N, 989.N, 994.N, 995.N, 1011.N; **Baboul**: 26.N, 27.N, 28.N, 29.N, 30.N, 50.N, 51.N, 55.N; **Cissia**: 1070.N; **Karosofoua**: 871.N, 889.N, 900.N; **Kéllé**: 638.N; **Kusa**: 219.N, 228.N, 647.N; **Saboulayi**: 168.N, 181.N, 183.N, 361.N, 382.N, 383.N, 926.N; **Tarka Dakouara**: 8.N, 9.N, 11.N, 12.N, 13.N, 14.N, 15.N, 16.N, 18.N, 19.N, 20.N, 21.N, 22.N, 23.N, 24.N, 25.N, 159.N, 413.N, 420.N, 422.N, 429.N, 430.N, 1119.N, 1134.N, 1139.N, 1140.N, 1163.N, 1184.N, 1186.N, 1188.N, 1192.N, 1219.N, 1221.N; **Tchintoulous**: TR.4453; **Tékhé**: 786.N, 789.N, 795.N, 807.N, 1359.N; **Tounga Yacouba**: 483.N, 494.N, 545.N, 547.N, 1688.N, 1697.N.

***Telescopus tripolitanus*. Aholé**: 1003.N, 1006.N, 1007.N, 1009.N, 1010.N, 1015.N, 1021.N, 1030.N, 585.N, 589.N, 592.N, 604.N, 614.N, 626.N, 629.N, 633.N, 634.N, 971.N, 975.N, 978.N, 982.N, 991.N, 993.N; **Baboul**: 31.N; **Gayia**: TR.2351; **Karosofoua**: 35.N, 902.N; **Kéllé**: 643.N; **Malbaza**: 459.N, 468.N, 951.N, 953.N, 965.N; **Piliki**: 332.N, 350.N, 708.N, 1401.N, 1456.N, 1460.N, 1461.N; **Saboulayi**: 367.N; **Tarka Dakouara**: 1117.N, 1122.N, 1231.N, 1246.N, 1264.N, **Tékhé**: 778.N, 779.N, 788.N, 791.N, 794.N, 804.N, 805.N, 806.N, 810.N, 812.N, 1278.N, 1289.N, 1292.N, 1293.N, 1311.N, 1326.N, 1377.N, 1385.N; **Téla**: 749.N; **Toundi Farkia**: 371.N, 1048.N; **Tounga Yacouba**: 32.N, 493.N, 521.N, 538.N, 540.N 1636.N, 1682.N.

***Tricheilostoma bicolor*. Niamey (airport)**: TR.4451.

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The tadpoles of eight West and Central African *Leptopelis* species (Amphibia: Anura: Arthroleptidae)

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***Abstract.*—The tadpoles of more than half of the African tree frog species, genus *Leptopelis*, are unknown. We provide morphological descriptions of tadpoles of eight species from Central and West Africa. We present the first descriptions for the tadpoles of *Leptopelis boulengeri* and *L. millsoni*. In addition the tadpoles of *L. aubryioides*, *L. calcaratus*, *L. modestus*, *L. rufus*, *L. spiritusnoctis*, and *L. viridis* are herein reinvestigated and their descriptions complemented, e.g., with additional tooth row formulae or new measurements based on larger series of available tadpoles.**

Key words. Anuran larvae, external morphology, diversity, mitochondrial DNA, DNA barcoding, lentic waters, lotic waters

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Introduction

Given that sequences of correctly determined species are available, the application of DNA-barcoding has facilitated species-assignment of tadpoles. Thus, tadpole morphology is more and more frequently included in species descriptions (e.g., Blackburn 2008a; Das and Haas 2010; Rödel et al. 2012; Lima et al. 2014; Portillo and Greenbaum 2014b; Vassilieva et al. 2014) and numerous publications even focus exclusively on tadpole descriptions. Insights from larval morphology have been important for recognizing, or hinting at, cryptic species (e.g., Randrianiaina et al. 2012; Pfalzgraff et al. 2015), have contributed to systematics (Haas 2003; Müller et al. 2005) or indicated the presence of range-restricted taxa and the appropriateness of a habitat for elusive, i.e., semi-fossorial species (e.g., *Cardioglossa*: Hirschfeld et al. 2012; *Leptodactylodon*: Cruz et al. 2013; Mapouyat et al. 2014).

Moreover, detection of tadpoles can be informative for habitat preferences of species and even more importantly, provides direct evidence of successful reproduction of recorded species even in the absence of adult vouchers (e.g., Hirschfeld et al. 2012). Thus, determination of tadpoles is beneficial for conservation assessments and long-term management strategies. However, due to the bi-phasic life-cycle of anurans, tadpoles and adults are exposed to different threats in their habitat or during migration, and conservation efforts should be considered accordingly (e.g., Becker et al. 2007; Wells 2007).

While four herpetological journals provided insight on tadpoles of more than 80 species in the last two years (2014–2015 those dealing with or describing African tadpoles were relatively few; e.g., *Herpetologica*: 0/4; *Zootaxa*: 11/70; *Salamandra*: 4/9; *The Herpetological Journal*: 1/1; accessed 30 September 2015) our knowledge is still far from complete (Channing et al. 2012).

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This likewise applies to the genus *Leptopelis* Günther, 1859 which is endemic to sub-Saharan Africa and currently comprises 53 species (Frost 2015). New species are continuously being added to this list (e.g., Lötters et al. 2005; Köhler et al. 2006; Rödel 2007; Portillo and Greenbaum 2014a,b; Gvoždík et al. 2014) and further species complexes are already known (Portillo et al. 2015; Barej and Rödel, unpubl. data). These medium to large-sized frogs inhabit a wide variety of vegetation types, from tropical and subtropical forests to open grasslands (Rödel 2000; Channing 2001; Minter et al. 2004; Channing and Howell 2006; Amiet 2012). The common name "treefrogs" is not applicable to the entire genus, as some species are adapted to burrowing and a terrestrial lifestyle (e.g., Poynton and Broadley 1987; Rödel 2000 and references therein).

Generally, knowledge of the biology and natural history of *Leptopelis* is rather incomplete although advertisement calls of more than half of the species are known (e.g., Amiet and Schiøtz 1974; Schiøtz 1999; Grafe et al. 2000; Rödel 2000; Köhler et al. 2006; Greenbaum et al. 2012; Portillo and Greenbaum 2014b) and anecdotal observations on predation events by spiders (Barej et al. 2009), death-feigning reflexes (de Witte 1941; Perret 1966; Kofron and Schmitt 1992; Schmitz et al. 1999; Rödel et al. 2000), cocoon building (Grafe 2000), and malacophagy (Perret 1966; Amiet 2012) have been documented. Furthermore, *Leptopelis* are featured as magical creatures used in traditional wars and modern sports (Pauwels et al. 2003).

Details on the reproduction of *Leptopelis* species are generally scarce. As far as known egg deposition occurs outside water in or on top of moist soil, the development is slow, and hatching starts when the eggs in their nest are inundated during the beginning of the rainy season. Hatched tadpoles then move towards the water where they develop and metamorphosis takes place (Schiøtz 1963, 1975; Oldham 1977; Wager 1986; Rödel 2007). It is presumed that tadpoles are exotrophic (developmental energy derived from ingested food as a free-living tadpole) and live in the thin muddy layer in the benthos of lentic waters (Altig and McDiarmid 1999a; Channing et al. 2012). However, Amiet (2012) also reports on reproduction in lotic waters. Direct development has been speculated for *L. brevirostris* (Schiøtz 1999).

A simplified morphological description of the described *Leptopelis* tadpoles comprises: an elongated and eel-like shape, in particular a very long tail with low fins, and a predominantly dark coloration of body and tail (Perret 1966; Channing et al. 2012).

Recently, Channing et al. (2012) compiled available data on African tadpoles including 22 *Leptopelis* tadpoles, nine being described for the first time. Since then, two more *Leptopelis* tadpoles have been described (Portillo and Greenbaum 2014b; Penske et al. 2015). However, several tadpole descriptions in Channing et al. (2012) were often based on single specimens and require a through comparison with larger series of specimens as it is well known that tadpole morphology can be very variable due to genetic and environmental factors as well as during development (e.g., Duellman and Trueb 1994; Laurila and Kujasalo 1999; Relyea 2001; Kraft et al. 2006; Wells 2007).

We herein use larger voucher series to re-describe the tadpoles of four Central African (*L. aubryioides n* = 20, *L. calcaratus n* = 16, *L. modestus n* = 3, *L. rufus n* = 18), and two West African *Leptopelis* species (*L. spiritusnoctis n* = 20, *L. viridis n* = 2). In addition, we provide the first descriptions of two other Central African species: *L. boulengeri* (*n* = 16) and *L. millsoni* (*n* = 1).

Materials and Methods

Sampling. Field surveys were carried out in Liberia and Guinea by M.F. Barej and J. Penner (June 2011); in Cameroon on Mt. Manengouba, Littoral and South-West Province by M. Hirschfeld and F. Grözinger (November 2010 to October 2011), in the Abo Forest, North West Province by T.M. Doherty-Bone (August 2012), in the Ebo forest, Littoral Province by M.-O. Rödel, M. Dahmen, F. Grözinger, and M. Hirschfeld (September 2010 to October 2011), on Mt. Nlonako, Littoral Province by M.F. Barej, H.C. Liedtke, N.L. Gonwouo, and M. Hirschfeld (October 2011), and around Kribi, South Province and Etome, South-West Province by M.F. Barej, H.C. Liedtke, and N.L. Gonwouo (October to November 2011). Detailed locality data of investigated tadpoles are provided in Appendix Table A1. Tadpoles were caught either by hand or with dip nets. They were anaesthetized in a tricaine methane sulphonate (MS222, Thomson & Joseph Ltd), chlorobutanol, or benzocaine solution. For molecular analyses a piece of tail muscle was removed and preserved in ethanol (99%) from at least one individual for each set of morphologically distinct tadpoles for every locality. All tadpoles were then fixed in formalin (8%) and later transferred into ethanol (75%).

Determination. Species identity of the tadpoles was verified by DNA-barcoding, comparing 16S ribosomal RNA sequences from tadpoles to those of adult vouchers and/or available GenBank sequences. For comparison of the partial 16S rRNA a total of 37 sequences (474–554 bp) has been generated and deposited in GenBank (KT967076-KT967112; Appendix Table A1). For details of extraction, primers, and PCR protocols, and sequencing see Barej et al. (2014). Sequences were aligned using ClustalX (Thompson et al. 1997; default parameters) and manually checked using the original chromatograph data in the program BioEdit (Hall 1999). Uncorrected p-distances for the partial 16S rRNA gene between included *Leptopelis* species were calculated with PAUP* 4.0b10 (Swofford 2002).

All tadpoles could be unambiguously assigned to a valid *Leptopelis* species. Intraspecific genetic divergences ranged from 0.0–0.8% (Table 1), except in *L. rufus* where a 1.5% difference indicated two distinct lineages herein referred to as *L. rufus*_1 and *L. rufus*_2. Voucher IDs and GenBank numbers of adults and tadpoles are provided in Appendix Table A1. For further synonyms and chresonyms used in older publications on *Leptopelis* tadpoles see Frost (2015).

Character assessment. Measurements were taken with a dissecting microscope or digital calliper by one person (TP). Summaries for several individuals are given as mean values. The following measurements were taken (for details see Appendix Figure A1): EL (entire length), BL (body length), TL (tail length), BH (body height at the point of the spiracle insertion), BW (maximum body width, in dorsal view), AW (width of the tail muscle [axis], at the tail base), AH (maximum tail muscle (axis) height), VF (maximum height of ventral fin), DF (maximum height of dorsal fin), TTH (total tail height), ED (horizontal eye diameter), IOD (interocular distance), IND (internostril distance), SND (snout-nostril distance), SED (snout-eye distance), ODW (oral disc width), SL (spiracle length), and SSD (snout-spiracle distance). Distances including eyes and/or nostrils were taken from respective centers (e.g., SED: centre of the eye to snout tip). Measurements of all examined specimens are provided in Appendix Table A2. The following ratios were calculated: BL/TL, BH/BL, BW/BL, SND/SED, ED/BL, IOD/IND, TL/EL, DF/VF, AH/DF, TTH/BH, AW/BW, AH/BH, SL/BL, ODW/BW, and SSD/BL. Ratios of all examined specimens are provided in Appendix Table A3; mean ratios for each species are provided in Appendix Table A4. The relation of body length to total length was mostly not measurable in genotyped vouchers, as tail tips have been removed for tissue sampling. Specimens were staged according to Gosner (1960) and labial tooth row formulae are based on Rödel (2000).

Illustrations of genotyped representatives in the best condition of each taxon were prepared with the help of a camera lucida on a dissecting microscope. Missing parts resulting from tissue sampling are drawn as outlines based on non-genotyped vouchers. Schematic sketches were made of the oral discs of genotyped tadpoles.

Comparative morphometrics. Morphological features like fin height, body shape or tail length point to adaptations to particular habitat types (e.g., Altig and McDiarmid 1999b). To assess morphological adaptations in *Leptopelis* tadpoles to particular habitats all 18 measurements were $\log_{10}$ transformed and subjected to a rigid rotation via a Principal Component Analysis. Only individuals with full sets of measurements were included, and so *L. viridis* and *L. rufus*_1 were not represented in the final dataset and *L. millsoni* and *L. modestus* were only represented by one and two individuals, respectively. The prcomp function was used in R v3.2 (R core team 2013), data was scaled and centered and the ordispider function in the vegan package (Oksanen et al. 2013) was used to add a cluster dendrogram to species groupings.

Table 1. Intraspecific genetic distances (uncorrected p) in the mitochondrial 16S ribosomal RNA between *Leptopelis* species, compared to adult individuals (for GenBank# see Appendix Table A1); SD = standard deviation, *n* = number of pairwise comparisons, alignment: 558 bp. Note that the maximum value in *L. rufus* results from two lineages in this species; if independently analysed both lineages show p-distance values within the range of remaining taxa: *rufus*_1 (*n* = 1): 0.43%; *rufus*_2 (*n* = 10): 0%.

Species	min	max	mean	SD	*n*
aubryioides	0	0.75	0.37	0.24	36
boulengeri	0	0.19	0.08	0.1	10
calcaratus	0.18	0.6	0.39	0.21	3
millsoni	—	—	0	—	1
modestus	0	0.2	0.13	0.11	3
rufus	0	1.5	0.66	0.68	21
spiritusnoctis	0	0.83	0.21	0.27	28
viridis	0	0.21	0.11	0.12	6
interspecies	1.92	13.03	8.8	2.2	712

Results and Discussion

The tadpoles of eight *Leptopelis* species are described herein: *Leptopelis aubryioides* (Andersson, 1907), *L. boulengeri* (Werner, 1898), *L. calcaratus* (Boulenger, 1906), *L. millsoni* (Boulenger, 1895), *L. modestus* Werner, 1898, *L. rufus* Reichenow, 1874 from Central Africa, and *L. spiritusnoctis* Rödel, 2007, and *L. viridis* (Günther, 1869) from West Africa. The morphology of the analyzed tadpoles is generally consistent with the simplified tadpole diagnosis of the genus *Leptopelis* provided by Altig and McDiarmid (1999a): oval/depressed body shape; generally uniformly dark colored; dorsal eyes; small nares, nearer snout than eye; labial tooth row formula 3–5/3, usually 2-n rows on upper labium broken medially and one row on lower labium may be broken; typical, anteroventral oral apparatus; wide dorsal gap on marginal distribution; uniserial dorsally and biserial ventrally; submarginal papillae absent; wide upper jaw sheath with medial indentation; wide, V-shaped lower jaw sheath; dextral vent tube; sinistral spiracle; low dorsal fin which originates near dorsal tail body junction ends in a pointed tip.

Leptopelis aubryioides (Andersson, 1907)

The description of *L. aubryioides* tadpoles is based on twenty tadpoles: ZMB 79604 (two tadpoles, at Gosner stages 30 and 36, near Etome, Cameroon, 4.8317°N; 9.9253°E, 476 m a.s.l., 23 October 2011, the tadpoles were found in a small muddy puddle along a stream bank; stream characterised by lots of little rapids), ZMB 79605 (one tadpole at Gosner stage 25) and ZMB 79606

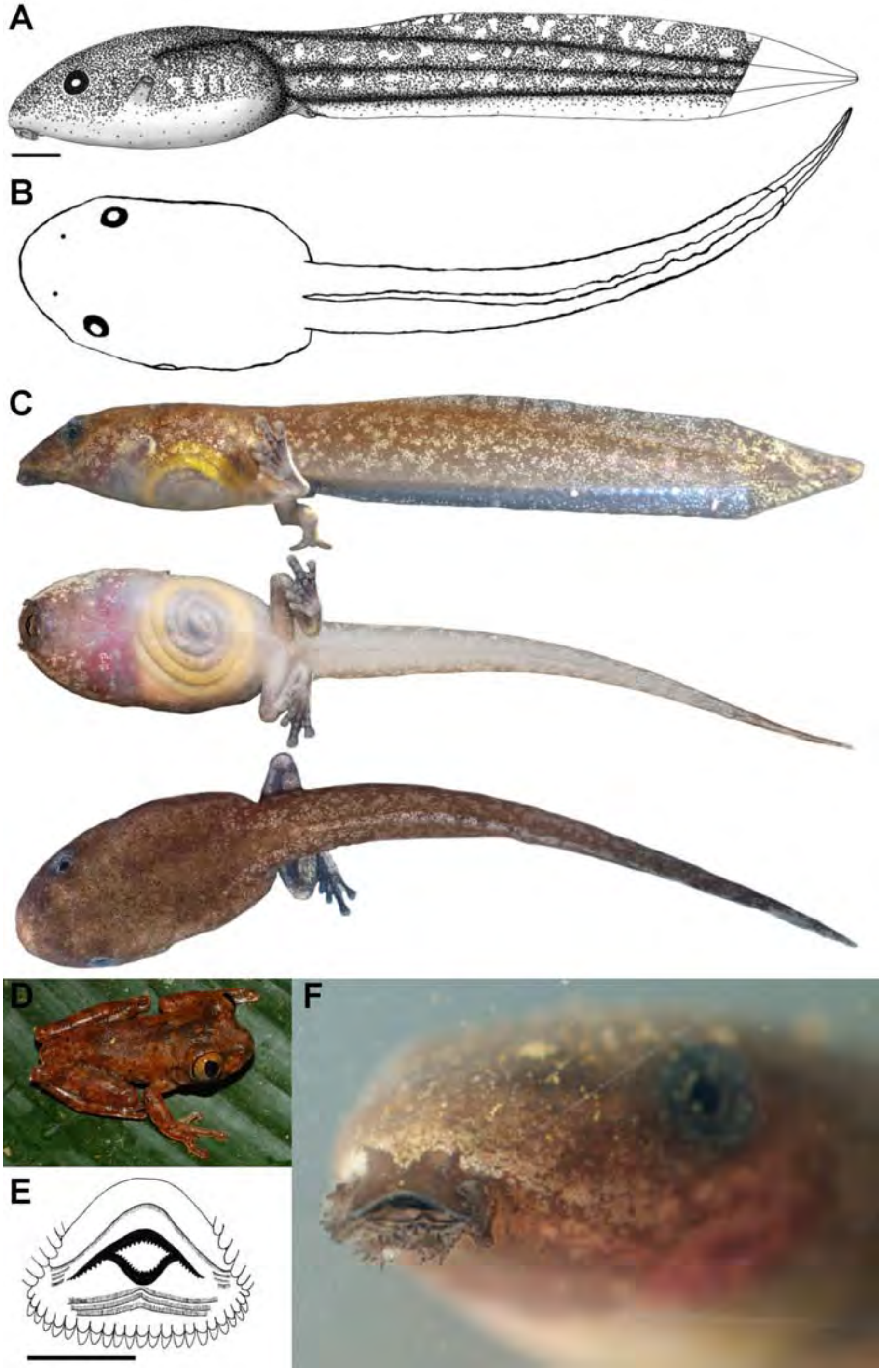

Fig. 1. Lateral (A) and dorsal (B) view of *Leptopelis aubryioides* (ZMB 79605) at Gosner stage 25; coloration of tadpole (ZMB 79604) in life (C); adult *L. aubryioides* (ZMB 83029) (D); oral disc opened in life (F); sketch of the oral disc (E); scale bars: 1 mm.

(nine tadpoles at Gosner stages 25 to 40, near Ekomtolo, at the foot of Mt. Nlonako, Cameroon, 4.8329°N; 9.9259°E, 477 m a.s.l., 24 October 2011, the tadpoles were found in a slow flowing forest stream), ZMB 79607 (three tadpoles, at Gosner stages 36 and 39, Njuma, Ebo Forest, Cameroon, 4.3483°N; 10.2329°E, 238 m a.s.l., 08 August 2011), ZMB 79608 (one tadpole, at Gosner stage 40, Njuma, Ebo Forest, Cameroon, 4.3483°N; 10.2329°E, 238 m a.s.l., 19 August 2011), ZMB 79609 (one tadpole, at Gosner stage 31, Njuma, Ebo Forest, Cameroon, 4.3394°N; 10.2458°E, 320 m a.s.l., 20 August 2011), ZMB 79610 (one tadpole, at Gosner stage 36, Njuma, Ebo Forest, Cameroon, 4.3483°N; 10.2329°E, 238 m a.s.l., 07 October 2011), ZMB 79611 (one tadpole, at Gosner stage 41, Njuma, Ebo Forest, Cameroon, 4.3483°N; 10.2329°E, 238 m a.s.l., 08 October 2011) and ZMB 79612 (one tadpole, at Gosner stage 34, Camp Njuma, Ebo Forest, Cameroon, 4.3480°N; 10.2323°E,

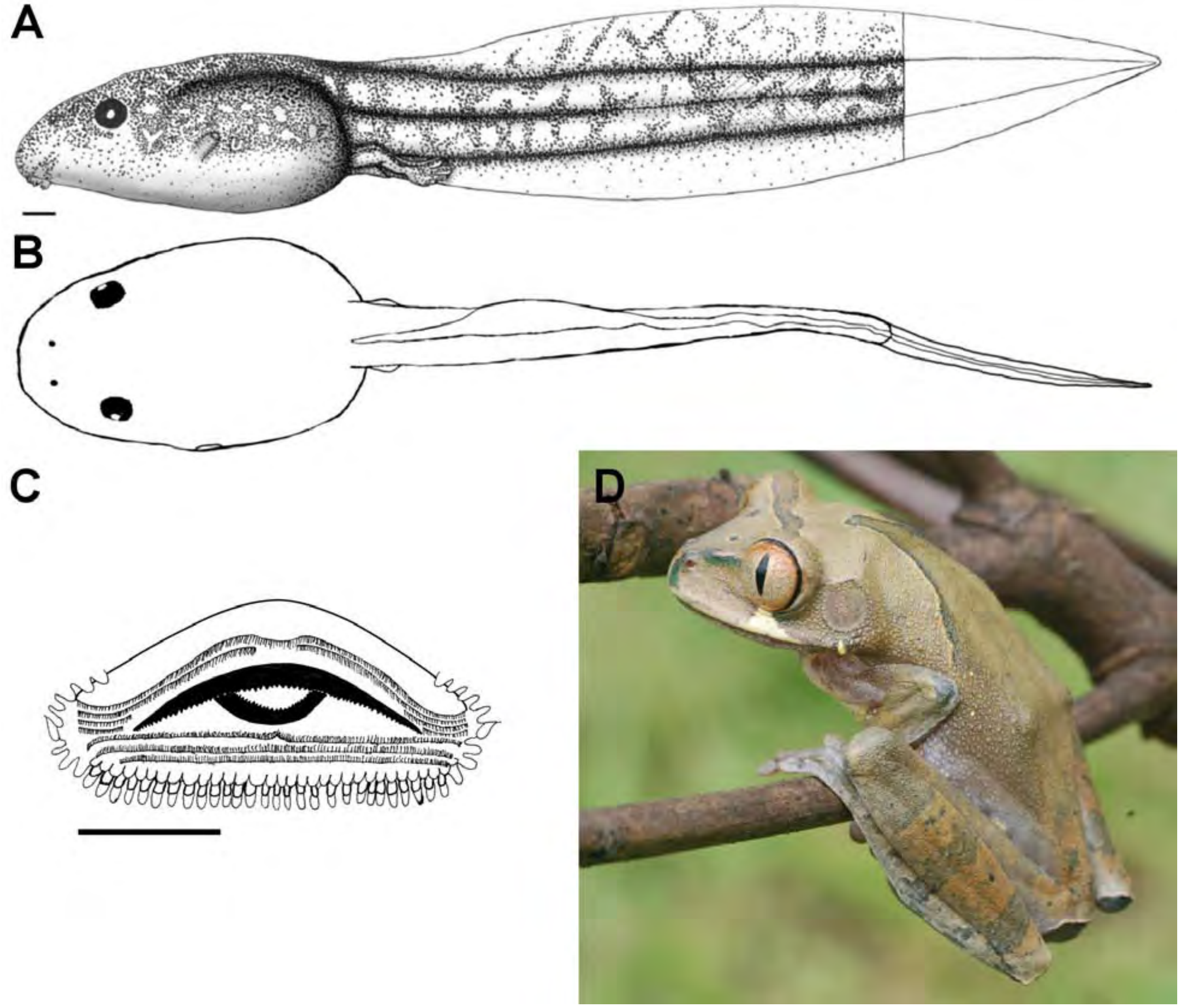

Fig. 2. Lateral (A) and dorsal (B) view of *Leptopelis boulengeri* (ZMB 79616) at Gosner stage 38; sketch of the oral disc (C); adult L. boulengeri (ZFMK 87857) (D); scale bars: 1 mm.

315 m a.s.l., 23 September 2011, the locality was situated in primary rainforest). Proportions including total or tail length were only available for non-genotyped individuals.

Description. Body oval with nearly rounded snout in dorsal view (Fig. 1B); ovoid to slightly compressed in lateral view (Fig. 1A); tail length-body length ratio 2.38 (TL/BL); body height 0.44 of body length (BH/BL); body width 0.58 of body length (BW/BL); maximum body width slightly behind the spiracle's posterior end; nostrils situated dorsally, slightly closer to snout tip than eyes (SND/SED = 0.42), distance snout-nostrils 0.20 of body length (SND/BL); eyes positioned laterally; eye diameter 0.11 of body length (ED/BL); interocular distance exceeds internostril distance by a factor of 1.93 (IOD/IND); tail length 0.70 of entire length (TL/EL), with moderately pronounced fins and narrow fin tip; dorsal fin originates at dorsal tail-body junction, barely rising at the first quarter of the tail; dorsal fin slightly curved with maximum height at three-quarters of the tail length; ventral fin originates on the ventral terminus of the body; ventral fin narrower than tail axis with maximum height at three-quarters of the tail length; maximum fin height in dorsal fin higher (DF/VF = 1.29); fin tip pointed; maximum tail height including fins lower than body height (TTH/BH = 0.90); tail axis width (in dorsal view) 0.42 of body width (AW/BW); maximum height of tail axis (at base) 0.56 of body height (AH/BH); tail axis height (at base) distinctly higher than maximum height of dorsal fin (AH/DF = 2.07); dextral vent tube, positioned basicaudally; spiracle sinistral, visible in dorsal view, originating anterior to mid-body (SSD/BL = 0.45); spiracle tube length 0.14 of body length (SL/BL); mouth opens anteroventrally; oral disc width less than quarter of body width (ODW/BW = 0.24); one row of papillae (with rounded tips) laterally at anterior lip with huge rostral gap, these connected to papillae in labial angles and posterior lip; second row of papillae caudal at posterior lip (Fig. 1F); labial tooth row formula 1/3+3//3 (Fig. 1E) or 1/2+2//3;

jaw sheaths black, of equal width and serrated; upper jaw widely V-shaped; lower jaw U-shaped.

Coloration in preservation. Dorsolateral part of the body, tail axis and dorsal fin mostly speckled dark brown on light brown ground at the body and yellowish ground at the tail; areas without brown spots shine through as yellow blots; ventral part of the body light brown with some dark brown spots at the anterior third of the body; vent tube translucent; spiracle translucent or pigmented; ventral fin predominantly translucent with few brown spots composed of dense melanophores towards tail tip.

Coloration in life (Fig. 1C). Pale brown with shiny golden speckles at dorsolateral part of the body, tail axis and dorsal fin; ventral fin translucent with few speckles; ventral part of the body translucent.

Remarks. *Leptopelis aubryioides* occurs from eastern Nigeria through Cameroon to Gabon and the Republic of the Congo (e.g., Schiøtz 1967, 1999, 2007; Frétey and Blanc 2001; Blanc and Frétey 2004; Amiet 2012). Amiet and Schiøtz (1974) and Amiet (2006, 2012) reported on habitat use and the call activity of the species. The tadpole of *L. aubryioides* has already been described by Channing et al. (2012) based on a single specimen, which belongs to a larger series of tadpoles examined herein (MH198 = ZMB 79612). Shape of body and tail, as well as tail shape and overall pigmentation are congruent with the available description. In addition to the labial

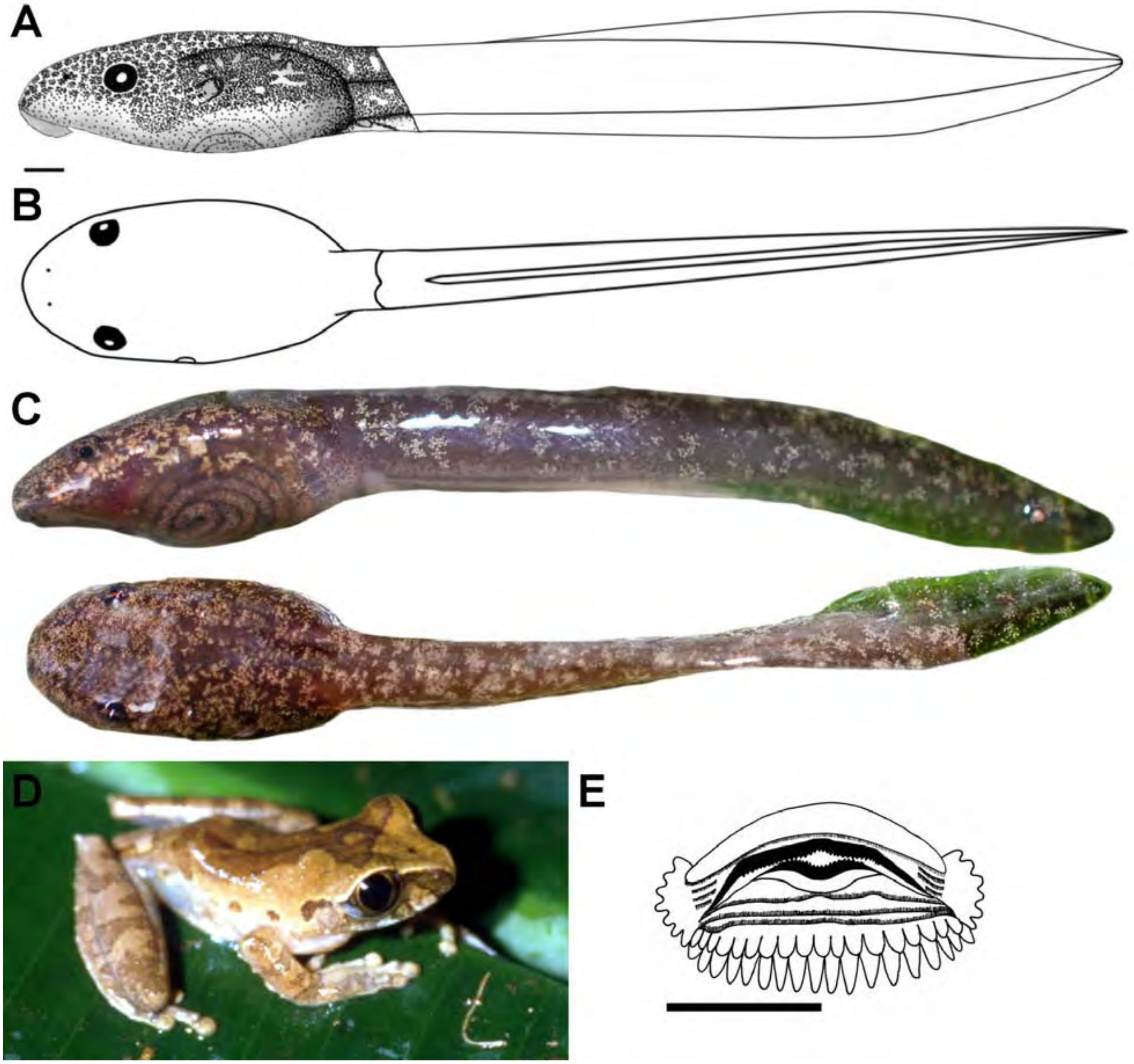

Fig. 3. Lateral (A) and dorsal (B) view of *Leptopelis calcaratus* (ZMB 79618) at Gosner stage 28; coloration in life of tadpole (ZMB 79618) in lateral (top) and dorsal (below) view (C); adult *L. calcaratus* (ZFMK 75590) (D); sketch of the oral disc (E); scale bars: 1 mm. Note that the greenish coloration at the tail tip results from a leaf used as the background.

tooth row formula presented by Channing et al. (2012: 1/2+2//3) a second labial tooth formula has been recognized 1/3+3//3 (Fig. 1E). While Channing et al. (2012) refer to a tail length-body length ratio of 2.2, the mean value of our measures was slightly higher (2.4) in the present series. Regarding the coloration, pale blotches are present in our material on the tail as well as the lateral part of the body (Fig. 1A, C). The spiracle was translucent, lacking any pigmentation.

Leptopelis boulengeri (Werner, 1898)

The description of *L. boulengeri* tadpoles is based on sixteen tadpoles: ZMB 79613 (one tadpole, at Gosner stage 37, Bekob, Ebo Forest, Cameroon, 4.3578°N; 10.4170°E, 921 m a.s.l., 27 August 2011), ZMB 79614 (four tadpoles, at Gosner stage 36 to 40, Bekob, Ebo Forest, Cameroon, 4.3578°N; 10.4170°E, 921 m a.s.l., 28 August 2011), ZMB 79615 (three tadpoles, at Gosner stage 36, Bekob, Ebo Forest, Cameroon, 4.3575°N; 10.4168°E, 903 m a.s.l., 29 August 2011), ZMB 79616 (one tadpole, at Gosner stage 38) and ZMB 79617 (seven tadpoles, at Gosner stages 36 to 40), Bekob, Ebo Forest, Cameroon, 4.3578°N; 10.4170°E, 921 m a.s.l., 08 September 2011. Proportions including total or tail length were only available for non-genotyped individuals.

Description. Body oval with subovoid snout in dorsal view (Fig. 2B); ovoid to slightly compressed in lateral view (Fig. 2A); tail length-body length ratio 2.44 (TL/BL); body height 0.43 of body length (BH/BL); body width 0.53 of body length (BW/BL); maximum body width on the level of the spiracle's posterior end; nostrils situated dorsally, closer to snout tip than eyes (SND/SED = 0.41), distance snout-nostrils 0.14 of body length (SND/BL); eyes positioned laterally; eye diameter 0.08 of body length (ED/BL); interocular distance exceeds internostril distance by a factor of 2.35 (IOD/IND); tail length 0.71 of entire length (TL/EL), with moderately pronounced fins with narrow fin tip; dorsal fin originates at dorsal tail-body junction with maximum height at half of the tail length; dorsal fin and ventral fin particularly curved; ventral fin originates on the ventral terminus of the body; ventral fin narrower than tail axis with maximum height at half of the tail length; maximum fin height in dorsal fin slightly higher (DF/VF = 1.12); fin tip pointed; maximum tail height including fins exceeds body height (TTH/BH = 1.20); the tail axis width (in dorsal view) 0.34 of body width (AW/BW); maximum height of tail axis (at base) 0.55 of body height (AH/BH); tail axis height (at base) higher than maximum height of dorsal fin (AH/DF = 1.63); dextral vent tube, positioned basicaudally; spiracle sinistral, visible in dorsal view, originating anterior to mid-body (SSD/BL = 0.43); spiracle tube length 0.18 of body length (SL/BL); mouth opens anteroventrally; oral disc width wider than a third of body width (ODW/BW = 0.36); one row of papillae (with rounded tips) laterally at anterior lip with huge rostral gap, these connected to papillae in labial angles and posterior lip; second and third row of papillae at posterior lip; labial tooth row formula 1/3+3//3 (Fig. 2C); jaw sheaths black, of equal width and serrated; upper jaw very widely U-shaped; lower jaw U-shaped.

Coloration in preservation. Dorsolateral part of the body mostly speckled dark brown on yellowish ground, tail axis and dorsal fin speckled with lighter brown spots on yellowish ground; areas without brown spots shine through as yellow blots; ventral part of the body yellow without any spots; spiracle and vent tube yellowish; ventral fin translucent without any brown spots.

Remarks. *Leptopelis boulengeri* is known from Nigeria to Gabon, the Republic of the Congo in the south and the Democratic Republic of the Congo to the east (e.g., de la Riva 1994; Schiøtz 1967, 1999; Amiet 2012). Similar to *L. aubryioides* the species inhabits dense forests with small rivulets and ponds (Schiøtz 1967; Amiet 2012). The call and call activity have been reported by Amiet and Schiøtz (1974) and Amiet (2006). The tadpole is herein described for the first time. The tadpole of *L. boulengeri* exhibits the generic diagnostic characters: elongated and slender body with a long thin tail (TL/BL = 2.4) and acute tip (Fig. 2A). The coloration is similar to other *Leptopelis* tadpoles with brown spots on yellowish ground, the spots however, being brighter than usual. The chromatophores on the dorsal part of the body and the tail are less dense in *L. boulengeri* than in the remaining examined species, the fin has dorsally only very few chromatophores and is translucent ventrally (Fig. 2A). Likewise, the labial tooth row formula 1/3+3//3 is common in the genus but the keratodonts are relatively long. Further typical characters of *L. boulengeri* tadpoles are small eyes (ED/BL= 0.08), a very high tail (including fins) in comparison to its congeners despite a narrow tail axis, and the presence of three rows of caudal papillae on the lower lip (Fig. 2C), the latter character being unique in the genus (compare Channing et al. 2012; Penske et al. 2015; Portillo and Greenbaum 2014b).

Leptopelis calcaratus (Boulenger, 1906)

The description of *L. calcaratus* tadpoles is based on eleven tadpoles: ZMB 79618 (one tadpole at Gosner stage 28) and ZMB 79619 (nine tadpoles at Gosner stages 25 to 40), all on Mt. Nlonako, Cameroon, 4.9250°N; 9.9817°E, 1,035 m a.s.l., 25 October 2011, the tadpoles were found in a stream near a village) and ZMB 79620 (one tadpole at Gosner stage 41, near Manengouba village, Mt. Manengouba, Cameroon, 4.9502°N; 9.8639°E, 1,116 m a.s.l., 23 November 2011, the tadpoles were found in a stream near the village). Proportions including total or tail length were only available for non-genotyped individuals and ZMB 79620.

Description. Body oval with nearly rounded snout in dorsal view (Fig. 3B); ovoid to slightly compressed in lateral view (Fig. 3A); tail length-body length ratio 2.27 (TL/BL); body height 0.43 of body length (BH/BL); body width 0.54 of body length (BW/BL); maximum body width on the level of the spiracle's posterior end; nostrils situated dorsally, closer to snout tip than eyes (SND/SED = 0.38), distance snout-nostrils 0.16 of body length (SND/BL); eyes positioned dorsolaterally; eye diameter 0.10 of body length (ED/BL); interocular distance exceeds internostril distance by a factor of 2.56 (IOD/IND); tail length 0.69 of entire length (TL/EL), with moderately pronounced fins with narrow fin tip; dorsal fin originates posterior to the dorsal tail-body junction with maximum height at three-quarters of the tail length; dorsal fin slightly curved; ventral fin originates on the ventral terminus of the body; ventral fin narrower than tail axis with maximum height at three-quarters of the tail length; maximum fin height in dorsal fin higher (DF/VF = 1.18); fin tip pointed; maximum tail height including fins equals body height (TTH/BH = 1.00); tail axis width (in dorsal view) 0.50 of body width (AW/BW); maximum height of tail axis (at base) 0.53 of body height (AH/BH); tail axis height (at base) higher than maximum height of dorsal fin (AH/DF = 2.15); dextral vent tube, positioned basicaudally; spiracle sinistral, visible in dorsal view, originating anterior to mid-body (SSD/BL = 0.43); spiracle tube length 0.17 of body length (SL/BL); mouth opens anteroventrally; oral disc width less than fifth of body width (ODW/BW = 0.19); one row of papillae (with rounded tips) laterally at anterior lip with huge rostral gap, these connected to papillae in labial angles and posterior lip; second row of papillae caudal at posterior lip with slightly pointed tips; labial tooth row

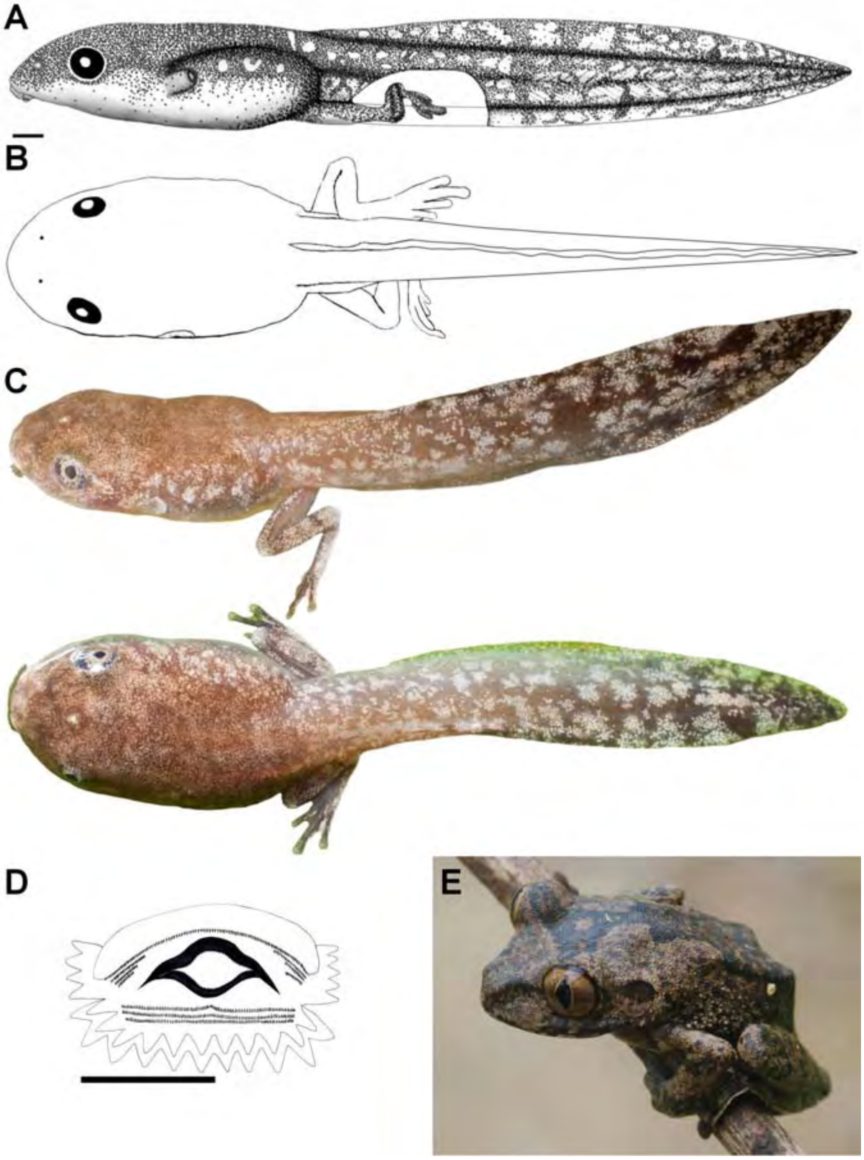

Fig. 4. Lateral (A) and dorsal (B) view of *Leptopelis millsoni* (ZMB 79621) at Gosner stage 39; coloration in life of tadpole (ZMB 79621) in lateral (top) and dorsal (below) view (C); sketch of the oral disc (D); adult *L. millsoni* (ZFMK 87708) (E); scale bars: 1 mm. Note that the greenish coloration on the lower fin results from a leaf used as the background.

formula 1/3+3//3 (Fig. 3E); jaw sheaths black, of equal width and serrated; upper jaw very widely U-shaped with median concavity; lower jaw widely V-shaped.

Coloration in preservation. Dorsolateral part of the body, tail axis and dorsal fin mostly mottled brown on yellowish ground; areas without brown spots shine through as yellow blots; ventral part of the body pale yellow with some homogeneously distributed brown spots; spiracle and vent tube translucent; ventral fin translucent without any brown spots.

Coloration in life (Fig. 3C). Dark brown with shiny golden speckles at dorsolateral part of the body, tail axis and dorsal fin; ventral fin predominantly translucent with few spots towards tail tip; ventral part of the body without golden speckles.

Remarks. *Leptopelis calcaratus* is known from Nigeria to Gabon and the Republic of the Congo in the south and the Central African Republic and the Democratic Republic of the Congo to the east (e.g., de la Riva 1994; Schiøtz 1963, 1999; Frétey and Blanc 2001; Frétey et al. 2006; Jackson and Blackburn 2007; Amiet 2012). Reproduction takes place in more or less swampy forests that are crossed by small rivers (Amiet 2012). Notes on habitat use and call activity of this species were documented by Schiøtz (1967, 1999), Amiet and Schiøtz (1974) and Amiet (2006, 2012). The tadpole of *L. calcaratus* has been described by Lamotte and Perret (1961) and Channing et al. (2012). Shape of body and tail, as well as overall pigmentation are congruent with the available tadpole descriptions. In addition to the above recorded labial tooth row formula Lamotte and Perret (1961) mention 1/2+2//3. The eyes are positioned dorsolaterally in our material, as described by Channing et al. (2012); in contrast, Lamotte and Perret (1961) refer to a dorsal position; however, it cannot be excluded that their series comprised material of different species (their descriptions were usually based on morphological series and not on tadpoles from known parents). The tail length-body length ratio of 2.3 was higher in comparison to both for-

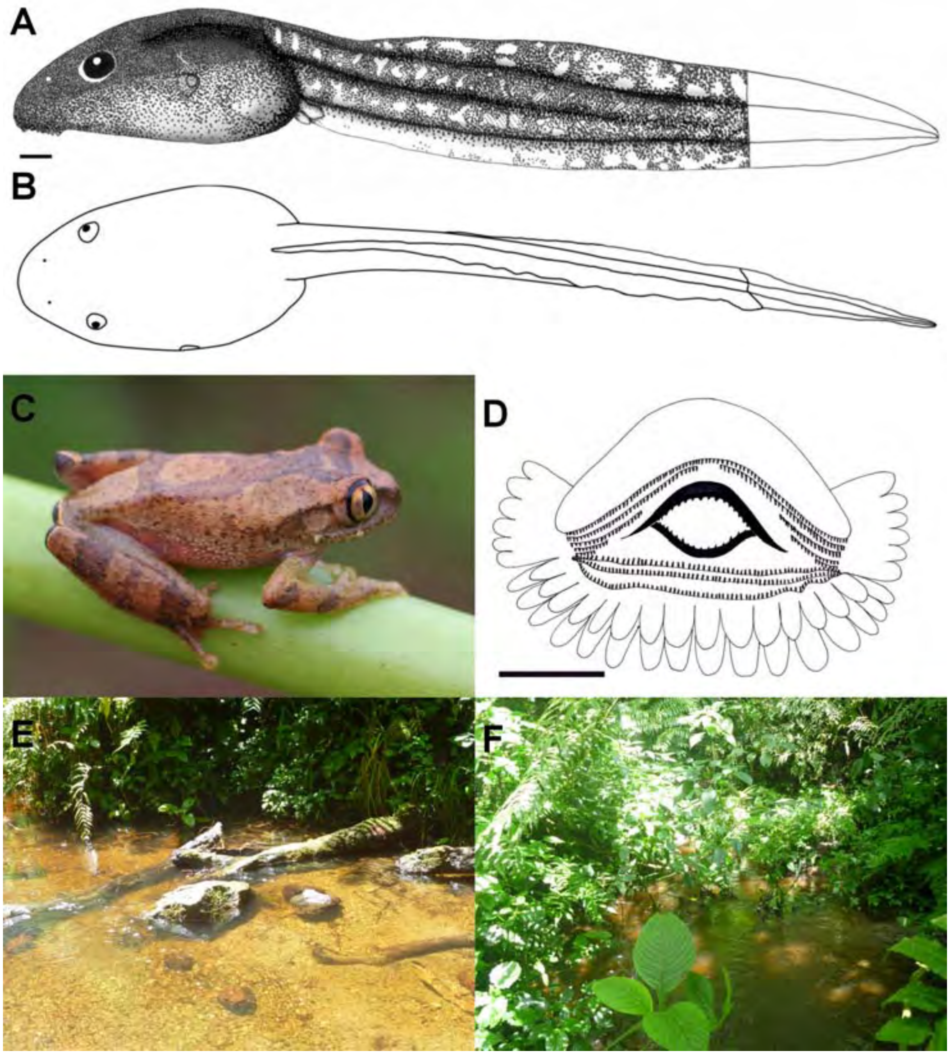

Fig. 5. Lateral (A) and dorsal (B) view of *Leptopelis modestus* (ZMB 79622) at Gosner stage 34; adult *L. modestus* (MCZ A138023, *photo courtesy David C. Blackburn*) (C); sketch of the oral disc (D); habitat of *L. modestus* on Mt. Manengouba (E and F); scale bars: 1 mm.

mer descriptions (1.9). Examined tadpoles also differed in coloration to the voucher examined by Channing et al. (2012). While these authors note black pigments on tail and fins, pigmentation in our material was mottled brown on a pale ground or forming large, almost uniform brown blotches, with a small translucent spiracle and vent tube as described by Lamotte and Perret (1961). Pigmentation tended to decrease from body to tail.

Leptopelis millsoni (Boulenger, 1895)

The description of *L. millsoni* tadpoles is based on one tadpole: ZMB 79621 (at Gosner stage 39, the tadpole was found in Kribi, near Miangasio Lendi, Cameroon, 2.8930°N; 9.9542°E, 31 m a.s.l., 04 November 2011, in a slow flowing, sandy bottom forest stream).

Description. Body oval with semi-circular snout in dorsal view (Fig. 4B); ovoid to slightly compressed in lateral view (Fig. 4A); tail length-body length ratio 1.82 (TL/BL); body height 0.38 of body length (BH/BL); body width 0.58 of body length (BW/BL); maximum body width on the level of the spiracle's anterior end; nostrils situated dorsally, slightly closer to snout tip than eyes (SND/SED = 0.43), distance snout-nostrils 0.16 of body length (SND/BL); eyes positioned laterally; eye diameter 0.12 of body length (ED/BL); interocular distance exceeds internostril distance by a factor of 2.33 (IOD/IND); tail length 0.65 of entire length (TL/EL), with moderately pronounced fins with narrow fin tip; dorsal fin originates at dorsal tail-body junction; dorsal fin moderately curved with maximum height at two-thirds of the tail length; ventral fin originates on the ventral terminus of the body; ventral fin narrower than tail axis with maximum height at half of the tail length; maximum fin height of dorsal fin higher (DF/VF = 1.25); fin tip pointed; maximum tail height including fins exceeds body height (TTH/BH = 1.06); tail axis width (in dorsal view) 0.52 of body width (AW/BW); maximum height of tail (axis at base) 0.69 of body height (AH/BH); tail axis height at its base higher than maximum height of dorsal fin (AH/DF = 2.50); dextral vent tube, positioned basicaudally; spiracle sinistral, visible in dorsal view, originating slightly anterior to mid-body (SSD/BL = 0.47); spiracle tube length 0.11 of body length (SL/BL); mouth opens anteroventrally; oral disc width more than a third of body width (ODW/BW = 0.36); one row of short papillae (with slightly pointed tips) laterally at anterior lip with huge rostral gap, these connected to papillae in labial angles and posterior lip; second row of papillae at posterior lip; labial tooth row formula 1/3+3//3 (Fig. 4D); jaw sheaths black, of equal width and serrated; upper jaw widely U-shaped with median concavity; lower jaw widely V-shaped.

Coloration in preservation. Body, tail axis, dorsal fin and ventral fin mostly speckled dark brown on yellowish ground, areas without brown spots shine through as yellow blots, ventral part of the body yellow with some light brown spots; spiracle and vent tube in the same color as body and tail.

Coloration in life (Fig. 4C). Dark brown with shiny golden speckles at dorsolateral part of the body, tail axis, dorsal fin and ventral fin; speckles very dense at dorsal part of the body; dorsoventral part of the body with few speckles.

Remarks. *Leptopelis millsoni* is known from Nigeria to Gabon and the eastern Democratic Republic of the Congo (e.g., Schiøtz 1967, 1999; Lötters et al. 2001; Blanc and Frétey 2004; Rödel et al. 2014). As in the other species male calling sites are found close to streams in the breeding season but reproduction most probably occurs in stagnant water (Amiet 2012). The call has been recorded by Amiet and Schiøtz (1974) and call activity is detailed in Amiet (2006). The tail with low fins is long (TL/BL = 1.8), but not as long as observed in other *Leptopelis* species. Because we had only one tadpole available we cannot check if this is a peculiarity of our specimen or a general trend in this Gosner stage. What distinguishes *L. millsoni* from the other studied tadpoles is the shape of the papillae. While all other *Leptopelis* species showed papillae with rounded tips, the papillae of *L. millsoni* had fairly pointed tips (Fig. 4D). The eyes of our voucher were relatively big compared to the other species (ED/BL = 0.12); only *L. viridis* had similar sized eyes in relation to body length. We cannot evaluate whether the TL/BL value reflects a species specific state, an individual character state or the advanced Gosner stage.

Leptopelis modestus (Werner, 1898)

The description of *L. modestus* tadpoles is based on three tadpoles: ZMB 79622 (one tadpole, at Gosner stage 34), ZMB 79623 (one tadpole, at Gosner stage 31), near summit of Mt. Manengouba, Cameroon, 5.0098°N; 9.8568°E, 2,135 m a.s.l., 27 September 2011, the tadpoles were found in a medium sized river in a gallery forest) and ZMB 79624 (one tadpole, at Gosner stage 36, North West Province Abo Forest, Cameroon, 24 August 2012). Proportions including total or tail length were only available for the non-genotyped individual and ZMB 79624.

Description. Body oval with nearly rounded snout in dorsal view (Fig. 5B); ovoid to slightly compressed in lateral view (Fig. 5A); tail length-body length ratio 2.27 (TL/BL); body height 0.49 of body length (BH/BL); body width 0.57 of body length (BW/BL); maximum body width slightly behind the level of the spiracle's posterior end; nostrils situated dorsally, closer to snout tip than eyes (SND/SED = 0.39), distance snout-nostrils 0.19 of body length (SND/BL); eyes positioned laterally; eye diameter 0.09 of body length (ED/BL); interocular distance exceeds internostril distance by a factor of

1.94 (IOD/IND); tail length 0.70 of entire length (TL/EL), with moderately pronounced fins with narrow fin tip; dorsal fin originates at dorsal tail-body junction rising barely at the first eighth of the tail length; dorsal fin slightly curved with maximum height at half of the tail length; ventral fin originates on the ventral terminus of the body; ventral fin narrower than tail axis with maximum height around half of the tail length; maximum fin height in dorsal fin higher (DF/VF = 1.25); fin tip pointed; maximum tail height including fins equals body height (TTH/BH = 1.00); tail axis width (in dorsal view) 0.36 of body width (AW/BW); maximum height of tail axis (at base) 0.46 of body height (AH/BH); tail axis height at its base higher than maximum height of dorsal fin (AH/DF = 1.55); dextral vent tube, positioned basicaudally; spiracle sinistral, visible in dorsal view, originating anterior to mid-body (SSD/BL = 0.53); spiracle tube length 0.07 of body length (SL/BL); mouth opens anteroventrally; oral disc width more than a third of body width (ODW/BW = 0.34); one row of papillae (with rounded tips) laterally at anterior lip with huge rostral gap, these connected to papillae in labial angles and posterior lip; second row of papillae at posterior lip, also with rounded tips; labial tooth row formula 1/3+3//3 or 1/4+4//3 (Fig. 5D); jaw sheaths black, of equal width and serrated; upper jaw and lower jaw widely U-shaped.

Coloration in preservation. Dorsolateral part of the body, tail axis and dorsal fin mostly speckled dark brown on brownish ground on the body and yellowish ground on the tail; areas without brown spots shine through as yellow blots; ventral part of the body yellowish with some homogeneously distributed dark brown spots at the anterior third of the body; spiracle and vent tube translucent; ventral fin at the anterior part translucent with some brown spots towards tail tip.

Remarks. Since a record of *Leptopelis modestus* from eastern Congo (Laurent 1972) and subsequent recognition as a distinct sub-species (Laurent 1973), *L. modestus* has been regarded as a species with a disjunct distribution with known occurrences in Nigeria, Cameroon, and Bioko – Equatorial Guinea (Schiøtz 1967, 1999; Amiet 2012; Frétey et al. 2012) and the eastern Democratic Republic of the Congo and Kenya (Köhler et al. 2006; Portillo and Greenbaum 2014b). However, the latter populations have been recently recognized as several distinct species (Schiøtz 1975: *L. fiziensis* from South Kivu Province, DRC; Köhler et al. 2006: *L. mackayi* from the Western Province, Kenya; Portillo and Greenbaum 2014b: *L. mtoewaate* from South Kivu Province, DRC). Although males congregate close to streams and torrents during the

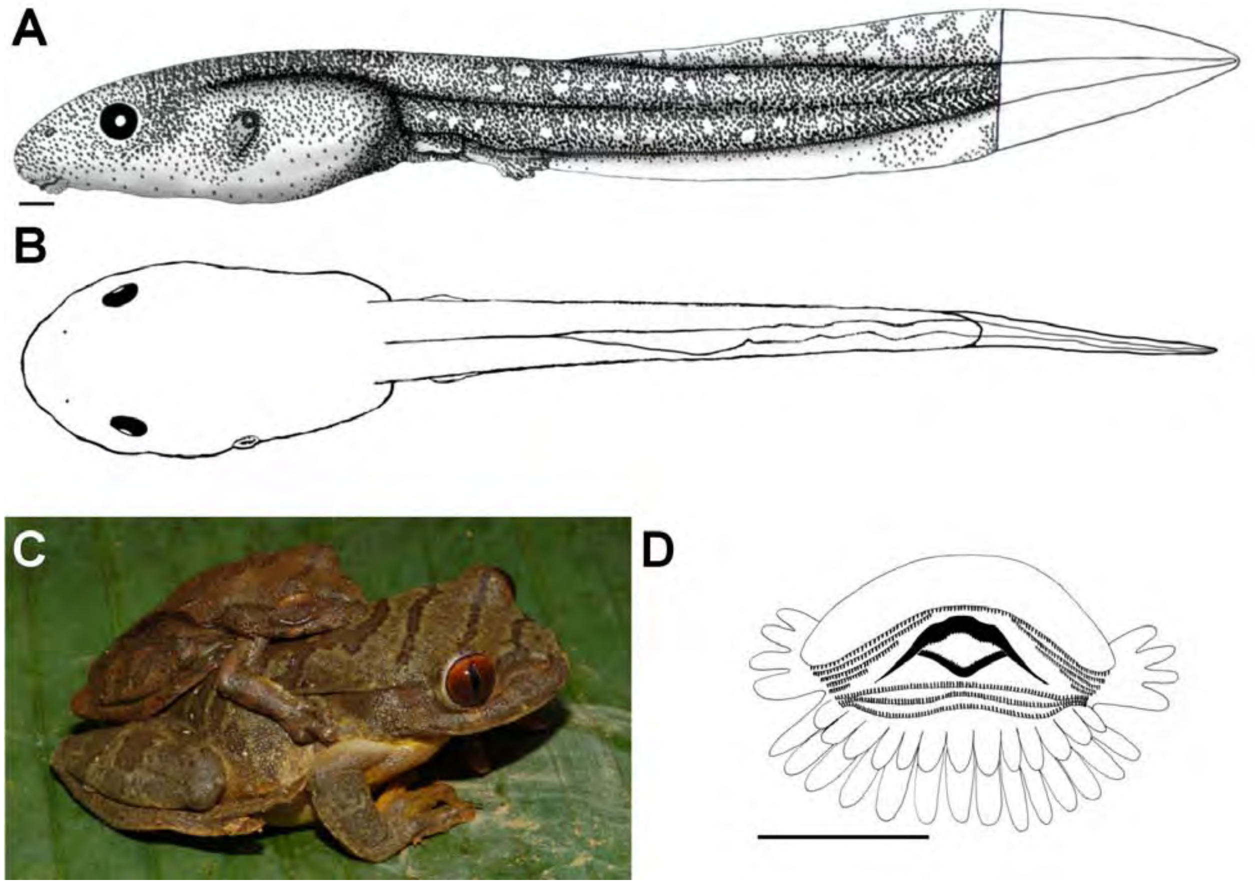

Fig. 6. Lateral (A) and dorsal (B) view of *Leptopelis rufus* (ZMB 79627) at Gosner stage 36; adult *L. rufus* (female: ZMB 78398 and male: ZMB 78399) (E); sketch of the oral disc (D), scale bars: 1 mm.

breeding season, reproduction takes place in slow running and stagnant water bodies (Amiet 2012). Further notes on call activity and the advertisement call are provided by Schiøtz (1999) and Amiet (2006). Based on two vouchers the tadpole has been described by Channing et al. (2012). Our observations are in agreement with their description. Minor differences refer to coloration and the interocular distance-internostril distance ratio and an additional labial tooth row formula (1/4+4//3; Fig. 5D). The IOD/IND was marginally lower (1.94) in comparison to the value of 2 recorded by Channing et al. (2012). Noteworthy, the tail length-body length ratio differed between different Gosner stages (stage 31: TL/BL= 2.1; stage 36: TL/BL= 2.5). Concerning the coloration, the anterior half of the ventral fin lacked speckles in Gosner stages 31 and 34 (Fig. 5A) while it was pigmented in the more developed tadpole (Gosner stage 36).

Taxonomic remark. Amiet (2012) discussed the possibility of cryptic speciation based on a *modestus*-like female from Mwandong, West Cameroon, which differed in coloration of skin and iris, size of tympanum, and snout-vent length from remaining populations and co-occurred with congeneric species (*L. brevirostris*, *L. calcaratus*, and *L. modestus*). The herein investigated tadpoles have been collected on Mt. Manengouba, in close proximity to Mwandong, and in the Abo Forest. The barcoded sequences included a specimen (MCZ A138023; Fig. 5C) collected near Nsoung on Mt. Manengouba. MCZ A138023 exhibits characters that assign the specimen to the "true" *L. modestus*. Although the two genotyped tadpoles originate from high elevation localities on Mt. Manengouba and Mt. Oku (both app. 2,150 m a.s.l.), with a distance of more than 150 km between them, they show no difference in the analysed 16S fragment and point to the occurrence of the same taxon on both mountain ranges.

Leptopelis rufus Reichenow, 1874

The description of *L. rufus* tadpoles is based on eighteen tadpoles (remark: two different molecular lineages have been recognized in *L. rufus* in the course of the present analyses, thus we herein refer to *L. rufus*_1 and *L. rufus*_2 in order to assure differentiation of the examined material): ZMB 79625 (*L. rufus*_1, three tadpoles, at Gosner stages 26 and 29, Camp Bekop, Ebo Forest, Cameroon, 4.3519°N; 10.4244°E, 845 m a.s.l., 07 January 2011, the tadpoles were found in secondary forest), ZMB 79626 (*L. rufus*_2; two tadpoles, at Gosner stages 28 and 29, Mt. Nlonako, Cameroon, 4.8309°N; 9.9255°E, 459 m a.s.l., 23 October 2011, the tadpoles were found in a small rock pool of approximately 50 cm diameter), ZMB 79627 (*L. rufus*_2; one tadpole, at Gosner stage 36, Njuma, Ebo Forest, Cameroon, 4.3394°N; 10.2458°E, 320 m a.s.l., 20 August 2011, the tadpole was found in primary rainforest), ZMB 79628 (*L. rufus*_2; one tadpole, at Gosner stage 29, Ndogbanguengue, Ebo Forest, Cameroon, 4.4069°N; 10.1653°E, 96 m a.s.l., 19 September 2010, the tadpole was found in farmbush) and ZMB 79629 (*L. rufus*_2; seven tadpoles, at Gosner stages 28 to 36, Ekom Khan, Mt. Manengouba, Cameroon, 5.0633°N; 10.0163°E, 587 m a.s.l., 29 December 2010, the tadpoles were found in a medium sized river in a forest fragment). Proportions including total or tail length were only available for non-genotyped individuals.

Description. Body oval with nearly rounded snout in dorsal view (Fig. 6B); ovoid to slightly compressed in lateral view (Fig. 6A); tail length-body length ratio 2.04 (TL/BL); body height 0.37 of body length (BH/BL); body width 0.53 of body length (BW/BL); maximum body width between the level of the eyes and the spiracle's anterior end; nostrils situated dorsally, closer to snout tip than eyes (SND/SED = 0.40), distance snout-nostrils 0.20 of body length (SND/BL); eyes positioned laterally; eye diameter 0.10 of body length (ED/BL); interocular distance exceeds internostril distance by a factor of 1.78 (IOD/IND); tail length 0.67 of entire length (TL/EL), with moderately pronounced fins with narrow fin tip; dorsal fin originates at dorsal tail-body junction, but very low, not visible in lateral view; rising behind anterior sixth of tail length; dorsal fin moderately curved with maximum height at three-quarters of the tail length; ventral fin originates on the ventral terminus of the body; ventral fin narrower than tail axis with maximum height at three-quarters of the tail length; maximum fin height higher in dorsal fin (DF/VF = 1.18); fin tip pointed; maximum tail height including fins nearly equals body height (TTH/BH= 0.98); tail axis width (in dorsal view) 0.36 of body width (AW/BW); maximum height of tail axis (at base) 0.65 of body height (AH/BH); tail axis height at its base higher than maximum height of dorsal fin (AH/DF = 1.75); dextral vent tube, positioned basicaudally; spiracle sinistral, visible in dorsal view, originating at mid-body (SSD/BL = 0.50); spiracle tube length 0.13 of body length (SL/BL); mouth opens anteroventrally; oral disc width more than a third of body width (ODW/BW = 0.36); one row of papillae (with rounded tips) laterally at anterior lip with huge rostral gap, these connected to papillae in labial angles and posterior lip; second row of longer papillae caudal at posterior lip, also with rounded tips; labial tooth row formula 1/3+3//3 or 1/4+4//3 (Fig. 6D); jaw sheaths black and serrated, upper jaw sheath thicker; upper jaw widely U-shaped with median concavity; lower jaw widely V-shaped.

Coloration in preservation. Dorsolateral part of the body, tail axis and dorsal fin mostly speckled dark brown on brownish ground at the body and yellowish ground at the tail; areas without brown spots shine through as small yellow blots; ventral part of the body yellowish with many homogeneously distributed dark brown spots at the anterior third of the body and fewer spots at the

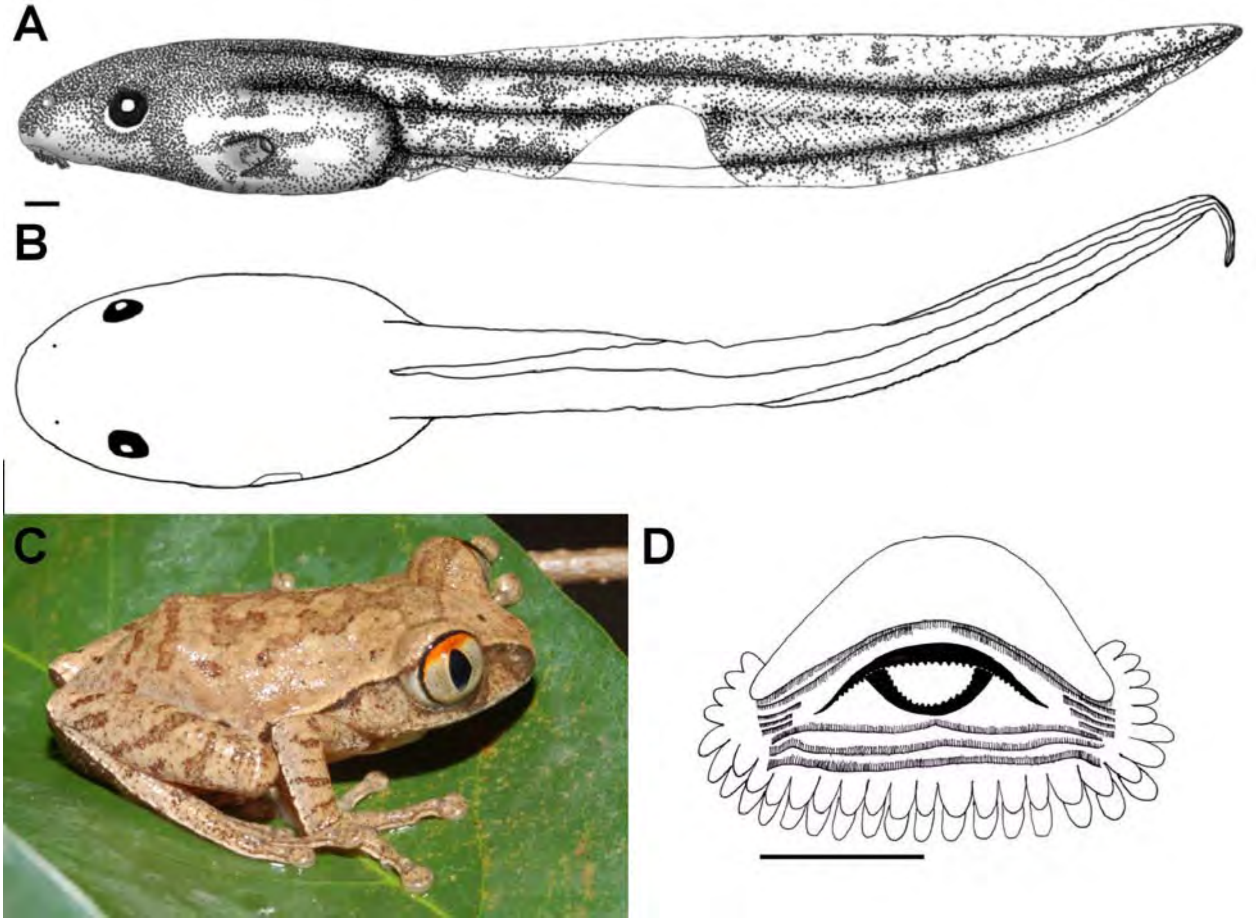

Fig. 7. Lateral (A) and dorsal (B) view of *Leptopelis spiritusnoctis* (ZMB 79634) at Gosner stage 34; adult *L. spiritusnoctis* (ZMB 79578) (C); sketch of the oral disc (D), scale bars: 1 mm.

posterior two-thirds of the body; spiracle and vent tube translucent; ventral fin at the anterior part translucent with some brown spots towards tail tip.

Remarks. *Leptopelis rufus* is known from Nigeria to northern Angola (de la Riva 1994; Schiøtz 1963, 1999; Amiet 2012). Adults are common on branches and lianas in proximity to streams during the breeding season (Amiet 1975). The call has been reported by Amiet and Schiøtz (1974). The tadpole of has been described by Channing et al. (2012) based on a single tadpole belonging to a larger series examined herein (MH399 = ZMB 79629; herein assigned to *L. rufus*_2). Generally our observations of the larger series coincide with the former description. However, while early tadpole stages of *L. rufus* exhibit the labial tooth row formula 1/3+3//3, also reported in Channing et al. (2012), we observed an increase of tooth rows on the upper lip in more developed tadpoles (Gosner stage 29: 1/4+4//3; Fig. 6D). Further differences refer to a lower tail length-body length ratio (TL/BL= 2.0) than in Channing et al. (2012; TL/BL = 2.6).

Taxonomic remark. A comparison of 16S sequences of adults and tadpoles revealed two molecular lineages in *L. rufus*, diverging by app. 1.5% in the mitochondrial 16S gene (Tab. 2). Each lineage could be assigned to adult specimens that have morphologically been assigned to *L. rufus*. While no obvious differences have been assessed, neither in tadpoles nor adults, we herein refer to *L. rufus*_1 and *L. rufus*_2 in order to highlight this molecular divergence beyond intraspecific variance in remaining species analysed herein. A similar genetic divergence (0.9–1.1% in 16S) has recently been uncovered between two species in the eastern Democratic Republic of the Congo (Portillo and Greenbaum 2014a) warranting further morphological and bio-acoustical analyses to examine the status of lineages of *L. rufus* in western Central Africa.

Leptopelis spiritusnoctis Rödel, 2007

The description of *L. spiritusnoctis* tadpoles is based on twenty tadpoles: ZMB 79630 (five tadpoles, at Gosner stages 25 to 40, 7.2347°N; 9.3096°E, 398 m a.s.l.), ZMB 79631 (one tadpole, at Gosner stage 40, 7.2347°N; 9.3096°E, 398 m a.s.l.), ZMB 79632 (one tadpole, at Gosner stage 31, 7.2316°N; 9.3118°E, 382 m a.s.l.), ZMB 79633 (eight tadpoles, at Gosner stages 25 to 36, 7.2308°N; 9.3023°E, 387 m a.s.l.), ZMB 79634 (one tadpole, at Gosner stage 36, 7.2308°N; 9.3023°E, 387 m a.s.l.), ZMB 79635 (three tadpoles, at Gosner stages 25 and 27, 7.2376°N; 9.3117°E, 417 m a.s.l.), and ZMB 79636 (one tadpole, at Gosner stage 25, 7.2376°N; 9.3117°E, 417 m a.s.l.). All *L. spiritusnoctis* tadpoles were caught near Gbanju, Liberia, 08 June 2011. Proportions including total or tail length were only available for non-genotyped individuals, ZMB 79630, 79632, 79634, and 79636.

Description. Body oval with subovoid snout in dorsal view (Fig. 7B); ovoid to slightly compressed in lateral view (Fig. 7A); tail length-body length ratio 2.33 (TL/BL); body height 0.49 of body length (BH/BL); body width 0.60 of body length (BW/BL); maximum body width on the level of the spiracle's anterior end; nostrils situated dorsally, closer to snout tip than eyes (SND/SED = 0.37), distance snout-nostrils 0.21 of body length (SND/BL); eyes positioned laterally; eye diameter 0.09 of body length (ED/BL); interocular distance exceeds internostril distance by a factor of 1.76 (IOD/IND); tail length 0.70 of entire length (TL/EL), with moderately pronounced fins with narrow fin tip; dorsal fin originates at dorsal tail-body junction; dorsal fin moderately curved with maximum height at three-quarters of the tail length; ventral fin originates on the ventral terminus of the body; ventral fin narrower than tail axis with maximum height at three-quarters of the tail length; maximum fin height in dorsal fin higher (DF/VF = 1.28); fin tip pointed; maximum tail height including fins slightly exceeds body height (TTH/BH = 1.08); tail axis width (in dorsal view) 0.41 of body width (AW/BW); maximum height of tail axis (at base) 0.56 of body height (AH/BH); tail axis height at its base higher than maximum height of dorsal fin (AH/DF = 1.93); dextral vent tube, positioned basicaudally; spiracle sinistral, visible in dorsal view, originating at mid-body (SSD/BL = 0.50); spiracle tube length 0.12 of body length (SL/BL); mouth opens anteroventrally; oral disc width more than a quarter of body width (ODW/BW = 0.30); one row of papillae (with rounded tips) laterally at anterior lip with huge rostral gap, these connected to papillae in labial angles and posterior lip; second row of papillae (also with rounded tips) at posterior lip; labial tooth row formula 1/4+4//3 (Fig. 7D); jaw sheaths black, of equal width and serrated; upper jaw widely U-shaped; lower jaw U-shaped.

Coloration in preservation. Dorsolateral part of the body mostly speckled dark brown on yellowish ground, tail axis, dorsal fin and spiracle speckled with less brown spots on yellowish ground; ventral part of the body yellow with some homogeneously distributed brown spots

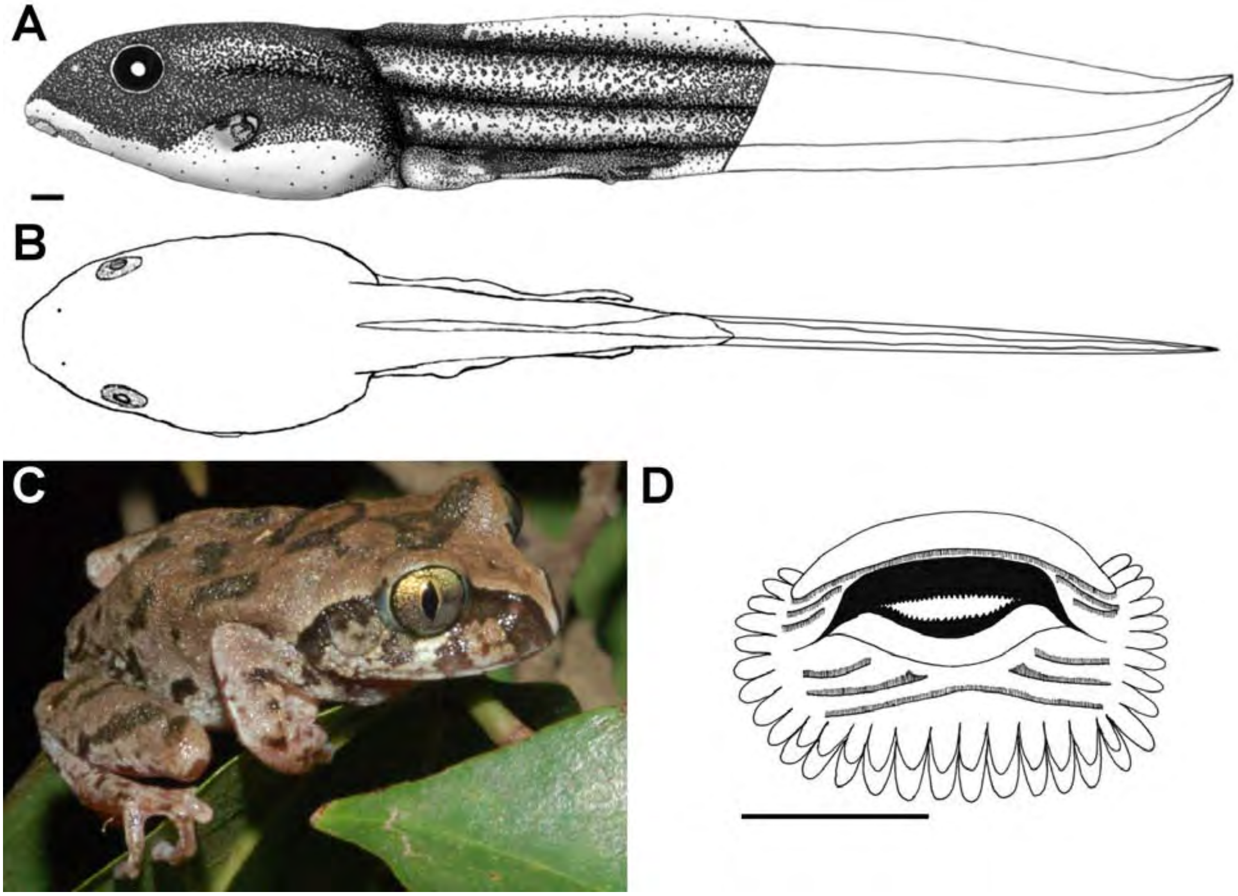

Fig. 8. Lateral (A) and dorsal (B) view of *Leptopelis viridis* (ZMB 79638) at Gosner stage 40; adult *L. viridis* (ZMB 83028) (C); sketch of the oral disc (ZMB 79637) at Gosner stage 30 (D), scale bars: 1 mm.

at the anterior third of the body; vent tube translucent; ventral fin translucent at anterior part with some brown spots towards tail tip.

Remarks. *Leptopelis spiritusnoctis* is known from the entire West African forest belt ranging from Guinea, through Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Togo, Benin to western Nigeria (e.g., Schiøtz 1963, 1967; Rödel et al. 2000, 2004; Hillers and Rödel 2007; Rödel 2007; Segniagbeto et al. 2007). Male calling sites have been reported from close to various water bodies, from fast flowing creeks with rocky bed to tiniest puddles on the forest floor (Rödel 2007). Females deposit up to 140 eggs below the soil surface (Schiøtz 1963; Rödel 2007). After three weeks tadpoles hatch and wriggle up to 50 cm towards the water (Schiøtz 1963; Oldham 1971). The tadpole was described by Lamotte and Perret (1961), Schiøtz (1963, 1967), Rödel (2007), and Channing et al. (2012). Prior to the description of *L. spiritusnoctis* by Rödel (2007) records of the species, including tadpole descriptions, have been named *L. hyloides*. Generally the observations of our larger series agree with former descriptions. However, an additional labial tooth row formula has been encountered 1/4+4//3 (Fig. 7D). Lamotte and Perret (1961) reported a change of the number of tooth rows during tadpole growth. The observed tail length-body length ratio was marginally higher (TL/BL= 2.3) than in the previous descriptions of Channing et al. (2012: TL/BL= 2.2) and Lamotte and Perret (1961: TL/BL= 2). The position of nostrils was closer to the snout tip than to the eyes while they are closer to the eye according to Channing et al. (2012).

Taxonomic remark. Amiet (2012) assumed the West African *L. spiritusnoctis* and the Central African *L. aubryi* to be conspecific. However, based on genetics and bioacoustics Rödel et al. (2014) recently confirmed their specific distinctness. This is herein further supported by tadpole morphology, as tadpoles of the two species differed in their size (tadpoles of *L. aubryi* growing larger 53 mm; Schiøtz 1963), tail length-body length ratio (higher in in *L. aubryi*; TL/BL = 3.4x) and labial tooth row formulae 1/3+3//3 in *L. aubryi*; diverse in *L. spiritusnoctis*; see above).

Leptopelis viridis (Günther, 1869)

The description of *L. viridis* tadpoles is based on two tadpoles: ZMB 79637 (one tadpole, at Gosner stage 30) and ZMB 79638 at (one tadpole, at Gosner stage 40). Both tadpoles were caught near Banambala, Guinea, 7.9899°N; 9.1312°E, 449 m a.s.l., 01 June 2011. Proportions including total or tail length for this species were not available, because there were only two individuals to examine, both with incomplete tail as tail tips were used for DNA analysis.

Description. Body oval with subelliptical snout in dorsal view (Fig. 8B); ovoid to slightly compressed in lateral view (Fig. 8A); body height 0.50 of body length (BH/BL); body width 0.58 of body length (BW/BL); maximum body width on the level of the spiracle's posterior end; nostrils situated dorsally, closer to snout tip than eyes (SND/SED = 0.35), distance snout-nostrils 0.20 of body length (SND/BL); eyes positioned laterally; eye diameter 0.12 of body length (ED/BL); interocular distance exceeds internostril distance by a factor of 1.92 (IOD/IND); tail with moderately pronounced fins; dorsal fin originates at dorsal tail-body junction; dorsal fin nearly parallel; ventral fin originates on the ventral terminus of the body; ventral fin narrower than tail axis and parallel to it; maximum fin height in dorsal fin higher (DF/VF = 1.60); maximum tail height including fins equals body height (TTH/BH= 1.00) at the level, where the tail was cut; tail axis width (in dorsal view) 0.49 of body width (AW/BW); maximum height of tail axis (at base) 0.61 of body height (AH/BH); tail axis height at its base higher than maximum height of dorsal fin (AH/DF = 2.19); dextral vent tube, positioned basicaudally; spiracle sinistral, visible in dorsal view, originating at mid-body (SSD/BL = 0.53); spiracle tube length 0.10 of body length (SL/BL); mouth opens anteroventrally; oral disc width about a quarter of body width (ODW/BW = 0.24); one row of papillae (with rounded tips) laterally at anterior lip with huge rostral gap, these connected to papillae in labial angles and posterior lip; second row of papillae (also with rounded tips) at posterior lip; labial tooth row formula 1/2+2//1+1/2 or 1/2+2//2+2/1 (Fig. 8D); jaw sheaths black and serrated, upper jaw sheath broader than lower jaw sheath; upper jaw widely U-shaped; lower jaw widely U-shaped as well.

Coloration in preservation. Dorsolateral part of the body mostly speckled dark brown on brownish ground; tail axis with less brown spots on yellow ground; ventral part of the body yellowish with some brown spots at the anterior third of the body; spiracle and vent tube translucent; ventral fin predominantly translucent with few brown spots composed of dense melanophores, dorsal fin brownish with some dark brown spots particularly at the anterior part of the tail.

Remarks. *Leptopelis viridis* covers a wide geographic range from Senegal to Nigeria and the north-eastern Democratic Republic of the Congo (e.g., Perret 1966; Schiøtz 1963, 1967, 1999; Rödel 2000; Amiet 2012). Females produce up to 220 eggs of 3.1–4.7 mm that are rich in yolk and of yellowish-white color (Barbault 1984; Rödel 2000). Rödel (2000) assumed egg deposition in rock-pools or transport of tadpoles by adults as the elevated surrounding was rocky and did not make digging of burrows possible. The tadpole of *Leptopelis viridis* has already been described in the past (Lamotte and Perret

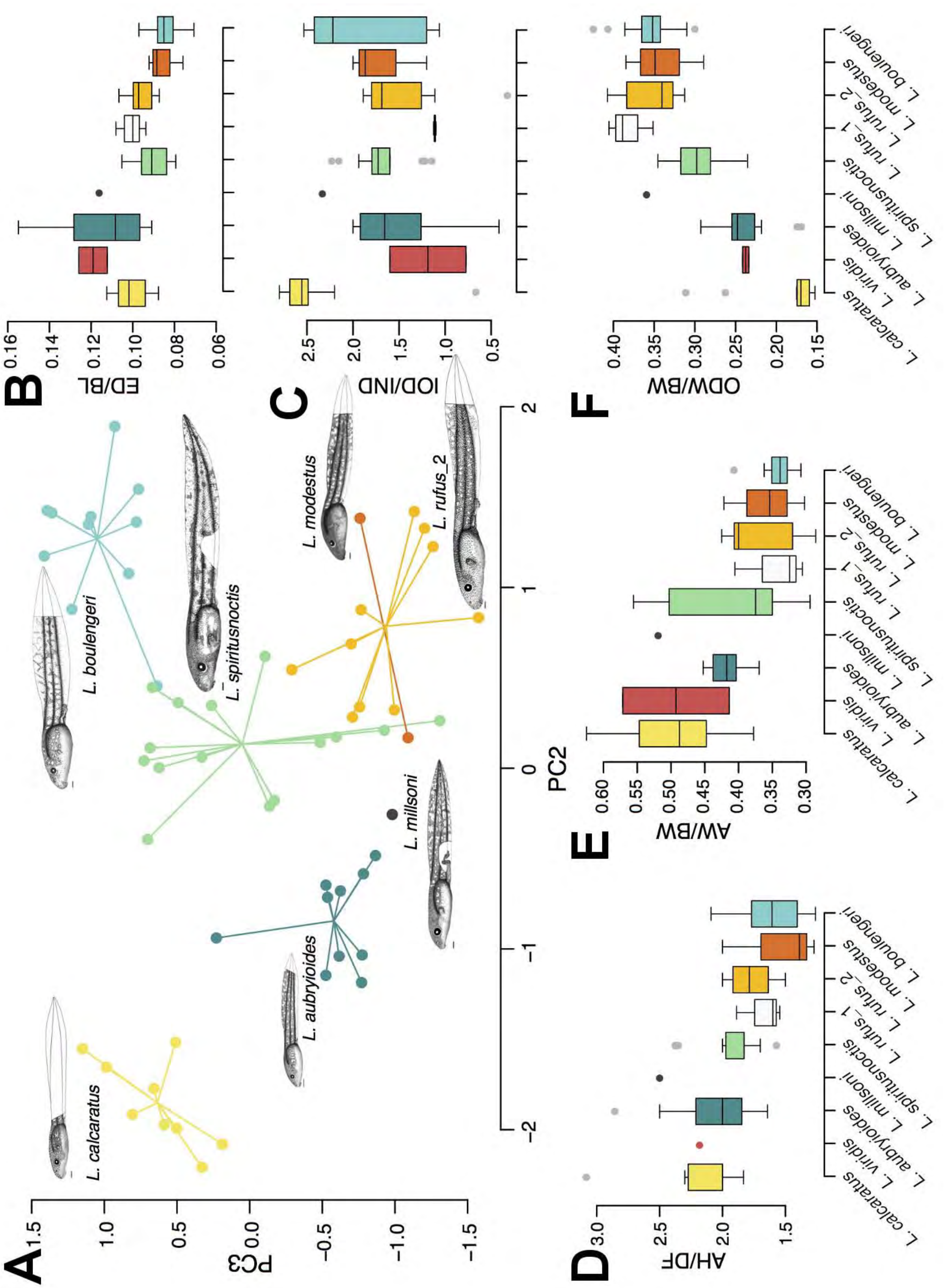

Fig. 9. Biplot of the second and third components of a Principal Component Analyses of morphological measures of *Leptopelis* tadpoles (A). Illustrations are of genotyped representatives (not necessarily included in the PCA) roughly to scale. Boxplots show morphometric ratios of variables contributing most to these components (B–F).

1961; Schiøtz 1963, 1967; Rödel 2000; Channing et al. 2012). Both of our tadpole vouchers had a cut tail, thus we can only refer to formerly reported tail length-body length ratios (Lamotte and Perret 1961: TL/BL = 2.1; Rödel 2000: TL/BL = 2.5; Channing et al. (2012): TL/BL = 2). In comparison to other *Leptopelis* species, the tooth rows are very variable. Rödel (2000) mentioned the labial tooth row formula of 1//2 for a tadpole two days after hatching and various formulae are known in more developed tadpoles: 1/2+2//3 (Lamotte and Perret 1961; Rödel 2000; Channing et al. 2012), 1/2+2//1+1/2 (Lamotte and Perret 1961; Channing et al. 2012; this study, in Gosner stage 40 in ZMB 79638), 1/3+3//3 and 1/3+3//1+1/2 (both Lamotte and Perret 1961) and 1/2+2//2+2/1 (this study, in Gosner stage 30 in ZMB 79637; Fig. 8D). A dark pigmentation of dorsal parts of the body has already been reported in the past and is more conspicuous than in other known *Leptopelis* tadpoles. While the spiracle was translucent in ZMB 79637, a condition also reported by Lamotte and Perret (1961) and Channing et al. (2012), it contained some chromatophores in ZMB 79638 (Fig. 8A). Lamotte and Perret (1961) reported the presence of pigmentation on the fins, ventral body parts and absence of chromatophores at the intestinal region, which could be confirmed herein. Likewise the presence of low and nearly parallel fins of similar height (Channing et al. 2012) and large eyes (Lamotte and Perret 1961) is in agreement with our observations (ED/BL = 0.12).

Comparative Morphometrics and Habitat

Morphometric patterns in *Leptopelis* tadpoles were compared to investigate whether species occupy different areas of morpho-space. This was achieved by subjecting $\log_{10}$-transformed body measurements to a rigid rotation (Principal Component Anlaysis; PCA) and by comparing morphometric ratios based on measurements that are contributing most to PC1 and PC2. The first component of the PCA was largely dominated by overall size differences (likely also influenced by differences in Gosner stages), but the second and third components could clearly separate species into distinct morphological clusters (Fig. 9A). PC2 is loaded negatively by AW, ED, and IOD, and positively by ODW, VF, and DF. This means that species clusters with negative PC2 values (*L. calcaratus*, *L. aubryioides*) have wider, more muscular tails, bigger eyes and wider interocular distances, compared to clusters with positive PC2 values (*L. boulengeri*, *L. rufus*, and *L. modestus*), which have wider oral discs and deeper tail fins. *Leptopelis millsoni* and *L. spiritusnoctis* are intermediate for these traits (PC2 values close to 0). *Leptopelis rufus*, *L. modestus*, and *L. boulengeri* show strongly overlapping values for these traits, but *L. boulengeri* is distinct from the other two, by having a narrower internarial distance (similar to *L. calcaratus*), the main loading of PC3. The relevant ratios (AH/DF, AW/BW, OWD/BW, IOD/IND, ED/BL; Fig. 9B–F) reiterate these patterns and in addition, show that *L. rufus*_1 tadpoles have similar body proportions to *L. rufus*_2 and that *L. viridis* is most similar to *L. aubryioides* in morphology, with possibly a wider tail muscle, more similar to *L. calcaratus*.

It should be noted however, that tadpole morphology, especially tail shape, can be plastic in response to extrinsic conditions (Duellman and Trueb 1994; Laurila and Kujasalo 1999; Relyea 2001; Kraft et al. 2006; Wells 2007) and due to limited sampling, morphological variation due to differences in Gosner stage could not be investigated. Nonetheless, the eight tadpoles included in the analyses occur in differing microhabitats that can roughly be grouped into temporary ponds, marshes or slow running to stationary parts of streams (*L. viridis*, *L. spiritusnoctis*, *L. modestus*, and *L. aubryioides*), versus faster flowing running streams (*L. calcaratus*, *L. millsoni*, *L. rufus*, and *L. boulengeri*). Differences in features, such as the hydrodynamics of the tail shape, may thus be experiencing diverging selective pressures across these differing habitats (Altig and McDiarmid 1999b). Greater sampling and more empirical data on microhabitat of these tadpoles is needed however, to thoroughly test whether such morphological differences are indeed correlated to environmental parameters or a result of phenotypic plasticity or development.

Concluding Summary of Morphological Characters

On a continental scale, and taking into account the latest taxonomic decisions (Gvoždík et al. 2014; Portillo and Greenbaum 2014a), tadpoles of only 25 of the 53 recognized *Leptopelis* species have been described. This is astonishing as most species are abundant during the breeding season.

Generally, tadpoles in the genus *Leptopelis* are morphologically conservative and can be unambiguously assigned to that genus directly in the field. They possess either the labial tooth row formula 1/3+3//3 or 1/2+2//3. Only *L. gramineus* has strongly divergent formulae (LTRF: 1/4+4//4, 1/4+4//1+1/2), and the first anterior tooth row may sometimes be interrupted (Channing et al. 2012). Future studies on these tadpoles should consider a potential ontogenetic change as increase of tooth rows has been reported in *L. aubryioides* (this study), *L. calcaratus* (Lamotte and Perret 1961), and *L. viridis* (Rödel 2000).

West and western Central African regions experienced an increase in herpetological surveys and subsequent taxonomic works in the last decades. But despite this positive development and the present descriptions of eight *Leptopelis* tadpoles, detailed accounts of the larval morphology for ten western African congeners are still missing: West Africa: *Leptopelis bufonides*, *L. macrotis*, *L. occidentalis*; western Central Africa: *Leptopelis bocagii*, *L. brevirostris*, *L. bufonides*, *L. christyi*, *L. crystallinoron*, *L. palmatus*, and *L. zebra*.

Among the eight herein described tadpoles, a superficial similarity is conspicuous. However, preliminary analyses not only reveal their morphological distinctness but tentatively indicate morphological adaptations to the respective habitat (lentic or lotic). Two species were underrepresented (*L. millsoni*, *L. modestus*) or even missing completely (*L. viridis*) in the analysis.

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Michael F. Barej is interested in the diversity of African amphibians and reptiles, their biology, biogeographic patterns, as well as resulting puzzles in taxonomy and systematics. He received his Ph.D. from the Humboldt University Berlin (Germany) for unravelling patterns and systematics of African torrent frogs.

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Figure Appendix 1.

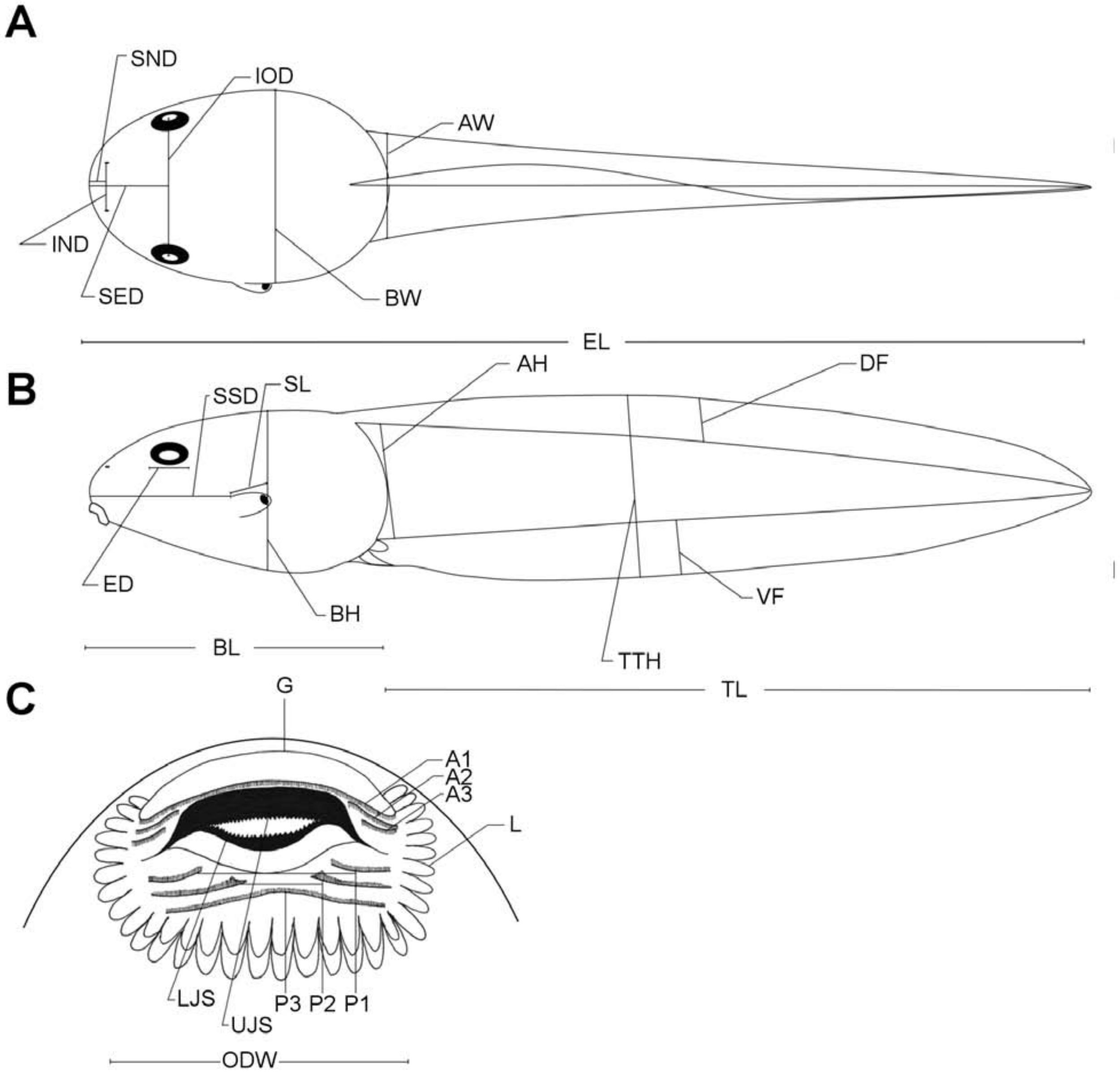

Fig. A1. Schematic tadpole in dorsal (A), lateral (B) view and sketch of the mouth part in ventral view (C) showing assessed distances and mouth parts. Abbreviations: G – dorsal gap; A1–A3 – anterior papillae; L – lateral papillae; P1–P3 – posterior papillae; LJS – lower jaw sheath; UJS – upper jaw sheath; for abbreviations of measurements see material and methods.

Table Appendix 1.

Table A1. Collection numbers (Museum für Naturkunde, Berlin, ZMB; Zoologisches Forschungsmuseum Alexander Koenig, Bonn, ZFMK), localities of *Leptopelis* tadpoles studied herein, and GenBank data analysed in our 16S DNA-barcoding analysis; *n* = number of tadpoles (a single one genotyped, see Appendix Tables A2 and A3).

Species	Collection number	Stage	*n*	Country	Region	Site	Latitude	Longitude	Elevation [m a.s.l.]	GenBank number	Reference
aubryioides	ZFMK 81604	adult	—	Cameroon	foot of Mt. Nlonako	near Ekomtolo	4.8397°N	9.9303°E	470	KT967076	this study
aubryioides	ZMB 79604	tadpole	2	Cameroon	Etome	near Etome	4.8317°N	9.9253°E	476	KT967077	this study
aubryioides	ZMB 79605	tadpole	1	Cameroon	foot of Mt. Nlonako	near Ekomtolo	4.8329°N	9.9259°E	477	KT967078	this study
aubryioides	ZMB 79606	tadpole	9	Cameroon	foot of Mt Nlonako	near Ekomtolo	4.8329°N	9.9259°E	477	—	—
aubryioides	ZMB 79607	tadpole	3	Cameroon	Ebo Forest	Njuma	4.3483°N	10.2329°E	238	KT967079	this study
aubryioides	ZMB 79608	tadpole	1	Cameroon	Ebo Forest	Njuma	4.3483°N	10.2329°E	238	KT967080	this study
aubryioides	ZMB 79609	tadpole	1	Cameroon	Ebo Forest	Njuma	4.3394°N	10.2458°E	320	KT967081	this study
aubryioides	ZMB 79610	tadpole	1	Cameroon	Ebo Forest	Njuma	4.3483°N	10.2329°E	238	KT967082	this study
aubryioides	ZMB 79611	tadpole	1	Cameroon	Ebo Forest	Njuma	4.3483°N	10.2329°E	238	KT967083	this study
aubryioides	ZMB 79612	tadpole	1	Cameroon	Ebo Forest	Camp Njuma	4.3480°N	10.2323°E	315	KT967084	this study
boulengeri	ZFMK 87860	adult	—	Cameroon	—	Amebishu	6.1239°N	9.6875°E	165	KT967085	this study
boulengeri	ZMB 79613	tadpole	1	Cameroon	Ebo Forest	Bekob	4.3578°N	10.4170°E	921	KT967086	this study
boulengeri	ZMB 79614	tadpole	4	Cameroon	Ebo Forest	Bekob	4.3578°N	10.4170°E	921	KT967087	this study
boulengeri	ZMB 79615	tadpole	3	Cameroon	Ebo Forest	Bekob	4.3575°N	10.4168°E	903	KT967088	this study
boulengeri	ZMB 79616	tadpole	1	Cameroon	Ebo Forest	Bekob	4.3578°N	10.4170°E	921	KT967089	this study
boulengeri	ZMB 79617	tadpole	7	Cameroon	Ebo Forest	Bekob	4.3578°N	10.4170°E	921	—	—
calcaratus	ZFMK 75509	adult	—	Cameroon	Mt Nlonako	Nguéngué	4.9172°N	9.9892°E	1140	KT967090	this study
calcaratus	ZMB 79618	tadpole	1	Cameroon	Mt Nlonako	—	4.9250°N	9.9817°E	1035	KT967091	this study
calcaratus	ZMB 79619	tadpole	9	Cameroon	Mt Nlonako	—	4.9250°N	9.9817°E	1035	—	—
calcaratus	ZMB 79620	tadpole	1	Cameroon	Mt Manengouba	Manengouba village	4.9502°N	9.8639°E	1116	KT967092	this study
millsoni	ZFMK 87708	adult	—	Cameroon	—	near Nkoelon	2.3972°N	10.0352°E	75	KF888342	Rödel et al. (2014)
millsoni	ZMB 79621	tadpole	1	Cameroon	Kribi	near Miangasio Lendi	2.8930°N	9.9542°E	31	KT967093	this study
modestus	MCZ A138023	adult	—	Cameroon	Mt. Manengouba	Nsoung	4.9814°N	9.8133°E	1346	JQ715683	Blackburn (2008b)
modestus	ZMB 79622	tadpole	1	Cameroon	Mt Manengouba	near summit	5.0098°N	9.8568°E	2135	KT967094	this study
modestus	ZMB 79623	tadpole	1	Cameroon	Mt Manengouba	near summit	5.0098°N	9.8568°E	2135	—	—
modestus	ZMB 79624	tadpole	1	Cameroon	North West Province	Abo Forest	6.2857°N	10.3580°E	2162	KT967095	this study

Table A1 (continued). Collection numbers (Museum für Naturkunde, Berlin, ZMB; Zoologisches Forschungsmuseum Alexander Koenig, Bonn, ZFMK), localities of *Leptopelis* tadpoles studied herein, and GenBank data analysed in our 16S DNA-barcoding analysis; *n* = number of tadpoles (a single one genotyped, see Appendix Tables A2 and A3).

Species	Collection number	Stage	*n*	Country	Region	Site	Latitude	Longitude	Elevation [m a.s.l.]	GenBank number	Reference
*rufus*_1	ZFMK 87897	adult	—	Cameroon	—	near Nkoelon	2.3972°N	10.0352°E	75	KT967096	this study
*rufus*_1	ZMB 79625	tadpole	3	Cameroon	Camp Bekop	Ebo Forest	4.3519°N	10.4244°E	845	KT967097	this study
*rufus*_2	ZFMK 67382	adult	—	Cameroon	Bakossi Mts.	Kodmin	4.9833°N	9.7000°E	1065	KT967098	this study
*rufus*_2	ZMB 79626	tadpole	2	Cameroon	Mt Nlonako	—	4.8309°N	9.9255°E	459	KT967099	this study
*rufus*_2	ZMB 79627	tadpole	1	Cameroon	Ebo Forest	Njuma	4.3394°N	10.2458°E	320	KT967100	this study
*rufus*_2	ZMB 79628	tadpole	5	Cameroon	Ebo Forest	Ndogbanguengue	4.4069°N	10.1653°E	96	KT967101	this study
*rufus*_2	ZMB 79629	tadpole	7	Cameroon	Mt Manengouba	Ekom Khan	5.0633°N	10.0163°E	587	KT967102	this study
spiritusnoctis	ZMB 79582	adult	—	Liberia	—	near Jarwodee	5.4938°N	8.3636°W	220	KF888336	Rödel et al. (2014)
spiritusnoctis	ZMB 79630	tadpole	5	Liberia	—	near Gbanju	7.2347°N	9.3096°W	398	KT967103	this study
spiritusnoctis	ZMB 79631	tadpole	1	Liberia	—	near Gbanju	7.2347°N	9.3096°W	398	KT967104	this study
spiritusnoctis	ZMB 79632	tadpole	1	Liberia	—	near Gbanju	7.2316°N	9.3118°W	382	KT967105	this study
spiritusnoctis	ZMB 79633	tadpole	8	Liberia	—	near Gbanju	7.2308°N	9.3023°W	387	KT967106	this study
spiritusnoctis	ZMB 79634	tadpole	1	Liberia	—	near Gbanju	7.2308°N	9.3023°W	387	KT967107	this study
spiritusnoctis	ZMB 79635	tadpole	3	Liberia	—	near Gbanju	7.2376°N	9.3117°W	417	KT967108	this study
spiritusnoctis	ZMB 79636	tadpole	1	Liberia	—	near Gbanju	7.2376°N	9.3117°W	417	KT967109	this study
viridis	ZMB 83027	adult	—	Liberia	—	near Gbanju	7.3242°N	9.3035°W	380	KT967110	this study
viridis	ZMB 79637	tadpole	1	Guinea	—	near Banambala	7.9899°N	9.1312°W	449	KT967111	this study
viridis	ZMB 79638	tadpole	1	Guinea	—	near Banambala	7.9899°N	9.1312°W	449	KT967112	this study

Table A2. Morphometrics of *Leptopelis* tadpoles; G = Gosner stage; measurements in mm; genotyped specimens are marked with an asterisk "*," genotyped and drawn specimens are marked with two asterisks "**;" for abbreviations see Materials and Methods.

species	ZMB#	G	BL	TL	EL	BW	BH	AH	VF	DF	TTH	AW	IOD	IND	SND	SED	ED	SSD	ODW	SL
aubryioides	79604*	30	9	-	-	5.3	3.8	2	0.5	-	-	2.2	3.5	1.8	1	2.4	0.9	5	1.3	0.7
aubryioides	79604	36	10.4	-	-	6.5	5.1	2.5	1	1.3	4.3	2.5	3.8	2	1	2.5	1	4.5	1.1	0.9
aubryioides	79605**	25	5.5	-	-	3.2	2.4	1.5	0.4	0.6	1.9	1.3	2.1	1.3	0.7	1.5	0.5	2.2	0.8	0.9
aubryioides	79606	40	10.3	23.8	34.1	6.3	5	2.3	1	1.4	4.2	2.6	3.8	2	1.1	2.6	1	4.6	1.1	0.9
aubryioides	79606	27	7.4	18.7	26.1	4.1	3.4	2	0.6	0.7	2.9	1.8	3.1	1.6	0.8	2.2	1	3.3	1.2	1
aubryioides	79606	25	7.1	16.9	24	4.2	3.3	1.9	0.7	0.8	3	1.9	3	1.5	0.8	2.3	1.1	3.6	1.1	1.2
aubryioides	79606	27	7.9	18.9	26.8	4.6	3.5	2	0.6	0.9	3.1	1.7	2.9	1.6	0.8	2.1	1	3.4	1.1	1
aubryioides	79606	27	7.7	-	-	4.8	3.8	2.1	0.7	1	3.4	1.8	2.8	1.5	0.8	2.2	1.1	3.5	1.2	1.3
aubryioides	79606	28	8.2	19.5	27.7	5	4.1	2	0.8	1.1	3.5	1.9	3	1.5	0.8	2.2	1.1	3.8	1.1	1.5
aubryioides	79606	37	10.4	23.6	34	5.5	4.5	2.4	1	1.3	4.2	2.4	3.9	2	1.1	2.6	1.2	4.7	1.4	1.7
aubryioides	79606	37	10.3	23.8	34.1	5.8	4.6	2.5	1.1	1.4	4.5	2.6	4.1	2.2	1.1	2.5	1.1	4.6	1.5	1.5
aubryioides	79606	37	10.5	24.4	34.9	6.2	4.5	2.7	1	1.4	4.5	2.5	3.9	2	1.1	2.6	1.2	4.7	1.4	1.8
aubryioides	79607*	36	10.7	-	-	6.1	5	2.7	1.1	1.3	3.8	2.6	3.8	2.1	1.4	2.9	1	4.5	1.6	1.7
aubryioides	79607	39	11.6	26.3	37.9	6.6	4.8	2.9	1.2	1.6	5.1	2.9	4.3	2.3	1.2	2.7	1.2	4.9	1.5	1.8
aubryioides	79607	36	10	24.8	34.8	6	4.4	2.6	1.1	1.3	4.5	2.5	4	2.1	1.1	2.5	1.1	4.3	1.4	1.7
aubryioides	79608*	40	10.6	-	-	5.5	4.5	2.4	1	1.3	2.9	2.4	3.9	2	1.1	2.6	1.2	4.7	1.4	1.7
aubryioides	79609*	31	8.8	-	-	5.2	3.2	2.2	0.9	1	2.9	2.3	3.3	1.7	1	2.3	0.8	4.2	1.3	1.1
aubryioides	79610*	36	9.8	-	-	5.5	4.4	2.5	1	1.3	3	2.3	3.8	1.8	1	2.4	1	4.7	1.2	1.2
aubryioides	79611*	41	10	-	-	5.4	3.9	2.3	0.9	1	3	2.3	4.1	1.9	1.2	2.6	1.3	4.4	1.3	0.7
aubryioides	79612*	34	9.4	-	-	5.2	3.9	2.3	0.9	1.1	2.8	2.1	3.3	1.6	0.9	2	0.9	4.1	1.3	1.3
boulengeri	79613*	37	10.9	-	-	5.5	3.5	2.2	1	1.2	4.4	1.8	3.5	1.5	1.1	2.9	0.9	5	1.9	1.5
boulengeri	79614*	37	11.5	-	-	7	5.6	2.9	1.5	1.7	6.1	2.3	4	1.6	1.1	2.8	1	5.5	2.1	1.7
boulengeri	79614	40	12.3	-	-	6.3	5	2.9	2	2.3	7.2	2.2	4.3	1.9	1.5	3.3	1	4.9	2.3	2.2
boulengeri	79614	40	12.2	34.7	46.9	5.9	4.9	2.8	1.8	2	6.6	2.4	4.1	1.9	1.4	3.2	1	5	2.4	2.4
boulengeri	79614	36	11.7	28.9	40.6	5.8	4.7	2.6	1.7	1.9	6.2	2.1	4	1.8	1.3	3.1	1	4.5	2.1	2.1
boulengeri	79615*	36	10.3	-	-	5.7	4.5	2.4	1	1.2	4.6	2	3.5	1.5	1.2	3	1	4.6	2	2
boulengeri	79615	36	9.3	20.9	30.2	5.1	4.3	2.3	1	1.1	4.4	1.7	3	1.3	1	2.4	0.7	4.2	1.8	1.7
boulengeri	79615	36	9.9	23.8	33.7	5.2	4.4	2.2	1.2	1.4	4.8	1.6	3.1	1.4	1	2.3	0.7	4.3	1.9	1.8
boulengeri	79616**	38	11.6	-	-	7.1	5.7	2.8	1.6	1.7	6.1	2.4	4	1.6	1.1	2.8	1	5.1	2.2	2
boulengeri	79617	40	10.8	24.7	35.5	5.7	4.6	2.5	1.3	1.5	5.3	1.9	3.7	1.5	1.2	2.7	0.8	4.4	2.2	2
boulengeri	79617	40	11.5	30.1	41.6	5.9	4.8	2.6	1.5	1.6	5.7	2	3.8	1.7	1.3	3.1	1	4.8	2	2.1
boulengeri	79617	36	10	24.2	34.2	5.3	4.5	2.4	1.5	1.7	5.6	1.8	3.5	1.6	1.2	2.8	0.8	4.7	2.3	2
boulengeri	79617	40	11.7	28.8	40.5	6	4.9	2.7	1.6	1.7	6	1.9	3.8	1.5	1	2.9	1.1	4.3	2.1	2.2
boulengeri	79617	38	10.8	25.8	36.6	5.7	4.5	2.4	1	1.2	4.6	2	3.7	1.5	1.2	3	1	4.6	2	2
boulengeri	79617	40	11.2	27.1	38.3	5.8	4.7	2.8	1.7	1.8	6.3	2.1	3.8	1.6	1.3	3.1	1	4.8	2.1	2.3
boulengeri	79617	40	11.8	30.6	42.4	6.2	4.8	2.5	1.8	1.9	6.2	2	4	1.6	1.2	3	1	4.5	2.1	2.3
calcaratus	79618**	28	8.8	-	-	4.5	3.3	1.8	0.3	-	2.2	1.7	3.2	1.3	0.7	2.3	0.8	4.9	1.4	0.7
calcaratus	79619	27	9.7	18.7	28.4	5.3	4	2.2	0.9	1.2	4.3	2.4	4	1.5	1	2.7	1	4.5	0.9	1.9
calcaratus	79619	29	9.2	22.4	31.6	5.2	4.1	2.3	0.9	1	4.2	2.3	3.8	1.4	0.9	2.6	1	4.3	0.9	2
calcaratus	79619	25	6.5	15.5	22	4	3.2	1.5	0.7	0.8	3	1.6	3	1.2	0.6	2	0.7	2.9	0.7	1.2
calcaratus	79619	40	11.8	26.8	38.6	5.8	4.5	2.5	1	1.1	4.6	3.2	4.6	1.8	1.1	2.7	1.1	4.6	0.9	2.1
calcaratus	79619	40	12	28.2	40.2	6	4.8	2.6	1	1.2	4.8	3.3	4.7	1.9	1.2	2.8	1.2	4.8	1	2.3
calcaratus	79619	40	11.6	26.4	38	5.9	4.7	2.4	1.1	1.2	4.7	3.2	4.6	1.7	1.2	2.9	1.1	4.3	0.9	1.7
calcaratus	79619	25	8	18.7	26.7	4.6	4.2	2	0.8	1	3.8	2.2	3.6	1.4	0.8	2.2	0.9	4.4	0.8	1.5
calcaratus	79619	36	11.4	24.9	36.3	5.6	5	2.6	1.1	1.3	5	3.5	4.5	1.8	1.3	3	1	4.2	0.9	2
calcaratus	79619	38	10.8	24	34.8	5.7	4.5	2.4	1	1.2	4.6	3.1	4.2	1.5	1.2	2.8	1.1	4.1	0.9	1.8
calcaratus	79620*	41	13.2	30.2	43.4	8	6	3.7	1	1.2	5.9	3.9	5.5	2.5	1.3	3.3	1.4	5	2.1	NA
millsoni	79621**	39	9.5	17.3	26.8	5	3.6	2.5	0.8	1	3.8	2.6	3.5	1.5	1	2.3	1.1	4.5	1.8	1
modestus	79622**	34	11.3	-	-	6.5	6	2.5	1.5	1.8	5.8	2.3	4.3	2.2	1.2	2.8	1	6.2	2.5	0.7

Table A2 (continued). Morphometrics of *Leptopelis* tadpoles; G = Gosner stage; measurements in mm; genotyped specimens are marked with an asterisk "*," genotyped and drawn specimens are marked with two asterisks "**;" for abbreviations see Materials and Methods.

species	ZMB#	G	BL	TL	EL	BW	BH	AH	VF	DF	TTH	AW	IOD	IND	SND	SED	ED	SSD	ODW	SL
modestus	79623	31	7.9	16.8	24.7	4.3	3.3	1.4	0.9	1.1	3.4	1.3	2.8	1.5	0.9	2.5	0.6	4.7	1.5	0.5
modestus	79624*	36	14.1	35.2	49.3	8.3	7.5	4	1.5	2	7.5	3.5	5	2.5	1.1	2.8	1.3	6.5	2.4	1
*rufus*_1	79625*	26	6.4	-	-	3.7	2.9	1.7	0.8	0.9	2.9	1.5	2.5	1.4	0.7	2.1	0.6	3.3	1.3	0.8
*rufus*_1	79625	29	7	-	-	3.7	2.3	1.6	0.9	1	2.2	1.2	2.7	1.6	0.8	2	0.7	3.7	1.5	0.9
*rufus*_1	79625	29	7.4	-	-	3.6	2.2	1.7	1	1.1	2.1	1.1	2.6	1.5	0.9	2.1	0.8	3.5	1.4	0.9
*rufus*_2	79626*	29	7.2	-	-	3.7	2.3	1.5	0.3	-	-	1.2	2.8	1.7	0.7	2	0.7	3.7	1.5	0.9
*rufus*_2	79626	28	5.7	-	-	2.7	2	1.2	0.6	0.8	2	1.1	2.1	1.3	0.8	1.8	0.5	3.1	1.1	0.7
*rufus*_2	79627**	36	10.2	-	-	5.6	4	2.4	1.1	1.3	3.9	2.3	3.5	1.5	1	2.6	1	5.3	1.8	1.6
*rufus*_2	79628*	29	8.8	-	-	4.7	3.5	2	0.9	1	3.4	1.9	3	1.8	0.9	2.4	0.8	4.3	1.6	1.2
*rufus*_2	79628	36	8.6	16.4	25	4.9	3.1	1.9	0.9	1.1	3	1.4	2.9	1.6	0.9	2	0.8	3.9	1.6	1
*rufus*_2	79628	32	7.6	15.5	23.1	3.7	2.4	1.9	0.9	1.2	2.4	1.2	2.7	1.6	1	2.1	0.8	3.6	1.4	0.9
*rufus*_2	79628	31	7.1	14.4	21.5	3.7	2.3	1.5	0.7	0.9	2.2	1.2	2.8	1.7	0.7	2	0.7	3.7	1.5	0.9
*rufus*_2	79628	40	8.8	14.7	23.5	4.7	3.5	2	0.9	1	3.5	1.9	3	1.8	0.9	2.4	0.8	4.3	1.6	1.2
*rufus*_2	79629*	36	12.6	-	-	8	5.8	3.3	1.7	2	5.6	3.4	4.5	2.4	1.2	3.3	1.1	6.4	2.5	1.5
*rufus*_2	79629	28	6.7	14.2	20.9	3.7	2.9	1.7	0.8	0.9	2.8	1.5	2.5	1.4	0.7	2.1	0.6	3.3	1.3	0.8
*rufus*_2	79629	29	7.7	15.1	22.8	3.8	2.4	1.8	1	1.2	2.4	1.2	2.7	1.6	1	2.1	0.8	3.6	1.4	0.9
*rufus*_2	79629	29	7.5	15.6	23.1	3.6	2.2	1.8	1	1.1	2.1	1.1	2.6	1.5	0.9	2.1	0.8	3.5	1.4	0.9
*rufus*_2	79629	35	10.2	22.7	32.9	5.6	4	2.4	1.1	1.3	4	2.3	3.5	1.9	1	2.6	1	5.3	1.8	1.6
*rufus*_2	79629	31	8.5	20.5	29	4.8	3	2	0.9	1	2.9	1.5	3	1.6	0.9	2	0.8	3.9	1.6	1
*rufus*_2	79629	34	9.9	22	31.9	5.5	3.9	2.3	1	1.2	3.9	2.2	3.4	1.8	1	2.5	1	5.1	1.8	1.5
spiritusnoctis	79630*	-	9.5	18.8	28.3	4.8	4	-	1	1.3	-	2.5	3.1	1.9	1	2.6	0.8	4.3	1.6	1.2
spiritusnoctis	79630	25	4.4	11.1	15.5	3.4	2.7	1.2	0.4	0.6	2.2	1	1.8	1	0.5	1.3	0.4	2.4	0.8	0.5
spiritusnoctis	79630	29	7.8	19.8	27.6	4.5	3.4	1.9	1	1	3.9	1.6	2.9	1.3	0.8	2.1	0.7	3.9	1.3	1
spiritusnoctis	79630	36	10.7	25.8	36.5	5.5	4.3	3	1	1.6	5.6	3	3.6	2	1	3	1	4.8	1.9	1.5
spiritusnoctis	79630	40	10.5	26.1	36.6	5.4	4.1	2.9	1	1.5	5.4	2.9	3.4	1.9	1	2.9	1	4.6	1.8	1.4
spiritusnoctis	79631*	40	13.3	-	-	7.4	6.3	4	1.4	1.7	7.1	3.8	5	2.7	1.2	2.7	1.4	6.4	2.1	1.5
spiritusnoctis	79632*	31	12.5	26.8	39.3	7.2	5.2	3.7	1.4	1.9	7	4	4	2.4	1.5	3.9	1.2	6.5	2.1	1.5
spiritusnoctis	79633*	25	6.6	-	-	4	3.3	1.7	0.8	1	3.5	1.4	2.3	1.5	0.7	2	0.6	3.6	1.2	0.7
spiritusnoctis	79633	25	5	12.1	17.1	2.8	2.7	1.3	0.5	0.7	2.5	1.1	1.9	1.1	0.5	1.4	0.4	2.6	0.9	0.6
spiritusnoctis	79633	25	4.8	11.6	16.4	3	2.9	1.1	0.5	0.7	2.3	1.1	1.9	1.1	0.5	1.4	0.4	2.6	0.9	0.6
spiritusnoctis	79633	36	8.7	22.8	31.5	4.7	3.6	2.1	1.2	1.2	4.5	1.8	3.1	1.6	1	2.3	0.9	4.2	1.3	1.3
spiritusnoctis	79633	27	7.2	17.7	24.9	4.1	3.5	1.9	0.7	0.8	3.4	1.8	2.4	1.5	0.7	2	0.6	3.2	1.2	0.7
spiritusnoctis	79633	26	5.9	-	-	4	3.3	1.7	0.8	1	3.5	1.4	2.3	1.5	0.7	2	0.6	3.6	1.2	0.7
spiritusnoctis	79633	26	6.2	14.2	20.4	4.1	3.2	1.8	0.8	1	3.6	1.5	2.5	1.4	0.7	2	0.6	3.8	1.3	0.8
spiritusnoctis	79633	30	7.6	17.9	25.5	4.4	3.3	1.9	0.9	1	3.8	1.6	2.8	1.3	0.7	2.1	0.7	3.9	1.3	1
spiritusnoctis	79634**	34	11.5	26.1	37.6	6.3	4.5	3.2	1.1	1.7	6	3.1	3.8	2.2	1.1	3.1	1.1	5.3	2	1.6
spiritusnoctis	79635*	27	6.3	-	-	3.8	3.2	1.5	0.7	0.8	3	1.3	2.2	1.3	0.6	1.7	0.5	2.9	1	0.7
spiritusnoctis	79635	25	5.5	12.2	17.7	3.6	3	1.4	0.6	0.7	2.7	1.2	2	1.2	0.6	1.5	0.5	2.7	1	0.6
spiritusnoctis	79635	25	4.9	10.7	15.6	3.5	2.8	1.3	0.5	0.7	2.5	1.1	1.9	1.1	0.5	1.4	0.4	2.6	0.9	0.6
spiritusnoctis	79636*	25	6.8	17.1	23.9	3.8	3.5	1.9	0.7	0.8	3.4	1.8	2.4	1.5	0.7	2	0.6	3.2	1.2	0.7
viridis	79637*	30	9.8	-	-	5.8	5.3	3.4	-	-	4.1	2.4	3.5	2.1	1	2.7	1.1	5.4	1.4	0.9
viridis	79638**	40	13.5	-	-	7.7	6.1	3.5	1	1.6	6	4.4	5.2	2.4	1.1	3.3	1.7	7	1.8	1.4

Table A3. Ratios of *Leptopelis* tadpoles; G = Gosner stage; measurements in mm; genotyped specimens are marked with an asterisk "*;" genotyped and drawn specimens are marked with two asterisks "**;" for abbreviations see Materials and Methods.

Species	ZMB#	BL/ TL	BH/ BL	BW/ BL	SND/ SED	ED/ BL	IOD/ IND	TL/ EL	DF/ VF	AH/ DF	TTH/ BH	AW/ BW	AH/ BH	SL/ BL	ODW/ BW	SSD/ BL
aubryioides	79604*	-	0.42	0.59	0.42	0.10	1.94	-	-	-	-	0.42	0.53	0.08	0.25	0.56
aubryioides	79604	-	0.49	0.63	0.40	0.10	1.90	-	1.30	1.92	0.84	0.38	0.49	0.09	0.17	0.43
aubryioides	79605**	-	0.44	0.58	0.47	0.09	1.62	-	1.50	2.50	0.79	0.41	0.63	0.16	0.25	0.40
aubryioides	79606	0.43	0.49	0.61	0.42	0.10	1.90	0.70	1.40	1.64	0.84	0.41	0.46	0.09	0.17	0.45
aubryioides	79606	0.40	0.46	0.55	0.36	0.14	1.94	0.72	1.17	2.86	0.85	0.44	0.59	0.14	0.29	0.45
aubryioides	79606	0.42	0.46	0.59	0.35	0.15	2.00	0.70	1.14	2.38	0.91	0.45	0.58	0.17	0.26	0.51
aubryioides	79606	0.42	0.44	0.58	0.38	0.13	1.81	0.71	1.50	2.22	0.89	0.37	0.57	0.13	0.24	0.43
aubryioides	79606	-	0.49	0.62	0.36	0.14	1.87	-	1.43	2.10	0.89	0.38	0.55	0.17	0.25	0.45
aubryioides	79606	0.42	0.50	0.61	0.36	0.13	2.00	0.70	1.38	1.82	0.85	0.38	0.49	0.18	0.22	0.46
aubryioides	79606	0.44	0.43	0.53	0.42	0.12	1.95	0.69	1.30	1.85	0.93	0.44	0.53	0.16	0.25	0.45
aubryioides	79606	0.43	0.45	0.56	0.44	0.11	1.86	0.70	1.27	1.79	0.98	0.45	0.54	0.15	0.26	0.45
aubryioides	79606	0.43	0.43	0.59	0.42	0.11	1.95	0.70	1.40	1.93	1.00	0.40	0.60	0.17	0.23	0.45
aubryioides	79607*	-	0.47	0.57	0.48	0.09	1.81	-	1.18	2.08	0.76	0.43	0.54	0.16	0.26	0.42
aubryioides	79607	0.44	0.41	0.57	0.44	0.10	1.87	0.69	1.33	1.81	1.06	0.44	0.60	0.16	0.23	0.42
aubryioides	79607	0.40	0.44	0.60	0.44	0.11	1.90	0.71	1.18	2.00	1.02	0.42	0.59	0.17	0.23	0.43
aubryioides	79608*	-	0.42	0.52	0.42	0.11	1.95	-	1.30	1.85	0.64	0.44	0.53	0.16	0.25	0.44
aubryioides	79609*	-	0.36	0.59	0.43	0.09	1.94	-	1.11	2.20	0.91	0.44	0.69	0.13	0.25	0.48
aubryioides	79610*	-	0.45	0.56	0.42	0.10	2.11	-	1.30	1.92	0.68	0.42	0.57	0.12	0.22	0.48
aubryioides	79611*	-	0.39	0.54	0.46	0.13	2.16	-	1.11	2.30	0.77	0.43	0.59	0.07	0.24	0.44
aubryioides	79612*	-	0.41	0.55	0.45	0.10	2.06	-	1.22	2.09	0.72	0.40	0.59	0.14	0.25	0.44
boulengeri	79613*	-	0.32	0.50	0.38	0.08	2.33	-	1.20	1.83	1.26	0.33	0.63	0.14	0.35	0.46
boulengeri	79614*	-	0.49	0.61	0.39	0.09	2.50	-	1.13	1.71	1.09	0.33	0.52	0.15	0.30	0.48
boulengeri	79614	-	0.41	0.51	0.45	0.08	2.26	-	1.15	1.26	1.44	0.35	0.58	0.18	0.37	0.40
boulengeri	79614	0.35	0.40	0.48	0.44	0.08	2.16	0.74	1.11	1.40	1.35	0.41	0.57	0.20	0.41	0.41
boulengeri	79614	0.40	0.40	0.50	0.42	0.09	2.22	0.71	1.12	1.37	1.32	0.36	0.55	0.18	0.36	0.38
boulengeri	79615*	-	0.44	0.55	0.40	0.10	2.33	-	1.20	2.00	1.02	0.35	0.53	0.19	0.35	0.45
boulengeri	79615	0.44	0.46	0.55	0.42	0.08	2.31	0.69	1.10	2.09	1.02	0.33	0.53	0.18	0.35	0.45
boulengeri	79615	0.42	0.44	0.53	0.43	0.07	2.21	0.71	1.17	1.57	1.09	0.31	0.50	0.18	0.37	0.43
boulengeri	79616**	-	0.49	0.61	0.39	0.09	2.50	-	1.06	1.65	1.07	0.34	0.49	0.17	0.31	0.44
boulengeri	79617	0.44	0.43	0.53	0.44	0.07	2.47	0.70	1.15	1.67	1.15	0.33	0.54	0.19	0.39	0.41
boulengeri	79617	0.38	0.42	0.51	0.42	0.09	2.24	0.72	1.07	1.63	1.19	0.34	0.54	0.18	0.34	0.42
boulengeri	79617	0.41	0.45	0.53	0.43	0.08	2.19	0.71	1.13	1.41	1.24	0.34	0.53	0.20	0.43	0.47
boulengeri	79617	0.41	0.42	0.51	0.34	0.09	2.53	0.71	1.06	1.59	1.22	0.32	0.55	0.19	0.35	0.37
boulengeri	79617	0.42	0.42	0.53	0.40	0.09	2.47	0.70	1.20	2.00	1.02	0.35	0.53	0.19	0.35	0.43
boulengeri	79617	0.41	0.42	0.52	0.42	0.09	2.38	0.71	1.06	1.56	1.34	0.36	0.60	0.21	0.36	0.43
boulengeri	79617	0.39	0.41	0.53	0.40	0.08	2.50	0.72	1.06	1.32	1.29	0.32	0.52	0.19	0.34	0.38
calcaratus	79618**	-	0.38	0.51	0.30	0.09	2.46	-	-	-	0.67	0.38	0.55	0.08	0.31	0.56
calcaratus	79619	0.52	0.41	0.55	0.37	0.10	2.67	0.66	1.33	1.83	1.08	0.45	0.55	0.20	0.17	0.46
calcaratus	79619	0.41	0.45	0.57	0.35	0.11	2.71	0.71	1.11	2.30	1.02	0.44	0.56	0.22	0.17	0.47
calcaratus	79619	0.42	0.49	0.62	0.30	0.11	2.50	1.29	1.14	1.88	0.94	0.40	0.47	0.18	0.18	0.45
calcaratus	79619	0.44	0.38	0.49	0.41	0.09	2.56	0.69	1.10	2.27	1.02	0.55	0.56	0.18	0.16	0.39
calcaratus	79619	0.43	0.40	0.50	0.43	0.10	2.47	0.70	1.20	2.17	1.00	0.55	0.54	0.19	0.17	0.40
calcaratus	79619	0.44	0.41	0.51	0.41	0.09	2.71	0.69	1.09	2.00	1.00	0.54	0.51	0.15	0.15	0.37
calcaratus	79619	0.43	0.53	0.58	0.36	0.11	2.57	0.70	1.25	2.00	0.90	0.48	0.48	0.19	0.17	0.55
calcaratus	79619	0.46	0.44	0.49	0.43	0.09	2.50	0.69	1.18	2.00	1.00	0.63	0.52	0.18	0.16	0.37
calcaratus	79619	0.45	0.42	0.53	0.43	0.10	2.80	0.69	1.20	2.00	1.02	0.54	0.53	0.17	0.16	0.38
calcaratus	79620*	0.44	0.45	0.61	0.39	0.11	2.20	0.70	1.20	3.08	0.98	0.49	0.62	-	0.26	0.38
millsoni	79621**	0.55	0.38	0.53	0.43	0.12	2.33	0.65	1.25	2.50	1.06	0.52	0.69	0.11	0.36	0.47
modestus	79622**	-	0.53	0.58	0.43	0.09	1.95	-	1.20	1.39	0.97	0.35	0.42	0.06	0.38	0.55

Table A3 (continued). Ratios of *Leptopelis* tadpoles; G = Gosner stage; measurements in mm; genotyped specimens are marked with an asterisk "*;" genotyped and drawn specimens are marked with two asterisks "**;" for abbreviations see Materials and Methods.

Species	**ZMB#**	**BL/ TL**	**BH/ BL**	**BW/ BL**	**SND/ SED**	**ED/ BL**	**IOD/ IND**	**TL/ EL**	**DF/ VF**	**AH/ DF**	**TTH/ BH**	**AW/ BW**	**AH/ BH**	**SL/ BL**	**ODW/ BW**	**SSD/ BL**
modestus	79623	0.47	0.42	0.54	0.36	0.08	1.87	0.68	1.22	1.27	1.03	0.30	0.42	0.06	0.35	0.59
modestus	79624*	0.40	0.53	0.59	0.39	0.09	2.00	0.71	1.33	2.00	1.00	0.42	0.53	0.07	0.29	0.46
rufus_1	79625*	-	0.45	0.58	0.33	0.09	1.79	-	1.13	1.89	1.00	0.41	0.59	0.13	0.35	0.52
rufus_1	79625	-	0.33	0.53	0.40	0.10	1.69	-	1.11	1.60	0.96	0.32	0.70	0.13	0.41	0.53
rufus_1	79625	-	0.30	0.49	0.43	0.11	1.73	-	1.10	1.55	0.95	0.31	0.77	0.12	0.39	0.47
rufus_2	79626*	-	0.32	0.51	0.35	0.10	1.65	-	-	-	-	0.32	0.65	0.13	0.41	0.51
rufus_2	79626	-	0.35	0.47	0.44	0.09	1.62	-	1.33	1.50	1.00	0.41	0.60	0.12	0.41	0.54
rufus_2	79627**	-	0.39	0.55	0.38	0.10	2.33	-	1.18	1.85	0.98	0.41	0.60	0.16	0.32	0.52
rufus_2	79628*	-	0.40	0.53	0.38	0.09	1.67	-	1.11	2.00	0.97	0.40	0.57	0.14	0.34	0.49
rufus_2	79628	0.52	0.36	0.57	0.45	0.09	1.81	0.66	1.22	1.73	0.97	0.29	0.61	0.12	0.33	0.45
rufus_2	79628	0.49	0.32	0.49	0.48	0.11	1.69	0.67	1.33	1.58	1.00	0.32	0.79	0.12	0.38	0.47
rufus_2	79628	0.49	0.32	0.52	0.35	0.10	1.65	0.67	1.29	1.67	0.96	0.32	0.65	0.13	0.41	0.52
rufus_2	79628	0.60	0.40	0.53	0.38	0.09	1.67	0.63	1.11	2.00	1.00	0.40	0.57	0.14	0.34	0.49
rufus_2	79629*	-	0.46	0.63	0.36	0.09	1.88	-	1.18	1.65	0.97	0.43	0.57	0.12	0.31	0.51
rufus_2	79629	0.47	0.43	0.55	0.33	0.09	1.79	0.68	1.13	1.89	0.97	0.41	0.59	0.12	0.35	0.49
rufus_2	79629	0.51	0.31	0.49	0.48	0.10	1.69	0.66	1.20	1.50	1.00	0.32	0.75	0.12	0.37	0.47
rufus_2	79629	0.48	0.29	0.48	0.43	0.11	1.73	0.68	1.10	1.64	0.95	0.31	0.82	0.12	0.39	0.47
rufus_2	79629	0.45	0.39	0.55	0.38	0.10	1.84	0.69	1.18	1.85	1.00	0.41	0.60	0.16	0.32	0.52
rufus_2	79629	0.41	0.35	0.56	0.45	0.09	1.88	0.71	1.11	2.00	0.97	0.31	0.67	0.12	0.33	0.46
rufus_2	79629	0.45	0.39	0.56	0.40	0.10	1.89	0.69	1.20	1.92	1.00	0.40	0.59	0.15	0.33	0.52
spiritusnoctis	79630*	0.51	0.42	0.51	0.38	0.08	1.63	0.66	1.30	-	-	0.52	-	0.13	0.33	0.45
spiritusnoctis	79630	0.40	0.61	0.77	0.38	0.09	1.80	0.72	1.50	2.00	0.81	0.29	0.44	0.11	0.24	0.55
spiritusnoctis	79630	0.39	0.44	0.58	0.38	0.09	2.23	0.72	1.00	1.90	1.15	0.36	0.56	0.13	0.29	0.50
spiritusnoctis	79630	0.41	0.40	0.51	0.33	0.09	1.80	0.71	1.60	1.88	1.30	0.55	0.70	0.14	0.35	0.45
spiritusnoctis	79630	0.40	0.39	0.51	0.34	0.10	1.79	0.71	1.50	1.93	1.32	0.54	0.71	0.13	0.33	0.44
spiritusnoctis	79631*	-	0.47	0.56	0.44	0.11	1.85	-	1.21	2.35	1.13	0.51	0.63	0.11	0.28	0.48
spiritusnoctis	79632*	0.47	0.42	0.58	0.38	0.10	1.67	0.68	1.36	1.95	1.35	0.56	0.71	0.12	0.29	0.52
spiritusnoctis	79633*	-	0.50	0.61	0.35	0.09	1.53	-	1.25	1.70	1.06	0.35	0.52	0.11	0.30	0.55
spiritusnoctis	79633	0.41	0.54	0.56	0.36	0.08	1.73	0.71	1.40	1.86	0.93	0.39	0.48	0.12	0.32	0.52
spiritusnoctis	79633	0.41	0.60	0.63	0.36	0.08	1.73	0.71	1.40	1.57	0.79	0.37	0.38	0.13	0.30	0.54
spiritusnoctis	79633	0.38	0.41	0.54	0.43	0.10	1.94	0.72	1.00	1.75	1.25	0.38	0.58	0.15	0.28	0.48
spiritusnoctis	79633	0.41	0.49	0.57	0.35	0.08	1.60	0.71	1.14	2.38	0.97	0.44	0.54	0.10	0.29	0.44
spiritusnoctis	79633	-	0.56	0.68	0.35	0.10	1.53	-	1.25	1.70	1.06	0.35	0.52	0.12	0.30	0.61
spiritusnoctis	79633	0.44	0.52	0.66	0.35	0.10	1.79	0.70	1.25	1.80	1.13	0.37	0.56	0.13	0.32	0.61
spiritusnoctis	79633	0.42	0.43	0.58	0.33	0.09	2.15	0.70	1.11	1.90	1.15	0.36	0.58	0.13	0.30	0.51
spiritusnoctis	79634**	0.44	0.39	0.55	0.35	0.10	1.73	0.69	1.55	1.88	1.33	0.49	0.71	0.14	0.32	0.46
spiritusnoctis	79635*	-	0.51	0.60	0.35	0.08	1.69	-	1.14	1.88	0.94	0.34	0.47	0.11	0.26	0.46
spiritusnoctis	79635	0.45	0.55	0.65	0.40	0.09	1.67	0.69	1.17	2.00	0.90	0.33	0.47	0.11	0.28	0.49
spiritusnoctis	79635	0.46	0.57	0.71	0.36	0.08	1.73	0.69	1.40	1.86	0.89	0.31	0.46	0.12	0.26	0.53
spiritusnoctis	79636*	0.40	0.51	0.56	0.35	0.09	1.60	0.72	1.14	2.38	0.97	0.47	0.54	0.10	0.32	0.47
viridis	79637*	-	0.54	0.59	0.37	0.11	1.67	-	-	-	0.77	0.41	0.64	0.09	0.24	0.55
viridis	79638**	-	0.45	0.57	0.33	0.13	2.17	-	1.60	2.19	0.98	0.57	0.57	0.10	0.23	0.52

Table A4. Ratios of morphometrics in *Leptopelis* tadpoles. Given are mean values and range [minimum – maximum] of ratio values; *n*(max) = number of vouchers; genotyped specimens were inapplicable in some ratios, e.g., BL/TL, for details see Appendices A2 and A4. Ratios for *L. rufus* are provided for both lineages independently and combined vouchers (*rufus*_1 & *rufus*_2); for abbreviations see Materials and Methods.

species	*n*(max)	BL/TL	BH/BL	BW/BL	SND/SED	ED/BL	IOD/IND	TL/EL	DF/VF	AH/DF	TTH/BH	AW/BW	AH/BH	SL/BL	ODW/BW	SSD/BL
aubryioides	20	0.42 [0.40-0.44]	0.44 [0.36-0.50]	0.58 [0.52-0.63]	0.42 [0.35-0.48]	0.11 [0.09-0.15]	1.93 [1.62-2.16]	0.70 [0.69-0.72]	1.29 [1.11-1.50]	2.07 [1.64-2.86]	0.86 [0.64-1.06]	0.42 [0.37-0.45]	0.56 [0.46-0.69]	0.14 [0.07-0.18]	0.24 [0.17-0.29]	0.45 [0.40-0.56]
boulengeri	16	0.41 [0.35-0.44]	0.43 [0.32-0.49]	0.53 [0.48-0.61]	0.41 [0.34-0.45]	0.08 [0.07-0.10]	2.35 [2.16-2.53]	0.71 [0.69-0.74]	1.12 [1.06-1.20]	1.63 [1.26-2.09]	1.20 [1.02-1.44]	0.34 [0.31-0.41]	0.55 [0.49-0.63]	0.18 [0.14-0.21]	0.36 [0.30-0.43]	0.43 [0.37-0.48]
calcaratus	11	0.44 [0.41-0.52]	0.43 [0.38-0.53]	0.54 [0.49-0.62]	0.38 [0.30-0.43]	0.10 [0.09-0.11]	2.56 [2.20-2.80]	0.75 [0.66-1.29]	1.18 [1.09-1.33]	2.15 [1.83-3.08]	0.97 [0.67-1.08]	0.50 [0.38-0.63]	0.53 [0.47-0.62]	0.17 [0.08-0.22]	0.19 [0.15-0.31]	0.43 [0.37-0.56]
millsoni	1	0.55	0.38	0.53	0.43	0.12	2.33	0.65	1.25	2.50	1.06	0.52	0.69	0.11	0.36	0.47
modestus	3	0.44 [0.40-0.47]	0.49 [0.42-0.53]	0.57 [0.54-0.59]	0.39 [0.36-0.43]	0.09 [0.08-0.09]	1.94 [1.87-2.00]	0.70 [0.68-0.71]	1.25 [1.20-1.33]	1.55 [1.27-2.00]	1.00 [0.97-1.03]	0.36 [0.30-0.42]	0.46 [0.42-0.53]	0.07 [0.06-0.07]	0.34 [0.29-0.38]	0.53 [0.46-0.59]
*rufus*_1	3	—	0.36 [0.30-0.45]	0.53 [0.49-0.48]	0.39 [0.33-0.43]	0.10 [0.09-0.11]	1.74 [1.69-1.79]	—	1.11 [1.10-1.13]	1.68 [1.55-1.89]	0.97 [0.95-1.00]	0.35 [0.31-0.41]	0.68 [0.59-0.77]	0.13 [0.12-0.13]	0.38 [0.35-0.41]	0.51 [0.47-0.53]
*rufus*_2	15	0.49 [0.41-0.60]	0.37 [0.29-0.46]	0.53 [0.47-0.63]	0.40 [0.33-0.48]	0.10 [0.09-0.11]	1.78 [1.62-2.33]	0.67 [0.63-0.71]	1.19 [1.10-1.33]	1.77 [1.50-2.00]	0.98 [0.95-1.00]	0.36 [0.29-0.43]	0.64 [0.57-0.82]	0.13 [0.12-0.16]	0.36 [0.31-0.41]	0.50 [0.45-0.54]
*rufus*_1&2	18	0.49 [0.41-0.60]	0.37 [0.29-0.46]	0.53 [0.47-0.63]	0.40 [0.33-0.48]	0.10 [0.09-0.11]	1.78 [1.62-2.33]	0.67 [0.63-0.71]	1.18 [1.10-1.33]	1.75 [1.50-2.00]	0.98 [0.95-1.00]	0.36 [0.29-0.43]	0.65 [0.57-0.82]	0.13 [0.12-0.16]	0.36 [0.31-0.41]	0.50 [0.45-0.54]
spiritusnoctis	20	0.43 [0.38-0.51]	0.49 [0.39-0.61]	0.60 [0.51-0.77]	0.37 [0.33-0.44]	0.09 [0.08-0.11]	1.76 [1.53-2.23]	0.70 [0.66-0.72]	1.28 [1.00-1.60]	1.93 [1.57-2.38]	1.08 [0.79-1.35]	0.41 [0.29-0.56]	0.56 [0.38-0.71]	0.12 [0.10-0.15]	0.30 [0.24-0.35]	0.50 [0.44-0.61]
viridis	2	—	0.50 [0.45-0.54]	0.58 [0.57-0.59]	0.35 [0.33-0.37]	0.12 [0.11-0.13]	1.92 [1.67-2.17]	—	1.60	2.19	0.88 [0.77-0.98]	0.49 [0.41-0.57]	0.61 [0.57-0.64]	0.10 [0.09-0.10]	0.24 [0.23-0.24]	0.53 [0.52-0.55]

Ecnomiohyla rabborum. Rabb's Fringe-limbed Treefrog is one of the most significantly threatened amphibians in Central America. This species is one of the most unusual anurans in the region because of its highly specialized reproductive mode, in which the eggs are laid in water-containing tree cavities and are attached to the interior of the cavity just above the water line. Females depart the tree cavity after oviposition, leaving the males to brood the eggs and the developing tadpoles, and parental care apparently extends to feeding the tadpoles flecks of skin from the male's body (AmphibiaWeb site: accessed 24 July 2014). Mendelson et al. (2008) described this tree canopy treefrog from "montane cloudforest in the immediate vicinity of the town of El Valle de Antón" (AmphibiaWeb site: accessed 24 July 2014) in central Panama, at elevations from 900 to 1,150 m. This mode of reproduction is typical of the members of the genus *Ecnomiohyla*, which now comprises 14 species (Batista et al. 2014) with a collective distribution extending from southern Mexico to northwestern South America (Colombia and Ecuador). This treefrog appears to be one of the many casualties of a sweep-through of Panama by the fungal pathogen *Batrachochytrium dendrobatidis* in 2006. The arrival of this pathogen was anticipated by a team of amphibian biologists, who observed the disastrous effects of *B. dendrobatidis* on the populations of anurans in the El Valle de Antón region. Individuals of *E. rabbororum* were taken into captivity and housed at Zoo Atlanta, but only a single male remains alive. We determined its EVS as 20, placing it at the upper end of the high vulnerability category, and its IUCN status is Critically Endangered. Since the species is known to survive only in captivity, its IUCN status should be considered as Extinct in the Wild. Additionally, since the animal now is known from a single male, its IUCN status should change to Extinct once it dies. This individual is from the type locality. *Photo by Brad Wilson.*

Bothriechis guifarroi. This green palm-pitviper is known only from the type locality in the Refugio de Vida Silvestre Texíguat in north-central Honduras, where it occurs in Premontane Wet Forest at elevations of 1,015 to 1,450 m. We calculated its EVS as 19, placing it in the upper portion of the high vulnerability category, but its IUCN status has not been determined. Its EVS is the highest for any snake in Central America. Molecular analysis of this species indicates that it is part of a clade containing the Lower Central American taxa *B. lateralis* and *B. nigroviridis*. Two pattern phases are seen in juveniles, of which one resembles the juveniles of its apparent closest relative, *B. lateralis*, which is distributed in the chain of mountains in the central portions of Costa Rica and western Panama. This snake was named in honor of the Honduran environmental leader Mario Guifarro, who was slain by unknown assailants while heading grassroots attempts to stop illegal logging in the indigenous Tawahka territory in the Mosquitia of eastern Honduras. Don Mario was the guide on several herpetological expeditions undertaken in the Mosquitia by Wilson and co-researchers during the last decade. This individual is from the type locality. *Photo by Josiah H. Townsend.*

DEDICATION

We are pleased to dedicate this contribution to our friend and colleague Louis W. Porras, for the many ways he has supported our efforts to conserve the rich herpetodiversity of Mesoamerica. As editor, publisher, and contributor to *Conservation of Mesoamerican Amphibians and Reptiles* (2010), he remained solidly behind this multi-year project. In addition, his amazing skills as a copy-editor and knowledge of graphic design were extremely important in the production of the *Amphibian & Reptile Conservation* Special Mexico Issue, published in 2013. Most recently, he has become the force behind the journal *Mesoamerican Herpetology* in which a number of our contributions have appeared. In general, we continually find it worthwhile to seek his counsel on a broad range of matters relating to herpetology and conservation. Most importantly, however, we consider it an honor to call him friend.

Porthidium porrasi. The White-tailed Hognosed Pitviper is endemic to the region of the Osa Peninsula of southwestern Costa Rica, where it occurs in Lowland Moist Forest at elevations from near sea level to 200 m. We assessed its EVS as 18, placing it in the upper portion of the high vulnerability category, and its IUCN status is Least Concern. This individual is from Rincón, province of Puntarenas. *Photo by Alejandro Solórzano.*

Louis W. Porras photographed on 19 April 2014 with a pair of Mormon Racers (*Coluber mormon*) in the Lake Shore Mountains in Utah County, Utah. Louis said the following: “I’ve been monitoring a den in these mountains for about 25 years. In the spring I often hike up there with my grandson and other family members. This was an unusually productive day, because we found 25 snakes of four species.” *Photo by Robbie Eagleston.*

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A conservation reassessment of the Central American herpetofauna based on the EVS measure

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***Abstract.*—Mesoamerica, the area composed of Mexico and Central America, is the third largest of the world's biodiversity hotspots. The Central American herpetofauna currently consists of 493 species of amphibians and 559 species of crocodylians, squamates, and turtles. In this paper, we use a revised EVS measure to reexamine the conservation status of the native herpetofauna of this region, utilize the General Lineage Concept of Species to recognize species-level taxa, and employ phylogenetic concepts to determine evolutionary relationships among the taxa. Since the publication of *Conservation of Mesoamerican Amphibians and Reptiles*, in 2010, 92 species of amphibians and squamates have been described, resurrected, or elevated from subspecies to species level, and one species of anuran has been synonymized. The herpetofaunal diversity of Central America is comparable to that of Mexico, an especially significant finding because the land area of Mexico is 3.75 times larger. The number of amphibian species is 1.3 times greater in Central America, whereas the number of species of turtles, crocodylians, and squamates is 1.5 times greater in Mexico. Endemicity also is significant in Central America (65.6% among amphibians, 46.5% among turtles, crocodylians, and squamates), with a combined average of 55.6%. We regard the IUCN system as expensive, time-consuming, tending to fall behind systematic advances, and over-dependent on the Data Deficient and Least Concern categories. Conversely, the EVS measure is economical, can be applied when species are described, is predictive, simple to calculate, and does not "penalize" poorly known species. Our EVS analysis of amphibians demonstrates that on average salamanders are more susceptible to environmental deterioration, followed by caecilians, and anurans. Among the remainder of the herpetofauna, crocodylians are the most susceptible and snakes the least, with turtles and lizards in between. We compared the EVS results for the Central American herpetofauna with those reported for Mexico; the results from those regions show an increase in numbers and percentages from low through medium to high. Arguably, attempting to conserve biodiversity is one of the most important and intransigent issues facing humanity, a situation partially due to humanity's lack of appreciation for its most serious concerns, and brought about by its anthropocentric focus.**

Key words. EVS, anurans, salamanders, caecilians, crocodylians, turtles, lizards, snakes, IUCN categorizations, survival prospects

***Resumen.*—Mesoamérica, el área comprendida por México y Centroamérica, es el centro de biodiversidad más grande del planeta. La herpetofauna de Centroamérica actualmente consiste de 493 especies de anfibios y 559 especies de crocodílidos, esquamados, y tortugas. En este artículo, usamos la medida de EVS revisada para reexaminar el estado de conservación de la herpetofauna nativa de esta región, usamos el Concepto del Linaje General de Especie para reconocer taxones al nivel de especie, y empleamos conceptos filogenéticos para determinar relaciones evolutivas entre taxones. Desde la publicación del libro *Conservation of Mesoamerican Amphibians and Reptiles*, en 2010, 92 especies de anfibios y esquamados han sido descritas, resucitadas, o elevadas de subespecie al nivel de especie y una especie de anuro ha sido sinonimizada. La diversidad herpetofaunística en Centroamérica es comparable a la de México, un resultado especialmente significativo dado que la superficie de México es 3.75 veces más grande. El número de especies de anfibios es 1.3 veces mayor en Centroamérica, mientras que el número de especies de tortugas, cocodrílidos y esquamados es 1.5 veces mayor en México. El endemismo es también significativo en Centroamérica (65.6% entre anfibios, 46.5% entre tortugas, cocodrílidos y esquamados), con un**

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promedio combinado de 55.6%. Consideramos el sistema de UICN como costoso, consume mucho tiempo, con una tendencia a quedarse rebasado por los avances sistemáticos, y sobre dependiente de las categorías de Datos Deficientes y de Preocupación Menor. Inversamente, la medida de EVS es económica, puede ser aplicada cuando una especie es descrita, es predictiva, es fácil de calcular y no “penaliza” especies por ser pobremente conocidas. Nuestro análisis del EVS en anfibios demuestra que en promedio las salamandras son las más susceptibles al deterioro ambiental, seguidas por las cecilias y los anuros. Entre el resto de la herpetofauna, los cocodrílidos son los más susceptibles y las serpientes las menos susceptibles, con las tortugas y las lagartijas en medio. Comparamos los resultados del EVS de la herpetofauna de Centroamérica con la herpetofauna de México; los resultados para ambas regiones muestran un incremento en los números y porcentajes de baja a mediana, a alta vulnerabilidad. Posiblemente, intentar conservar la biodiversidad es uno de los problemas más importantes y arduos que enfrenta la humanidad, una situación parcialmente debida a la falta de apreciación de las preocupaciones más serias por parte de la humanidad, y exacerbada por su enfoque antropocéntrico.

Palabras claves. EVS, anuros, salamandras, cecilias, cocodrílidos, tortugas, lagartijas, culebras, categorías de UICN, perspectivas de supervivencia

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> *Currently, the global extinction rate far exceeds the rate of speciation, and consequently, loss of species is the primary driver of changes in global biodiversity…Since the advent of the Anthropocene, humans have increased the rate of species extinction by 100–1,000 times the background rates that were typical over Earth’s history … Until recently, most extinctions (since 1500) occurred on oceanic islands. In the last 20 years, however, about half of the recorded extinctions have occurred on continents, primarily due to land-use change, species introductions, and increasingly climate change, indicating that biodiversity is now broadly at risk throughout the planet.*
>
> Rockström et al. 2009: 14

Introduction

The most significant problem facing humanity is biodiversity decline. Our attempts to estimate the total number of species and our knowledge and appreciation of environmental relationships within and among the large planetary spheres are woefully inadequate. Strangely enough, given the immense diversity of life on our planet and the endless intellectual fulfillment its study can foster, humans have become increasingly focused on their own activities and become increasingly removed from the rest of the living world. In spite of this loss of perspective, we are beginning to learn that our existence as a species depends on our understanding of how life on this planet operates, and the role we play in this process.

In a Special Mexico Issue of the journal *Amphibian & Reptile Conservation*, we conducted a conservation reassessment of the reptiles (Wilson et al. 2013a) and amphibians (Wilson et al. 2013b) of Mexico based on the use of the Environmental Vulnerability Score (EVS). These works allowed us to examine the results obtained by the International Union for Conservation of Nature (IUCN) and published in the Red List website (www.iucnredlist.org), and compare them to our EVS results. In total, we assayed 1,227 species (378 amphibians, 849 reptiles) of the Mexican herpetofauna. Our conclusions from those studies were that, “both groups are highly imperiled, especially the salamanders, lizards, and turtles” (Wilson et al. 2013b: 98). Because the term “reptile” has been demonstrated increasingly to have a paraphyletic standing in phylogenetic systematics (www.iflscience.com/plants-and-animals/there-s-no-such-thing-reptiles-any-more-and-here-s-why), instead we use the names “crocodylians, squamates, and turtles” when referring to these groups.

The purpose of this paper is to reexamine the conservation status of the herpetofauna of Central America, updating and broadening the treatments that appeared in *Conservation of Mesoamerican Amphibians and Reptiles* (CMAR; Wilson et al. 2010). A substantial amount of systematic work has been published since the cutoff point of 31 December 2008 used by Wilson and Johnson (2010); our cutoff date for the present paper was 1 March 2015. In the interim, 92 species-level taxa have been described, resurrected, or elevated, and one species was synonymized. In addition, 30 species have undergone status changes (usually placement in another genus). In this study, therefore, we treat 1,052 species (493 amphibians; 559 crocodylians, squamates and turtles) and use a revised EVS designed to encompass all of Central America.

Our Taxonomic Positions

Transitions in systematics. — For herpetologists working in Mesoamerica, these are interesting times. We live in a period of transition, from conditions characterizing the past to those we envision will come in the future. The element of transition is evident in much of what we present in this paper and in our taxonomic positions, which we deliberate below.

In trying to understand the biological aspects of the Mesoamerican herpetofauna, we must be interested in systematics, the study of the pattern of relationships among living taxa (www.ucmp.berkeley.edu/clad/clad4.html). Most systematists today practice phylogenetic systematics, defined as "the way that biologists reconstruct the pattern of events that has led to the distribution and diversity of life" (www.ucmp.berkeley.edu/clad/clad4.html). The word "phylogenetic" refers to a system based on evolutionary relationships, in this case among members of biotic groups that commonly are depicted as segments on a phylogeny (an evolutionary tree). As with any reasoned system that has developed over time, today's phylogenetic systematics represents our current understanding of the way life has diversified and changed over time (www.ucmp.berkeley.edu/clad/clad4.html). The degree that phylogenetic systematics has influenced our present understanding of Mesoamerican herpetofaunal diversity has depended on the group of amphibians, crocodylians, squamates, or turtles studied, and by the level of acceptance of modern philosophical ideas and techniques by taxonomists. Thus, our understanding of phylogenetic systematics is in a state of transition, as we keep moving from the ideas and techniques of the past into those of the present and future.

Our predecessors attempted to catalogue all life, and from Carolus Linnaeus we received a system of binomial nomenclature that provided a means for biologists to communicate. Under the Linnaean system of nomenclature, first and second names (generic and specific epithets) are provided for living organisms. A system for the placement of organisms into a set of hierarchically positioned taxonomic categories followed. Another idea that nearly all biologists embrace is that life changes over time. Charles Darwin delivered his theories of biotic evolution, of which some still constitute fundamental themes of modern-day biology. Presently, we combine the ideas of Linnaeus and Darwin and recognize the species category as the fundamental starting point of taxonomic inquiry. Anything systematically linked to populations, below the species level, is consigned to the ecologically regulated expression of individual and geographic variation within a species' genotypic and related phenotypic characters; geographic variation is how individual variation within a species fluctuates in space. Genera and all other higher taxonomic categories are not applicable until species are recognized. Once recognized, species are named, and in doing so must be placed within an existing genus or a new one erected to incorporate the newly named species. According to the rules of zoological nomenclature, named taxa also are placed into a specified set of higher taxonomic categories; major ones are genera, families, orders, classes, phyla, kingdoms, and domains.

Species concepts and their evolution. — Biologists also have inherited the part of systematics that deals with understanding how species come to exist and how they can be defined, and throughout history have provided a suite of species concepts. Within the context of these conceptions, the Biological Species Concept (BSC) proposed ideas of definitive reproductive isolation and the use of subspecies as a formal taxonomic category. The BSC gained primacy as a means of objectively defining and recognizing a species during the early to mid 20th century. In those days, the modern synthesis of evolutionary thought established genetic background as the source for evolutionary processes, through the early works of groundbreaking geneticists like Thomas H. Morgan and Wilhelm Johannsen, and later by the systematists Theodosius Dobzhansky and especially Ernst Mayr, whose book *Systematics and the Origin of Species from the Viewpoint of a Zoologist* (1942) served as a turning point for views about what constitutes a species. Together with like-minded biologists, such as the herpetologist and anatomist Hobart M. Smith, Mayr viewed a species as a group of populations of organisms that are capable of reproducing with each other and are reproductively isolated from other species. This species concept enjoyed great popularity among biologists who worked with sexually reproducing organisms, such as Mayr, who was an ornithologist. Nonetheless, the BSC never appealed much to biologists who focused on asexually reproducing organisms, because these creatures do not enjoy sexual reproductive compatibility. Although the BSC still holds sway in some corners of the biological world, it has gradually been replaced by species concepts that purport to work for all organisms, irrespective of their means of reproduction, and which are part of an overarching view of how life has changed over time.

These efforts gained remarkable focus and became part of the modern theory and practice of phylogenetic systematics, which rests on a foundation of cladistic theory pioneered by Willi Hennig in the 1930's. Cladistic analysis provided a means of erecting testable hypotheses about evolutionary initiated connections among organisms, and currently is considered by many as the best means for phylogenetic analysis (www.ucmp.berkeley.edu/clad/clad1.html), which now we recognize predomi-

Abronia vasconcelosii. This arboreal alligator lizard is endemic to the Guatemalan Plateau in the south-central portion of the country, where occurs in Lower Montane Wet Forest at elevations from 2,000 to 2,100 m. We assessed its EVS as 16, placing it in the middle portion of the high vulnerability category, and its IUCN status is Vulnerable. This individual is from Cerro Alux, department of Sacatepéquez, Guatemala. *Photo by Gunther Köhler.*

Andinobates claudiae. This poison dart frog is endemic to islands on the Atlantic side of Panama, where occurs in Lowland Moist Forest at elevations from 5 to 140 m. We gauged its EVS as 18, placing it in the upper portion of the high vulnerability category, and its IUCN status is Data Deficient. This individual is from Isla Colón, province of Bocas del Toro. *Photo by Brian Freiermuth.*

nantly among groups at higher taxonomic categories (see below). Most importantly, cladistic analysis gives biologists a way to use scientific methodology to study how organisms are related to one another on an accepted ancestor-descendent evolutionary basis. Cladistic protocols recognize synapomorphies, namely shared derived homologous characteristics, which uniquely distinguish the related groups in which they are present from all other such groups, most specifically by sharing the derived traits that originated during evolutionary modification of the direct ancestor to the descendants comprising phylogenetic segments of an evolutionary lineage. Therefore, cladistic systematics does not use reproductive capacity as a universal character to identify sister species on a phylogeny.

Reproduction is a characteristic of life, and sexual reproduction is common to a large portion of living species. Today, however, speciation in bisexual organisms is properly recognized to arise by cladogenesis, which is the splitting of a single lineage into two new genetically separate lineage segments. This idea, in part, dates to at least Darwin and his supporters, and was expanded upon by more modern phylogenetically-based species concepts, like the Evolutionary and Phylogenetic Species Concepts of George G. Simpson and Edward O. Wiley for the former, and Niles Eldridge and Joel Craycraft for the latter, among others. It was Kevin de Queiroz, in a series of papers dating from the late 1990s (e.g., de Queiroz 2005, 2007) that proposed a General Lineage Concept of Species (GLCS) that reiterated species to be genetically separated lineages, but uniquely embraced both clonal (asexual) and bisexual reproductive systems. We interprete the GLCS and its inclusive phylogenetically based principles to falsify some traditionally used doctrines that are deemed unusable in a modern phylogenetically assembled taxonomic system; below we identify the major ones associated with bisexual species.

As a consequence of modern phylogenetic theory, the BSC as a universal definition for bisexual species essentially was relegated to the systematics of the past, because reproductive capability is not a synapomorphic state but rather a plesiomorphic one, which is the ancestral state before the feature evolved into the derived condition in groups making up separate lineage segments found on a phylogeny. Plesiomorphic characters cannot be used to show sister relationships among other members of a phylogeny, because they can remain in that primitive condition in some or all taxa making up lineage segments of the phylogeny. The demise of the BSC to depict phylogenetic relationships among related taxa because of its reliance on an unusable trait (reproductive isolation) to show sister relationships also led to the finale for the short-lived impact of numerical taxonomy (Sneath and Sokal 1973). Numerical taxonomy used the overall similarity of many unweighted phenetic traits to cluster sister taxa together on a supposed phylogeny (actually a similarity phenogram). The high number of plesiomorphic traits shared among closely related species, however, makes the phenograms untenable for depicting phylogenetic sister relationships because such primitive traits cannot reflect evolutionary sister relationships among them.

Taxonomic processes at the species-lineage level usually do not follow cladistic principles, because speciation regularly does not rely on shared synapomorphies to specify sister relationships. In many of those cases evolutionary relationships were established when new evolutionary lineage segments were formed during allopatric speciation (geographic separation of ancestor into two separate evolutionary lineage segments), so features identifying separate sister species at that level can be an assortment of traits that were present in the ancestor to the two new lineage segments. Allopatric speciation typically is not due to genetic changes, but rather to spatial separation that eliminates gene flow. In other words, newly defined sister species can be very similar (if not identical) in genotypic structure and phenotypic expression during early periods of their lineage diversification. Still, a synapomorphy could define sister species if its attainment in the ancestral lineage is the reason for speciation, which generally would be expected in a sympatric situation. The primary function of taxonomists working at the species level is to determine if gene flow has ceased or not, and then decide what suite of taxonomic characters will define the taxon as a new separate evolutionary lineage segment.

A lineage is "any series of organisms connected by reproduction by parent of offspring" (www.ucmp.berkeley.edu/glossary/gloss1phylo.html). Thus, in bisexual organisms, speciation occurs as soon as an ancestral gene pool splits into two genetically isolated gene pools (lineage segments), as depicted at the nodes of a phylogeny. Consequently, there are no "stages of speciation," other than the initial complete separation of an ancestral lineage into two new sister lineages, which can be rapid or prolonged depending on the source of separation. Evolutionary character divergences are not stages of speciation, but rather changes within a single lineage's gene pool during its evolutionary lifespan. Some people consider stages of speciation alongside some speculative rule when they report that their sampled population has not changed adequately in genetic distance or morphological divergence to be considered a full species, as though some indefinable amount of evolutionary change is necessary to be considered a different species. Frost and Hillis (1990) correctly pointed out that "invoking a particular arbitrary level of genetic distance or morphological divergence as a species criterion is neither appropriate nor fruitful." This means that a species currently is defined only as a separate evolutionary lineage and not by some subjective amount of evolutionary change. Because a single lineage, say a species, does not develop into a new taxon without a genetic split, the idea of anagenesis (development of a new taxon without a genetic split) is negated, along with the related idea that stages of speciation occur

Agkistrodon howardgloydi. The Southern Cantil is distributed from southern Honduras to northwestern Costa Rica, where it occurs in Lowland Arid and Dry forests at elevations from near sea level to 470 m. We determined its EVS as 17, placing it in the middle portion of the high vulnerability category, but its IUCN status has not been determined. This individual is from Volcán Masaya, Nicaragua. *Photo by Javier Sunyer.*

within a single lineage. Anagenesis has been considered a valid concept in the past, but in order to form a new species gene pool separation must exist.

The demise of the subspecies category. — Even though the subspecies category has been associated with taxonomically recognized geographic variants within a species that are connected by gene flow (intergradation), some tend to consider a subspecies as a stage of speciation, even in light of clinal intergradation (gene-flow between members of the same species along a geographic cline). Thus, the subspecies category no longer is useful in systematics as a formal taxon, because by definition it does not constitute a separate evolutionary lineage, nor is it a stage of speciation. Disposing with this category also eliminates the conundrum created with another definition of a subspecies, as an entity consisting of organisms capable of interbreeding and producing fertile offspring with other subspecies of the same species, but cannot do so in nature because of geographic isolation or other factors. This "they can but they don't" paradox remains because it is not a testable hypothesis through scientific methodology. This definition also is misleading because allopatric populations, by definition, are separate evolutionary lineages due to genetic isolation and should be considered full species, not subspecies. If supposedly allopatric populations do not exhibit distinct genetic or morphological differences at a particular point in time, the only reasonable conclusion is that their gene pools are not incontrovertibly separated, so those populations should continue to be considered the same species until empirical data reverse that conclusion. So again, a foremost issue for taxonomists is to determine if gene pool separation has transpired or not.

Our understanding of the lowest-level phylogenetic relationships is that only species are separate evolutionary lineages and, thus, only species can be depicted appropriately on phylogenetic trees as lineage segments diverging from the nodes. Inserting subspecies as a lineage segment branching at nodes might seem to give subspecies a legitimate position as a formal taxonomic category, but it does not because a population that is not a separate evolutionaly lineage legitimately cannot be placed onto a resolved phylogeny.

In summary, our position is that subspecies, as formerly defined, are not separate evolutionary lineages and cannot be placed into a phylogeny. Furthermore, subspecies do not conform to an anagenetic stage of speciation because those stages do not exist. The focus of phylogenetic systematics, therefore, including its association with conservation biology, requires species to be the fundamental unit of diversification as identified by their binomial scientific name.

In addition, hybridization between two species in a contact zone should not be a factor in determining the presence of one or two species, because the ability to successfully reproduce is a plesiomorphic characer that cannot be used to identify phylogenetic sister relationships among the species being investigated. Hybridization in contact zones often is observed in natural situations; hybrids have no taxonomic status unless they lead to a separate lineage segment.

Persistent issues in publication of systematic results. — Another aspect of this discussion is our need to comment on the GLCS theory and its practice in modern systematics, because of its scientific relevance in officially published and unpublished literature. With the focus of modern phylogenetic systematics being centered on evolutionary divergence at the species level, our recognition of amphibians, crocodylians, squamates, and turtles in Central America is based on our interpretation of the information available in peer-reviewed scientific literature. With continued advances in communication, especially through the Internet, recognition of taxa should not be founded on what one might find on a Facebook page, in a blog, from someone's tweet, or in a private non-peer-reviewed journal (see Kaiser et al. 2013), no matter what attempts are made to masquerade them as legitimate scientific contributions. Thus, in documenting the makeup of the Cental American herpetofauna, we cite our sources as in Wilson et al. (2013a, b). Unfortunately, problems in scientific publication still persist, which are identified to clarify our position, as follows: (a) a lack of appropriate taxon representation; (b) a lack of appropriate taxonomic follow-through; and (c) taxon recognition based on non-phylogenetic grounds. We discuss some of these problems below and in the section entitled "Controversial Taxonomic Issues."

An example of lack of appropriate taxon representation is evident in the manner in which recognition of the genus *Masticophis* has been treated in recent literature. We believe efforts to synonymize *Masticophis* with *Coluber* have been hampered by a serious lack of appropriate taxon representation by previous investigators (e.g., Utiger et al. 2005; Pyron et al. 2013; and others). As traditionally recognized (e.g., Wallach et al. 2014), *Masticophis* contains at least 11 species, and no taxonomic analysis to date has included more than a small sample of those. In addition, little effort has been made to examine the phylogenetic relationships of the 11 species to more than a handful of the other genera and their constituent species that likely are close relatives of *Masticophis* and *Coluber* (for elaboration, see section on Controversial Taxonomic Issues).

Another example of a lack of appropriate taxon representation regarding racers in the Burbrink et al. (2008) study is the absence of samples of *C. constrictor* from Mexico, Belize, or Guatemala, where the "subspecies" *C. c. oaxaca* has been recognized (Köhler 2008). Lack of appropriate taxon representation is a common inconsistency in taxonomic studies of the herpetofauna that occur in the United States and neighboring Latin America, where taxon sampling often stops at or near the United States and Mexico border.

The single species recognized in the genus *Coluber* (*C. constrictor*) is what used to be recognized as the generotype of a much larger constellation of species that mostly occur in the Old World, which now have been segregated into seven genera (including the six listed in Wallach et al. 2014, and another genus, *Argyrogena*, resurrected by Wilson 1967, to contain the species *A. fasciolatus*). Wallach et al. (2014) noted that Burbrink et al. (2008) studied *C. constrictor* from a phylogenetic perspective and recognized "six unnamed clades." The clades or lineages they recognized are reminiscent of the "subspecies" arrangement held prior to the publication of their study (e.g., Conant and Collins 1998; Stebbins 2003). Burbrink et al. (2008) concluded that, "according to the general lineage concept of species, the racer may not be a single taxon, particularly since several lineages are well-defined geographically and are of very ancient origin." So, our questions to these authors are: (1) what happened to the taxonomic follow-through; (2) what is the taxonomic status of the six recognized but unnamed lineages; and (3) given that the lineages are noticeably not named in Burbrink et al. (2008), is there somewhere else where they are, or will be named? The logical place to find this information would be at the Center for North American Herpetology website, but the standard complement of 11 subspecies is listed there (accessed 1 March 2015). Nonetheless, it would be simple to figure out the names of the six lineages recognized in Burbrink et al. (2008), but it is not our responsibility to second-guess the authors and apply the designations to their recognized lineages. We believe, however, that the authors of this study and others like it are responsible for providing the necessary taxonomic follow-through and place some binomial on the lineages in question, at least until someone else reports different conclusions.

The last issue is taxon recognition based on non-phylogenetic grounds. Recognition of taxa must be founded on conclusions reached in phylogenetic studies using evidence-based data published in peer-reviewed scientific outlets. Once published, the information can be applied to resolve a variety of problems, such as determining conservation status. Importantly, such resolutions must be founded entirely on solid phylogenetic grounds. We cite a perplexing recent example to the contrary. Sanders et al. (2013) studied the phylogeny of the viviparous

Bolitoglossa cerroensis. This web-footed salamander is distributed in the Cordillera de Talamanca in central Costa Rica, where it occurs Lower Montane and Montane Wet forests at elevations from 2,530 to 2,990 m. We determined its EVS as 16, placing it in the middle portion of the high vulnerability category, and its IUCN status is Least Concern. This individual is from near Cerro de la Muerte. *Photo by Tobias Eisenberg.*

Bolitoglossa diaphora. This Cusuco web-footed salamander is known only from Parque Nacional Cusuco, Sierra de Omoa, in northwestern Honduras, where it occurs in Lower Montane Wet Forest at elevations from 1,450 to 2,200 m. We calculated its EVS as 18, placing it in the upper portion of the high vulnerability category, and its IUCN status is Critically Endangered. This individual is from the vicinity of the type locality. *Photo by Todd Pierson.*

Bolitoglossa centenorum. This web-footed salamander is only known from the type locality on Cerro Bobic in west-central Guatemala, in the Sierra de Cuchumatanes, department of Huehuetenango, where it occurs in Montane Wet Forest at en elevation of 3,250 m. We gauged its EVS as 18, placing it in the upper portion of the high vulnerability category, but its IUCN status has not been determined. This individual is from near San Mateo Ixtatán. *Photo by Todd Pierson.*

Bolitoglossa aureogularis. The Yellow-throated Web-footed Salamander is known only from two localities in Costa Rica, of which one is the vicinity of the type locality on the Atlantic versant of the Cordillera de Talamanca; it occurs in Lower Montane Wet forest (cloud forest) at elevations from 1,680 to 2,100 m. We estimated its EVS as 18, placing it in the upper portion of the high vulnerability category, but its IUCN status has not been determined. This individual is from the headwaters of the Río Coén, province of Limón. *Photo by Roney Santiago and Eduardo Boza Oviedo.*

seasnakes using both mitochondrial and nuclear markers from 39 of 62 species and 15 of 16 genera. We found one of their conclusions of particular interest because they allocated the long-recognized genus *Pelamis*, with its single species, to the genus *Hydrophis* (the name thus became *Hydrophis platurus*). This view later was supported by the broader study of Pyron et al. (2013), so we accept it based on the suggestions presented in both studies. We take issue, however, with the last sentence in Sanders et al. (2013), which reads: "The taxon *Hydrophis* is well known as comprising dangerously venomous sea snakes; hence, retaining this name (instead of adding multiple new genera) will create less confusion for conservationists, medical professionals, and fishing industries/communities as well as herpetologists." The level of confusion agonized over by the types of people indicated, including those compiling taxonomic lists (taxonomic inflation - Isaac et al. 2004; Will et al. 2005) is not a valid reason for reaching taxonomic conclusions, in this case whether one genus (*Hydrophis*) should be recognized or multiple genera (including, according to the authors, five new genera). Making life easier for persons not evolutionarily driven is not a valid motive for disregarding phylogenetic conclusions.

We also contend that recognizing subspecies as a formal taxonomic category, or placing them as separate evolutionary lineage segments on a phylogeny, are examples of taxon recognition based on non-phylogenetic grounds. Unfortunately, many studies continue this practice and sometimes unnessessarily confound taxonomic issues. In particular, the wrongful use of subspecies as a formal taxonomic category can obscure the issue when geographic pattern classes (Grismer 2002) of the same species are acknowledged with official taxonomic names. Such variation can be erratic when it expresses vastly inconsistent spatial features in ecological conditions and in the size of intergrade zones, and is a non-phylogenetic and speculative concept without basis in authenticity. In a similar context, Uetz et al. (2014) unfairly criticized Wallach et al. (2014) for not recognizing subspecies in their Snakes of the World, which in our opinion was the correct thing for the latter authors to do because of the invalid status of subspecies in modern phylogenetically based taxononmy. Identifying subspecies today only has relevance in historical perspectives.

Controversial Taxonomic Issues

Our work deals with over one thousand species of amphibians, crocodylians, squamates, and turtles occurring in Central America. Thus, differences in taxonomic opinion are expected between our position and those held by other systematic herpetologists. We discussed some of these differences above in Our Taxonomic Positions section, and discuss others below.

***Trachemys* in Central America.** — In recent years, the taxonomy of the turtle genus *Trachemys* in Mesoamerica has been examined numerous times with inconsistent results. Seidel and Smith (1986) transferred the taxon *Pseudemys scripta* and its subspecies into the genus *Trachemys*. Legler (1990) continued recognizing *Pseudemys* as the genus containing *T. scripta* and acknowledged the Central American forms as *P. s. venusta* (Caribbean versant of southern Mexico and the Yucatan Peninsula), *P. s. grayi* (Pacific side from the Isthmus of Tehuantepec to western Guatemala), and *P. s. emolli* (Nicaraguan lakes and Costa Rica). Ernst (1990) accepted the genus *Trachemys* and similarly recognized the subspecies *T. s. venusta* and *T. s. grayi*, but considered *T. s. ornata* as occurring from Honduras to Panama. Seidel (2002) later elevated two of the Central American forms to *T. emolli* and *T. venusta*. Bonin et al. (2006) considered *T. ornata* to be a Mexican Pacific versant endemic, *T. venusta* as occurring on the Atlantic slopes from Veracruz, Mexico, to Panama and on the Pacific side from southeastern Oaxaca, Mexico, to Guatemala, and *T. emolli* as restricted to Nicaragua and adjacent Costa Rica. Köhler (2008) reviewed the most recent literature on this species complex, but preferred to take a “conservative approach” and relegated all Central American populations to indeterminate status as part of the wide-ranging *Trachemys scripta*, but commented that he expected the taxonomy to be revised.

Fritz et al. (2011) examined the molecular phylogeny of the slider turtles of Mexico, Central America, and South America and determined previous allocations to be incorrect, therein identifying two species in Central America: *T. grayi* and *T. ornata*. Their evidence indicated that *T. grayi* occurred intermittently on the Pacific lowlands of Oaxaca, Mexico, through Panama and included species or subspecies of taxa previously considered as *T. venusta panamensis*, *T. v. grayi*, and *T. emolli*. Their information also specified that *T. ornata* ranged sporadically on the Pacific versant from Sinaloa, Mexico (type locality, Mazatlan), to a depicted allopatric population in the vicinity of Acapulco, Guerrero, the only locality in western Mexico from which they had samples. *Trachemys ornata* also was reported to occur from Tamaulipas, Mexico, on the Atlantic versant into South America. Populations of *T. ornata* from that area previously were listed as comprised of *T. venusta cataspila*, *T. v. venusta*, *T. v. uhrigi*, and two subspecies of *T. callirostris* in South America. In a paper associated primarily with Antillean *Trachemys*, Parham et al. (2013) continued to recognize *T. venusta* for Atlantic versant turtles without analyzing any *T. ornata* from western Mexico (except from the supposed isolated population around Acapulco), and *T. emolli* on the Pacific vesant of middle Central America because of its supposed allopatric distribution. McCranie et al. (2013), in reporting the taxon *T. g. emolli* in southern Honduras, added new data that corroborated the taxonomy of Fritz et al. (2011), although they cited the publication date of that paper as 2012. The main problem with both Fritz et al. (2011) and McCranie et al. (2013), as with most recent sources, is that these authors continued to utilize subspecies as a formal taxonomic category.

The question arises as to what these recent studies demonstrate regarding which species-level taxa of slider turtles should be recognized in Central America. In our effort to arrive at a decision, we examined the latest version of the world turtle checklist published by the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group (van Dijk et al. 2014). These authors adopted a position that allows users of the checklist to arrive at their own conclusion on what taxa at what level can or should be recognized, which leads to a curious situation. They recognized three taxa of slider turtles in Central America. One was *T. venusta*, which supposedly was distributed principally along the Atlantic versant from Tamaulipas, Mexico, to extreme northwestern Colombia, but also on the Pacific versant in Panama. van Dijk et al. (2014), however, suggested that this taxon also could be called, in addition to *T. venusta*, *T. ornata venusta*, or *T. venusta venusta*. They also listed *T. grayi* (Pacific versant of Oaxaca, Mexico, to eastern El Salvador), but indicated that it could also be called *T. venusta grayi*. Finally, they included *T. emolli* (Pacific versant from eastern El Salva-

Bolitoglossa indio. This web-footed salamander is known from the lowlands of the Río San Juan area in extreme southeastern Nicaragua and north-central Costa Rica, where it occurs in Lowland Moist Forest at elevations from 25 to 68 m. We evaluated its EVS as 17, placing it in the middle portion of the high vulnerability category, and its IUCN status is Data Deficient. This individual is from the type locality, Dos Bocas de Río Indio, department of Río San Juan, Nicaragua. *Photo by Javier Sunyer.*

dor to northwestern Costa Rica), but also listed the taxon as *T. grayi emolli*. So, the reader could make a choice among three species and/or subspecies (*grayi*, *ornata*, and *venusta*) into which to place the three Central American populations of slider turtles under a total of seven preferred names.

We then examined Legler and Vogt's (2013) book on Mexican turtles to see how they handled the issue, and quickly realized that their taxonomic arrangements were permeated with subspecies, and that they continued to treat all populations as subspecies of *T. scripta*. When we ignored the trinomials and just concentrated on the subspecific names as potential species names, Legler and Vogt's (2013) scheme would recognize the following: *T. ornata* as occurring on the Pacific side of Mexico from Sinaloa southwestward to the area around Acapulco, Guerrero, the latter location depicted as a broadly allopatric population (also illustrated that way by Legler 1990, and Seidel 2002); *T. venusta* as ranging on the Atlantic versant from southeastern Veracruz through Central America into Colombia, and on the Pacific side in western Panama and adjacent Costa Rica; and *T. grayi* as occurring on the Pacific versant from south-central Oaxaca into El Salvador. They did not recognize the taxon *emolli* that had been considered a subspecies of *P. scripta* by Legler (1990) and *T. scripta* by Iverson (1992), as a full species by Seidel (2002) and Jackson et al. (2008), and as *T. grayi* by Fritz et al. (2011).

McCranie et al. (2013) also produced a subspecies infused phylogeny, so again if their trinomials are ignored, their taxa as based on distributional information found on their phylogeny, included the following potential Central American forms: *T. ornata* ranging from Sinaloa, Mexico, on the Pacific versant to Acapulco, Guerrero, and on the Atlantic slope from Tamaulipas, Mexico, southward and eastward through Central America to Venezuela; and *T. grayi* occurring on the Pacific slope from southeastern Oaxaca, Mexico, to Panama. A major difference of Fritz et al. (2011) and McCranie et al. (2013), when compared to the other papers, was that of all the species of *Trachemys* in Central America, only *T. ornata* occurred on both Atlantic and Pacific versants of Mexico above the Isthmus of Tehuantepec and on the Atlantic slope of Central America. Below the Isthmus, however, only *T. grayi* was present on the Pacific side, from southwestern Mexico to Panama. The pattern of species distributed on the Pacific and Atlantic sides connected near the Isthmus of Tehuantepec, as in *T. ornata*, also is found among crocodylians, squamates, and other turtles (see maps in Köhler 2008).

Seidel (2002) and Legler and Vogt (2013) regarded the population of *Trachemys* located on the Pacific side of Panama and Costa Rica as *T. venusta*, a species that almost everywhere else in Mesoamerica was an Atlantic versant form. Parham et al. (2013) thought that *T. venusta* and *T. emolli* probably intergraded in southern Nicaragua and northern Costa Rica, although they apparently had no access to the information in McCranie et al. (2013). Fritz et al. (2011) and McCranie et al. (2013) both reported that *T. grayi* was the species present from Pacific Costa Rica and Panama, which was conspecific with other populations to the northwest on the Pacific slopes, and not to those on the Atlantic side. The question of what species name to use for the Atlantic versant population occurring from Tamaulipas into South America tentatively is answered by recognizing the conclusions of the published positions of Fritz et al. (2011) and McCranie (2013) that *T. ornata* is the valid name, because it has publication date priority over *T. venusta*. The decision by Parham et

Bothrops punctatus. This semiarboreal pitviper is distributed from extreme eastern Panama to northwestern Ecuador, where it occurs in Lowland Wet, Premontane Wet, and Lower Montane Wet forests at elevations from near sea level to 2,300 m. We evaluated its EVS as 16, placing it in the middle portion of the high vulnerability category, but its IUCN status has not been determined. This individual is from the Serranía de Pirre, province of Darién, Panama. *Photo by Abel Batista.*

Bothriechis marchi. The Honduran Emerald Tree Viper is endemic to northwestern and north-central Honduras, where it occurs in Premontane Wet and Lower Montane Wet forests at elevations from 500 to 1,840 m. We calculated its EVS as 16, placing it in the middle portion of the high vulnerability category, and its IUCN status is Endangered. This individual is from Parque Nacional Cusuco, Sierra de Omoa, department of Cortés. *Photo by Silviu Petrovan.*

Bradytriton silus. This salamander, the sole member of its genus, is endemic to the Sierra de Cuchumatanes in northwestern Guatemala, where it is known only from two localities in Premontane and Lower Montane Wet forests at elevations of 1,310 and 1,640 m. We established its EVS as 18, placing it in the upper portion of the high vulnerability category, and its IUCN status is Critically Endangered. This individual is from San José Maxbal, department of Huehuetenango. *Photo by Sean Michael Rovito.*

Bolitoglossa insularis. This web-footed salamander is endemic to Volcán Maderas on Ometepe Island in southwestern Nicaragua, where it occurs in Premontane Moist Forest at elevations from 800 to 1,050 m. We assessed its EVS as 18, and its IUCN status is Vulnerable. This individual is from Volcán Maderas, Isla de Ometepe, department of Rivas. *Photo by Javier Sunyer.*

al. (2013) to revert to calling the Atlantic versant turtles *T. venusta* is curious. These authors admitted that Atlantic and Pacific Mexico populations probably were conspecific and that the valid name would be *T. ornata*. Still, they decided to maintain the name *T. venusta* because they had no data from Mexican west coast *T. ornata* other than samples from the supposed allopatric population in the vicinity of Acapulco, which they thought might have been introductions, and speculated that genetic introgression was the reason for their alliance with *T. ornata;* to us, this indicates that wild *T. ornata* probably were present in the area. We also question the allopatric nature of the Acapulco population because another Guerrero locality for *T. ornata* was reported by Mertz et al. (2015) from 200 km NW of Acapulco, which bridges a portion of the distributional gap between Cabo Corrientes, Jalisco, and Acapulco (Legler and Vogt 2013).

For our purposes in this paper and to try to reduce the confusion created in the van Dijk et al. (2014) checklist and other papers, we consider that the equivalent data in Fritz et al. (2011) and McCranie (2013) best explain the present knowledge of the taxonomic status of *Trachemys* in Central America, so we recognize two species-level taxa of slider turtles: *T. grayi* on the Pacific lowlands and *T. ornata* on the Atlantic side, with their ranges as indicated above. Nonetheless, we reject all reference to subspecies due to taxonomic recognition based on nonphylogenetic grounds.

Taxonomy of *Chelonia mydas*. — The Green Turtle, *Chelonia mydas*, is a cosmopolitan species of marine turtle that occurs in all the tropical to temperate oceans, and has been regarded as showing considerable individual and geographic variation in morphological and genetic characters (see discussion in Ernst and Lovich 2009). *Chelonia agassizii*, a supposedly Pacific Ocean form, was named by Bocourt (1868) for an individual from the Pacific coast of Guatemala, which some authorities have determined to be a local variant of *C. mydas* (Karl and Bowen 1999), others have considered it a subspecies of *C. mydas* (Kamezaki and Matsui 1995), and still others as a full species (Iverson 1992; Pritchard 1999; Savage 2002; Bonin et al. 2006). In a morphological study of *C. mydas* from coastal waters around Japan, Okamoto and Kamezaki (2014) found differences between two samples of turtles that appeared to validate *C. mydas* and *C. agassizii* as separate species (at least around Japan), and they commented on other studies in the Pacific Ocean that agreed with their findings (e.g., Parker et al. 2011). We consider that the possibility of the two species arrangement eventually might stand or even expand. We also feel, however, that accepting the two species scenario is premature because of a serious lack of appropriate taxon representation, especially in the Atlantic and Indian Oceans, as well as the need for using more relevant phylogenetic criteria to decipher species-level taxonomic status within the composite of populations associated with *C. mydas*.

Status of *Cryptochelys*. — Taxon delimitation among the turtles historically placed in the family Kinosternidae has been challenging at all taxonomic levels, and this controversy continues to the present. Two recent studies are relevant to the status of members of this group in Central America. As noted in van Dijk et al. (2014), "Iverson et al. (2013) sequenced three mtDNA and three nuclear markers for every recognized species and most subspecies of kinosternids. Their analyses revealed three well-resolved clades within the Kinosternidae, corresponding to *Sternotherus*, a previously unnamed clade that they described as the new genus *Cryptochelys*, and *Kinosternon sensu stricto*. Their molecular data support for *Cryptochelys* was strong, but data support for non-monophyly of *Kinosternon* with respect to *Sternotherus* was weak. The identified groups are broadly consistent with morphological and biogeographical features. Their new genus *Cryptochelys* was diagnosed based on an extensive set of morphological and molecular characters, and contains the designated type species *leucostoma*, as well as *acuta*, *angustipons*, *creaseri*, *dunni*, and *herrerai*." van Dijk et al (2014) referenced "a parallel study of kinosternid phylogenetics … that reaches different taxonomic conclusions." The title of this paper by Spinks et al. (2014), "Multilocus phylogeny of the New-World mud turtles (Kinosternidae) supports the traditional classification of the group," indicated the principal conclusion of this paper, i.e., a rebuttal of the Iverson et al. (2013) classification, as well as an argument for maintaining stability in organismic classifications. Their abstract provides a good statement of their position, as follows: "A goal of modern taxonomy is to develop classifications that reflect current phylogenetic relationships and are as stable as possible given the inherent uncertainties in much of the tree of life. Here, we provide an in-depth phylogenetic analysis, based on 14 nuclear loci comprising 10,305 base pairs of aligned sequence data from all but two species of the turtle family Kinosternidae, to determine whether recent proposed changes to the group's classification are justified and necessary. We conclude that those proposed changes were based on (1) mtDNA gene tree anomalies, (2) preliminary analyses that do not fully capture the breadth of geographic variation necessary to motivate taxonomic changes, and (3) changes in rank that are not motivated by non-monophyletic groups. Our recommendation, for this and other similar cases, is that taxonomic changes be made only when phylogenetic results that are statistically well-supported and corroborated by multiple independent lines of genetic evidence indicate that non-phylogenetic groups are currently recognized and need to be corrected. We hope that other members of the phylogenetics community will join us in proposing taxonomic changes only when the strongest phylogenetic data demand such changes, and in so doing that we can move toward stable, phylogenetically informed classifications of lasting value." Operating on this basis, Spinks et al. (2014) rejected the Iverson et al. (2013) genus *Cryptochelys*, moved the six above-mentioned species back into the genus *Kinosternon*, and maintained recognition of the genus *Sternotherus*. The Spinks et al. (2014) arrangement appears to rest on a more secure basis, does not support recognition of *Cryptochelys*, and is the approach we tentatively adopted. Nonetheless, we wish to caution those same "members of the phylogenetics community" that attempting stability of organismic classification is only desirable if it does not limit scientific discourse. Given that humans will always be dealing with the inherent uncertainties in much of the tree of life, and that their scientific toolbox can only hope to recover phylogenies of organisms about which we are aware, systematic biologists must have the freedom to attempt such recovery in a spirit of cooperative enlightenment. After all, we are guided in this effort by the conventions of peer review in scientific publications and the principles of zoological nomenclature. Even with these conventions, it will never be possible for systematists to locate a comfortable armchair from which to reflect on stable, phylogenetically informed classifications of lasting value.

Staurotypinae vs. Staurotypidae. — Divergent approaches to the family-level classification of the genera *Claudius* and *Staurotypus* were taken in the Iverson et al. (2013) and Spinks et al. (2014) papers discussed above, with the former arguing for the placement of these genera

Craugastor laevissimus. This species is distributed from western and east-central Honduras to northern and southwestern Nicaragua, where it occurs in Lowland Moist, Lowland Dry, Premontane Wet, Premontane Moist, Premontane Dry, and Lower Montane Moist forests at elevations from near sea level to 2,000 m. We assessed its EVS as 12, placing it in the upper portion of the medium vulnerability category, and its IUCN status is Endangered. This individual is from Cerro Kilambé, department of Jinotega, Nicaragua. *Photo by Javier Sunyer.*

Craugastor chingopetaca. This rainfrog is known only from the type locality along the Río San Juan in extreme southeastern Nicaragua, department of Río San Juan, where it occurs in Lowland Wet Forest at an elevation of 40 m. We evaluated its EVS as 18, placing it in the upper portion of the high vulnerability category, and its IUCN status is Data Deficient. This individual is from Reserva de Vida Silvestre Río San Juan. *Photo by Javier Sunyer.*

Craugastor nefrens. The distribution of this ranita de hojarasca (little litter frog) is restricted to a narrow elevational band (800–1,000 m) of Premontane Wet Forest in the Sierra de Caral of eastern Guatemala, near the border with Honduras. We established its EVS as 18, placing it in the upper portion of the high vulnerability category, and its IUCN status is Data Deficient. This individual is from Finca la Firmeza, Morales, department of Izabal. *Photo by Sean Michael Rovito.*

Ctenosaura palearis. This Guatemalan spiny-tailed iguana is endemic to the Motagua Valley in eastern Guatemala, where it occurs in Lowland Arid and Premontane Dry forests at elevations from 150 to 700 m. We calculated its EVS as 19, placing it in the upper portion of the high vulnerability category, and its IUCN status is Endangered. This individual is from Zacapa, Motagua River Valley, department of Zacapa. *Photo by Antonia Pachmann.*

in the family Staurotypidae and the latter in the subfamily Staurotypinae. Iverson et al. (2013) followed Bickham and Carr (1983) in recognizing two clades, one consisting of *Claudius* and *Staurotypus* and another of *Kinosternon* and *Sternotherus*, as separate families, based on the estimated age of the clades and their unambiguously distinct morphologies and sex-determining mechanisms (genetic sex determination in the former clade and temperature-dependent sex determination in the latter), as well as the concatenated sequences of three nuclear and three mitochondrial genes. Spinks et al. (2014: 258), however, argued that, “in the interest of maintaining taxonomic stability … we suggest that the community maintain the historical treatment of Staurotypinae as a subfamily as has been done for decades.” We briefly explained our position on this matter above, and in this case follow the recommendations of Iverson et al. (2013) and recognize the genera *Claudius* and *Staurotypus* in the family Staurotypidae, distinct from the family Kinosternidae that includes the genera *Kinosternon* and *Sternotherus*.

Single-genus vs. multiple-genera approaches to anole classification. — A sizeable number of herpetologists are interested in anoles and their classification. Over the years, many herpetologists have tried to make sense of a group of lizards that presently contains 395 species

(Reptile Database website; accessed 28 February 2015), with more added each year (e.g., see our listing of presently added taxa to the Central American herpetofauna, in which we document the recognition of 15 additional species-level taxa since the publication of Wilson et al., 2010). Gunther Köhler and his colleagues undertook most of this work and with one exception (*Dactyloa ginaelisae*) described or resurrected the remainder under the genus *Anolis*. In our present work, we list 95 species of anoles in Central America, and Wilson et al. (2013a) recorded 50 species from Mexico; presently 129 species comprise the anole fauna of Mesoamerica (16 species occupy both regions; www.mesoamericanherpetology.com; accessed 28 February 2015). In Wilson et al. (2013a), we listed all 50 Mexican species under the genus *Anolis*. We took that position because a controversy was brewing over the classification proposed by Nicholson et al. (2012), especially with the harsh rebuttal of this paper by Poe (2013), and we were uncertain where the controversy would go. Since that time, however, Nicholson et al. (2014) provided a detailed response addressing Poe's concerns. Most anyone with an interest in anole systematics knows the backstory, beginning with Guyer and Savage's (1986) revolutionary cladistic analysis of the anoles. The effect of that study was to segment the huge and unwieldy genus *Anolis* into a series of eight genera. Subsequently, Williams (1989) authored a scathing critique of the Guyer-Savage approach, asking if the data were available to reclassify the anoles; herpetologists varied in their opinions. During the ensuing years, students of tropical American herpetology basically fell into two camps, those who supported or opposed the Guyer-Savage scheme. In recent years, we sided with the latter camp (Wilson and Johnson 2010; Johnson et al. 2010; Wilson et al. 2013a), but did not undertake an exhaustive study of the matter. Nonetheless, after the publication of Poe's (2013) critique of the Nicholson et al. (2012) paper and the Nicholson et al. (2014) rebuttal, we decided to take a fresh look at this issue. Principally, the controversy that developed over the last two years results from two approaches to the classification of anoles. The Nicholson et al. (2012, 2014) approach was to recognize eight genera of these lizards. Poe's (2013) tactic was to jettison entirely the Nicholson et al. (2012) approach and to recognize a single genus that contained 391 species, the largest genus of squamates. Fundamentally, Poe's criticism of the eight-genus approach was two-fold, i.e., that "some of the proposed genera are not monophyletic" and that Nicholson et al. (2012) did not study enough taxa or enough characters. Nicholson et al. (2014) presented their rebuttal "to explain how Poe erred in characterizing our work, and missed the opportunity to present an alternative comprehensive taxonomy to replace the one against which he argues so strenuously. In this contribution we explain, and correct, Poe's errors and misrepresentations, and argue that our taxonomy is likely to be adopted because it (1) eliminates the obvious problem that will arise if the family Dactyloidae contains only a single large genus (i.e., that a single genus obscures the evolution and diversity within the group and misrepresents or cloaks it), (2) it conforms with the long historical trend of dissecting large, cumbersome groups into smaller sub-units, (3) is consistent with all recent phylogenetic studies for anoles in membership within clades we recognize as genera, and (4) aids in associating these lizards with the ancient land masses that shaped their history." We consider that Nicholson and her coauthors adequately responded to Poe's criticisms and we are confident in adopting the portion of their scheme relevant to the situation in Central America, and Mesoamerica as a whole. So, what impact does the Nicholson et al. approach have on the taxonomy of anoles in Mesoamerica? As it turns out, only three of the eight genera Nicholson et al. (2012, 2014) recognized contain Mesoamerican species as follows: *Anolis* (one species), *Dactyloa* (10 species), and *Norops* (118 species). The distribution of the genus *Anolis* is stated by Nicholson et al. (2012) to be in "the Bahamas, Cuba, and adjacent islands, Navassa Island, Little Cayman [I]sland, Hispaniola, and the southeastern United States west to Oklahoma and Texas." They further indicated that, "one Cuban species (*A. allisoni*) occurs on Isla Cozumel, Mexico and Islas de la Bahía, Honduras, and on coastal islands off Belize." Distribution of the genus *Dactyloa* is indicated by Nicholson et al. (2012) to be on the "Atlantic and Pacific slopes of Costa Rica and Panama, then south through the Chocó region of Colombia and Ecuador, including Malpelo Island; highlands of Colombia, Ecuador, Peru, and Venezuela; Caribbean slope of Colombia and Venezuela; Bonaire and Blanquilla Islands and the southern Lesser Antilles; south on the Atlantic versant through the Guayanas to Espiritu Santo State in eastern Brazil, and throughout the Orinoco and Amazon Basins in Colombia, Ecuador, Peru, Venezuela, Bolivia, and Brazil." The remainder of the anoles in Central America (as well as all of the species in Mexico except for *Anolis allisoni*) are placed in the genus *Norops*, which Nicholson et al. (2012) reported to occur in "Cuba, Jamaica, Bahamas, Grand and Little Cayman, Cayman Brac, Mexico, Central America, and many adjacent islands, including Cozumel, the Bay Islands, the Corn Islands, Swan Island, San Andres and Providencia (Caribbean) and Isla del Coco (Pacific); south to western Ecuador, northern South America (Colombia and Venezuela), including Isla Gorgona (Pacific), the islands of Aruba, Curaçao, and Margarita (Caribbean), Trinidad and Tobago; then south through the Guyanas to southeastern and southern Brazil, and Paraguay, and throughout the Orinoco and Amazon Basins (Colombia, Venezuela, Ecuador, Peru, Brazil, and Bolivia)." We agree that Nicholson and her coauthors provided a perceptive set of reasons why their classification will be accepted in time, just as with other classifications that sought to

Cryptotriton nasalis. This small salamander is endemic to the Sierra de Omoa in northwestern Honduras, where it occurs in Premontane and Lower Montane Wet forests at elevations from 1,220 to 2,200 m. We estimated its EVS as 18, placing it in the upper portion of the high vulnerability category, and its IUCN status is Endangered. This individual is from the Sierra de Omoa, department of Cortés. *Photo by Sean Michael Rovito.*

make sense of formerly unmanageable genera, such as *Eleutherodactylus*, which now not only is segmented into a number of genera, but also a number of families.

***Coluber* versus *Masticophis*.** — We base most of this commentary on information discussed in Wilson and Johnson (2010), along with a fresh look at the available data and on our reliance on the proper use of phylogenetic systematics to produce accurate conclusions. The major issue is: should the genus *Masticophis* be synonymized with the genus *Coluber* based on the information available today? This question has been contentious for many years, and the disagreement stems from a number of factors, including overall molecular, morphological, and ontogenetic similarities between the two genera; a prodigious lack of appropriate taxon representation in seminal papers of recent vintage (see Our Taxonomic Position section), especially those that reflected molecular comparisons; and the overt continuation of recognizing groups at the subspecies level.

Nagy et al. (2004), in a molecular study using mitochondrial and nuclear genes, agreed with Schätti's (1987) morphogical investigation that the genus *Coluber* (*sensu stricto*) should be restricted to the New World; both declined to synonymize *Masticophis* with *Coluber* based on their own data. Utiger et al. (2005), with low support, found *Masticophis flagellum* to be nested within *Coluber constrictor*, with *M. taeniatus* as the sister to the *C. constrictor-M. flagellum* clade, which made *Masticophis* paraphyletic, therein recommending the placement of *Masticophis* into *Coluber* (the older generic name). Burbrink et al. (2008) examined *C. constrictor* from throughout upper North America and concluded the species to be monophyletic and composed of six unnamed lineages; they also considered *M. flagellum* the sister species to *C. constrictor*, thus negating Utiger et al.'s. (2005) verdict that a population of *C. flagellum* was more closely related to *C. constrictor* than to other populations of *C. flagellum*. The Burbrink et al. (2008) treatment also is afflicted with a lack of taxonomic follow-through, inasmuch as the separate lineages within the *C. constrictor* complex they disclosed are not named. In addition, they did not indicate the species to which *M. flagellum* is the sister taxon. Collins and Taggart (2008) correctly noted that because of incomplete taxon sampling by Utiger et al. (2005), the generic status of certain taxa could not be addressed adequately. Wilson and Johnson (2010) also presented summary information on this debate, and commented that Utiger et al. (2005) did not provide adequate samples from throughout the range of the respective taxa (e.g., at least nine other species of *Masticophis* were not included in their study). Both Collins and Taggart (2008) and Wilson and Johnson (2010) recommended the continued recognition of both genera as separate taxa, although some publications have continued to use *Coluber* for all the species of *Masticophis*, most notedly *C. flagellum* and *C. taeniatus*, species occurring sympatrically in the southwestern United States.

Importantly, no comparison has been made between *M. flagellum* and the wide-ranging *M. mentovarius*, as presently envisioned, which long were thought to be sister species (e.g., Wilson 1970; Johnson 1977). Also, only a small amount of genetic material has been available to examine and compare the relationships of *Coluber* and *Masticophis* to other genera of North American racer-like colubrids (e.g., *Dendrophidion*, *Drymobius*, *Leptodrymus*, *Leptophis*, *Mastigodryas*, *Salvadora*), of which most do not occur northward outside of Mexico.

Craugastor polyptychus. This frog is distributed along the lowlands of the Atlantic versant from extreme southeastern Nicaragua to extreme northwestern Panama, where it occurs in Lowland Moist Forest at elevations from near sea level to 260 m. We estimated its EVS as 17, placing it in the middle portion of the high vulnerability category, and its IUCN status is Least Concern. This individual is from the Refugio Nacional de Vida Silvestre Gandoca-Manzanillo, province of Limón, Costa Rica. *Photo by Maciej Pabijan.*

Crocodylus acutus. The American Crocodile is broadly distributed in the Caribbean Basin from southern Florida and the Yucatan Peninsula south to Colombia and Venezuela, and on the Pacific coast of Latin America from Sinaloa in Mexico to Peru in South America. We evaluated its EVS as 14, at the lower end of the high vulnerability category, and its IUCN status is Vulnerable. This individual is from Isla Juan Venado, a barrier island constituting a nature reserve, department of León, Nicaragua. *Photo by Javier Sunyer.*

Dactyloa ibanezi. This anole is distributed on the Caribbean versant from southeastern Costa Rica to western Panama, where it occurs in Lowland Moist and Premontane Wet forests at elevations from 400 to 1,070 m. We established its EVS as 15, placing it in the lower portion of the high vulnerability category, but its IUCN status has not been determined. This individual is from Donoso, province of Colón, Panama. *Photo by Abel Batista.*

Dactyloa kunayalae. This anole is distributed in western and central Panama, where it occurs in Lowland Moist and Premontane Wet forests at elevations from 320 to 1,050 m. We estimated its EVS as 15, placing it in the lower portion of the high vulnerability category, but its IUCN status has not been determined. This individual is from the Río Tuquesa, province of Darién, Panama. *Photo by Abel Batista.*

In an extensive review of squamates, Pyron et al. (2013) also showed *C. constrictor* and *C. flagellum* as sister species and *C. taeniatus* as the sister to that clade, but didn't mention the overt lack of appropriate taxon representation when producing their phylogeny. Pyron et al. (2013) included some samples of other racer-like genera in their phylogeny, but still maintained a lack of sufficient taxon sampling in those genera, of which most have not undergone recent phylogenetic analyses. After all, if the phylogenetic interpretation is not accurate or based on inadequate taxonomic representation, it could lead to erroneous conclusions.

Another germane question about the generic status of *Masticophis* could be resolved by determining the phylogenetic position of *M. taeniatus* compared with that of the above-mentioned genera of racer-like species. After an all-encompasing phylogenetic comparison, the possibility exists that a monophyletic *M. taeniatus* group (eight species), could be assigned to a genus other than *Masticophis* or *Coluber*; which would remove the paraphyletic status of *Masticophis*, and make its inclusion into *Coluber* inconsequential.

In conclusion, because pertinent phylogenetic studies on the issue of *Coluber* versus *Masticophis* have not included appropriate taxonomic representation of members of the genera *Masticophis* and *Coluber* or genera of other Western Hemisphere racer-like colubrids, we accept the recommendations of Collins and Taggart (2008) and Wilson and Johnson (2010) and use the name *Masticophis* for the 11 species traditionally included in this genus, including *M. mentovarius* in Central America.

A Revised Environmental Vulnerability Measure

Wilson et al. (2013a, b) adapted the Environmental Vulnerability Score developed by Wilson and McCranie (2004) for use in Mexico. The Mexican EVS only differed from that used for Honduras by Wilson and McCranie (2004) in the design of the geographic component (considering, however, that the third component of the measure differed between amphibians and the remainder of the herpetofauna). Herein, we revised the same component for use with the Central American herpetofauna, as follows:

1 = distribution broadly represented both inside and outside of Central America (large portions of the range are both inside and outside of Central America)
2 = distribution prevalent inside of Central America, but limited outside of Central America (most of the range is inside of Central America)
3 = distribution limited inside of Central America, but prevalent outside of Central America (most of the range is outside of Central America)
4 = distribution limited both inside and outside of Central America (most of range is marginal to areas near the border of Central America and Mexico or South America, respectively)
5 = distribution only within Central America, but not restricted to the vicinity of the type locality
6 = distribution limited to Central America in the vicinity of the type locality

The second component of the EVS measure, for ecological distribution based on occurrence in different vegetaion formations, is the same for Central America as for Mexico, as follows:

1 = occurs in eight or more formations
2 = occurs in seven formations
3 = occurs in six formations
4 = occurs in five formations
5 = occurs in four formations
6 = occurs in three formations
7 = occurs in two formations
8 = occurs in one formation

The third component, for amphibians, deals with the type of reproductive mode, as follows:

1 = both eggs and tadpoles are found in large to small bodies of lentic or lotic water
2 = eggs are deposited in foam nests, and tadpoles are found in small bodies of lentic or lotic water
3 = tadpoles are found in small bodies of lentic or lotic water, and eggs elsewhere
4 = eggs are laid in moist situations on land or in moist arboreal situations, and tadpoles (larvae) are carried (or move) to water or undergo direct development
5 = eggs and/or tadpoles are carried in the dorsal pouch of the female or are imbedded in the dorsum of female, larval or direct development, or viviparous
6 = eggs and tadpoles are found in water-retaining arboreal bromeliads or in water-filled tree cavities

The third component, for crocodylians, squamates, and turtles, deals with the degree of human persecution, as follows:

1 = fossorial, usually escape human notice
2 = semifossorial, or nocturnal arboreal or aquatic, nonvenomous and usually non-mimicking, sometimes escape human notice
3 = terrestrial and/or arboreal or aquatic, generally ignored by humans
4 = terrestrial and/or arboreal or aquatic, thought to be harmful, might be killed on sight
5 = venomous species or mimics thereof, killed on sight
6 = commercially or non-commercially exploited for hides, meat, eggs and/or the pet trade

Once these three components are added, the EVS can range from 3 to 20 in both groups. Wilson and McCranie (2004) placed the range of scores for Honduran amphibians into three categories of vulnerability to environmental degradation, as follows: low (3–9); medium (10–13); and high (14–19). The categories for the rest of the herpetofauna were similar, with the high category encompassing values of 14–20. Herein, we employ the same categorizations: low (3–9); medium (10–13); and high (14–20). In Appendices 1 and 2, these categories are signified by the abbreviations L (low), M (medium), and H (high).

Recent Changes to the Central American Herpetofauna

Due to ongoing fieldwork in Central America by a number of herpetologists from around the globe, and the systematic research emanating from their fieldwork, the composition of the region's herpetofauna constantly is being updated. In most cases, the number of recognized taxa increases. These changes add or subtract from the taxonomic lists that appeared in Wilson et al. (2010);

Dactyloa latifrons. This anole is distributed from eastern Panama to northwestern Ecuador, where it occurs in Premontane Wet Forest at elevations from 665 to 780 m. We gauged its EVS as 13, placing it at the upper end of the medium vulnerability category, but its IUCN status has not been determined. This individual is from the Serranía de Pirre, province of Darién, Panama. *Photo by Abel Batista.*

since that work appeared, the following 92 species have been described, resurrected, or elevated to species level:

Anomaloglossus astralogaster: Myers et al. 2012. *American Museum Novitates* 3,763: 1–19. New species.

Anomaloglossus isthminus: Myers et al. 2012. *American Museum Novitates* 3763: 1–19. New species.

Atelopus chirripoensis: Savage and Bolaños. 2009. *Revista Biologia Tropical* 57: 381–386. New species.

Incilius aurarius: Mendelson et al. 2012. *Journal of Herpetology* 46: 473–479. New species.

Incilius karenlipsae: Mendelson and Mulcahy. 2010. *Zootaxa* 2396: 61–68. New species.

Craugastor evanesco: Ryan et al. 2010b. *Copeia* 2010: 405–409. New species.

Andinobates geminisae: Batista et al. 2014b. *Zootaxa* 3866: 333–352. New species.

Diasporus citrinobapheus: Hertz et al. 2012. *ZooKeys* 196: 23–46. New species.

Diasporus igneus: Batista et al. 2012. *Zootaxa* 3410: 51–60. New species.

Ecnomiohyla bailarina: Batista et al. 2014c. *Zootaxa* 3826: 449–474. New species.

Ecnomiohyla sukia: Savage and Kubicki. 2010. *Zootaxa* 2719: 21–34. New species.

Ecnomiohyla veraguensis: Batista et al. 2014c. *Zootaxa* 3826: 449–474. New species.

Pristimantis adnus: Crawford et al. 2010. *Herpetologica* 66: 171–185. New species.

Bolitoglossa aureogularis: Boza-Oviedo et al. 2012. *Zootaxa* 3309: 36–61. New species.

Bolitoglossa centenorum: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa chucantiensis: Batista et al. 2014d. *Mesoamerican Herpetology* 1: 96–121. New species.

Bolitoglossa daryorum: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa eremia: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa huehuetenanguensis: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa jugivagans: Hertz et al. 2013. *Zootaxa* 3636: 463–475. New species.

Bolitoglossa kamuk: Boza-Oviedo et al. 2012. *Zootaxa* 3309: 36–61. New species.

Bolitoglossa kaqchikelorum: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa la: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa ninadormida: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa nussbaumi: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa nympha: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa omniumsanctorum: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. Resurrection from synonymy.

Bolitoglossa pacaya: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa psephena: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa pygmaea: Bolaños and Wake. 2009. *Zootaxa* 1981: 57–68. New species.

Bolitoglossa robinsoni: Bolaños and Wake. 2009. *Zootaxa* 1981: 57–68. New species.

Bolitoglossa splendida: Boza-Oviedo et al. 2012. *Zootaxa* 3309: 36–61. New species.

Bolitoglossa suchitanensis: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa tenebrosa: Vásquez-Almazán and Rovito. 2014. *Journal of Herpetology* 48: 518–524. New species.

Bolitoglossa tzultacaj: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa xibalba: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Bolitoglossa zacapensis: Rovito et al. 2010. *Journal of Herpetology* 44: 516–525. New species.

Cryptotriton necopinus: McCranie and Rovito. 2014. Zootaxa 3795: 61–70. New species.

Cryptotriton sierraminensis: Vásquez-Almazán et al. 2009. *Copeia* 2009: 313–319. New species.

Dendrotriton chujorum: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Dendrotriton kekchiorum: Campbell et al. 2010. *Miscellaneous Publications, Museum of Zoology, University of Michigan* (200): i–iv, 1–60. New species.

Nototriton matama: Boza-Oviedo et al. 2012. *Zootaxa* 3309: 36–61. New species.

Nototriton mime: Townsend et al. 2013c. *Zootaxa* 3666: 359–368. New species.

Nototriton picucha: Townsend et al. 2011. *Systematics and Biodiversity* 9: 275–287. New species.

Oedipina chortiorum: Brodie et al. 2012. *Journal of Herpetology* 46: 233–240. New species.

Oedipina koehleri: Sunyer et al. 2011. *Breviora* 526: 1–16. New species.

Oedipina motaguae: Brodie et al. 2012. *Journal of Herpetology* 46: 233–240. New species.

Oedipina nica: Sunyer et al. 2010. *Zootaxa* 2613: 29–39. New species.

Oedipina nimaso: Boza-Oviedo et al. 2012. *Zootaxa* 3309: 36–61. New species.

Oedipina petiola: McCranie and Townsend. 2011. *Zootaxa* 2990: 59–68. New species.

Oedipina tzutujilorum: Brodie et al. 2012. *Journal of Herpetology* 46: 233–240. New species.

Dactyloa ginaelisae: Lotzkat et al. 2013. *Zootaxa* 3626: 1–54. New species.

Dactyloa ibanezi: Poe et al. 2009. *Phyllomedusa* 8: 81–87. New species.

Norops alocomyos: Köhler et al. 2014. *Zootaxa* 3915: 111–122. New species.

Norops beckeri: Köhler. 2010. *Zootaxa* 2354: 1–8. Resurrection from the synonymy of *A. pentaprion*.

Norops benedikti: Lotzkat et al. 2011. *Zootaxa* 3125: 1–21. New species.

Norops charlesmyersi: Köhler. 2010. *Zootaxa* 2354: 1–8. New species.

Norops gaigei: Köhler et al. 2012. *Zootaxa* 3348: 1–23. Resurrection of *A. gaigei* from the synonymy of *A. tropidogaster*.

Norops leditzigorum: Köhler et al. 2014. *Zootaxa* 3915: 111–122. New species.

Norops marsupialis: Köhler et al. 2015. *Zootaxa* 3915: 111–122. Resurrection of *A. marsupialis* from the synonymy of *A. humilis*. Previously recognized at the species level without comment by Bolaños et al. (2011).

Norops monteverde: Köhler. 2009. *Journal of Herpetology* 43: 11–20. New species.

Norops osa: Köhler et al. 2010a. *Zootaxa* 2718: 23–38. New species.

Norops tenorioensis: Köhler 2011. *Zootaxa* 3120: 29–42. New species.

Norops triumphalis: Nicholson and Köhler. 2014. *Zootaxa* 3895: 225–237. New species.

Norops unilobatus: Köhler and Vesely. 2010. *Herpetologica* 66: 186–207. New species.

Dendrotriton chujorum. This salamander is endemic to the northern portion of the Sierra de Cuchumatanes in northwestern Guatemala, where occurs in the lower extent of Montane Wet Forest at elevations from 2,697 to 2,792 m in. We gauged its EVS as 18, placing it in the upper portion of the high vulnerability category, and its IUCN status is Critically Endangered. This individual is from near San Mateo Ixtatán, Sierra de los Cuchumatanes, Guatemala. *Photo by Todd Pierson.*

Diasporus igneus. The Fiery Rainfrog is known only from the eastern and western slopes of Cerro Santiago in the Serranía de Tabasará in central Panama, where it occurs in Lower Montane Wet Forest at elevations from 1,699 to 1,815 m. We determined its EVS as 18, placing it in the upper portion of the high vulnerability category, but its IUCN status has not been determined. This individual is from Llano Tugri, in the Comarca Ngöbe Buglé. *Photo by Abel Batista.*

Diploglossus bilobatus. This anguid lizard is distributed along the Atlantic lowlands and premontane slopes of Costa Rica and northwestern Panama, where it occurs in Lowland Moist and Wet forests, Premontane Wet Forest and Premontane Rainforest at elevations from near sea level to 1,360 m. We determined its EVS as 16, placing in the middle of the high vulnerability category, and its IUCN status is Least Concern. This individual is from Isla Bopa, province of Bocas del Toro, Panama. *Photo by Abel Batista.*

Dipsas articulata. This slug-eating snake is found along the Atlantic versant from southeastern Nicaragua to western Panama, where it occurs in Lowland Moist and Wet forests at elevations from near sea level to 500 m. We assessed its EVS as 15, placing it in the lower portion of the high vulnerability category, and its IUCN status is Least Concern. This individual is from Greytown, department of Río San Juan, Nicaragua. *Photo by Javier Sunyer.*

Norops wellbornae: Köhler and Vesely. 2010. *Herpetologica* 66: 186–207. Resurrection from the synonymy of *A. sericeus*.

Ctenosaura praeocularis: Hasbún and Köhler. 2009. *Journal of Herpetology* 43: 192–204. New species.

Marisora magnacornae: Hedges and Conn. 2012. *Zootaxa* 3288: 1–244. New species.

Marisora roatanae: Hedges and Conn. 2012. *Zootaxa* 3288: 1–244. New species.

Phyllodactylus paralepis: McCranie and Hedges. 2013b. *Zootaxa* 3694: 51–58. New species.

Sphaerodactylus alphus: McCranie and Hedges. 2013a. *Zootaxa* 3694: 40–50. New species.

Sphaerodactylus continentalis: McCranie and Hedges. 2012. *Zootaxa* 3492: 65–76. Resurrection from synonymy.

Sphaerodactylus guanajae: McCranie and Hedges. 2012. *Zootaxa* 3492: 65–76. New species.

Sphaerodactylus leonardovaldesi: McCranie and Hedges. 2012. *Zootaxa* 3,492: 65–76. New species.

Sphaerodactylus poindexteri: McCranie and Hedges. 2013. *Zootaxa* 3694: 40–50. New species.

Ameiva praesignis: Ugueto and Harvey. 2011. *Herpetological Monographs* 25: 113–170. Elevation to species level from within *A. ameiva*.

Cnemidophorus duellmani: McCranie and Hedges. 2013c. *Zootaxa* 3722: 301–316. New species.

Dermophis occidentalis. This caecilian is endemic to the southern Pacific versant of Costa Rica, where it occurs in Lowland Moist and Premontane Wet forests at elevations from 50 to 970 m. We determined its EVS as 17, placing it in the middle portion of the high vulnerability category, and its IUCN status is Data Deficient. This individual is from Río Piro, province of Puntarenas. *Photo by Eduardo Boza Oviedo.*

Cnemidophorus ruatanus: McCranie and Hedges. 2013c. *Zootaxa* 3722: 301–316. Resurrection from the synonymy of *C. lemniscatus*.

Boa imperator: Hynková et al. 2009. *Zoological Science* 26: 623–631. Elevation to species level from within *B. constrictor*.

Dendrophidion apharocybe: Cadle 2012. *Bulletin of the Museum of Comparative Zoology* 160: 183–240. New species.

Dendrophidion crybelum: Cadle 2012. *Bulletin of the Museum of Comparative Zoology* 160: 183–240. New species.

Dendrophidion rufiterminorum: Cadle and Savage. 2012. *Zootaxa* 3513: 1–50. New species.

Tantilla olympia: Townsend et al. 2013a. *Journal of Herpetology* 47: 191–200. New species.

Tantilla psittaca: McCranie 2011b. *Zootaxa* 3037: 37–44. New species.

Omoadiphas cannula: McCranie and Cruz Díaz. 2010. *Zootaxa* 2690: 53–58. New species.

Sibon merendonensis: Rovito et al. 2012. *Zootaxa* 3266: 62–68. New species.

Sibon noalamina: Lotzkat et al. 2012. *Zootaxa* 3485: 26–40. New species.

Sibon perissostichon: Köhler et al. 2010b. *Herpetologica* 66: 80–85. New species.

Epictia magnamaculata: Adalsteinnsson et al. 2009. *Zootaxa* 2244: 1–50. Transfer from genus *Leptotyphlops* and resurrection from the synonymy of *E. goudotii*.

Bothriechis guifarroi: Townsend et al. 2013b. *ZooKeys* 298: 77–105. New species.

Cerrophidion sasai: Jadin et al. 2012. *Zoological Scripta* doi: 10.1111/j.1463-6409.2012.00547.x. New species.

Cerrophidion wilsoni: Jadin et al. 2012. *Zoological Scripta* doi: 10.1111/j.1463-6409.2012.00547.x. New species.

These 92 species represent an increase of 9.7% over the 952 species listed for Central America by Wilson and Johnson (2010: Appendix 1).

The following species has undergone synonymization:

Pristimantis educatoris: Ryan et al. 2010a. *Journal of Herpetology* 44: 193–200. Synonymized with *P. caryophyllaceus* (Batista et al. 2014).

The following 29 species have undergone status changes:

Incilius chompipe: Mendelson et al. 2011. *Zootaxa* 3138: 1–34. Transfer from genus *Crepidophryne*.

Incilius epioticus: Mendelson et al. 2011. *Zootaxa* 3138: 1–34. Transfer from genus *Crepidophryne*.

Incilius guanacaste: Mendelson et al. 2011. *Zootaxa* 3138: 1–34. Transfer from genus *Crepidophryne*.

Andinobates claudiae: Brown et al. 2011. *Zootaxa* 3083: 1–120. Transfer from genus *Ranitomeya*.

Andinobates fulguritus: Brown et al. 2011. *Zootaxa* 3083: 1–120. Transfer from genus *Ranitomeya*.

Andinobates minutus: Brown et al. 2011. *Zootaxa* 3083: 1–120. Transfer from genus *Ranitomeya*.

Agalychnis lemur: Faivovich et al. 2010. *Cladistics* 26: 227–261. Transfer from genus *Hylomantis*.

Trachycephalus typhonius: Lavilla et al. 2010. *Zootaxa* 2671: 17–30. New name for *T. venulosus*.

Leptodactylus insularum: Heyer and de Sá. 2011. Smithsonian Contributions to *Zoology* 635: i–vii, 1–58. Name *L. insularum* applied to populations in Costa Rica and Panama, as well as Colombia, Venezuela, and Trinidad. Called *L. bolivianus* in Wilson et al. (2010).

Ctenophryne aterrima: de Sá et al. 2012. BMC *Evolutionary Biology* 12: 241 (21 pp.). Formerly placed in the genus *Nelsonophryne*, now placed in synonymy of *Ctenophryne*.

Elachistocleis panamensis: de Sá et al. 2012. *BMC Evolutionary Biology* 12: 241 (21 pp.). Transfer from genus *Chiasmocleis*.

Elachistocleis pearsei: de Sá et al. 2012. *BMC Evolutionary Biology* 12: 241 (21 pp.). Return to genus *Elachistocleis* from *Relictivomer*. This species was not considered in Wilson et al. (2010), but was shown to occur in Panama by Köhler (2011b).

Hypopachus pictiventris: Streicher et al. 2012. *Molecular Phylogenetics and Evolution* 64: 645–653. Tentative transfer from genus *Gastrophryne*. Transfer supported by de Sá et al. 2012. *BMC Evolutionary Biology* 12: 241 (21 pp.).

Hypopachus ustus: Streicher et al. 2012. *Molecular Phylogenetics and Evolution* 64: 645–653. Tentative transfer from genus *Gastrophryne*. Spelling of specific epithet corrected by Frost (2013). Transfer supported by de Sá et al. 2012. *BMC Evolutionary Biology* 12: 241 (21 pp.).

Marisora alliacea: Hedges and Conn. 2012. *Zootaxa* 3288: 1–244. Transfer from the genus *Mabuya*.

Marisora brachypoda: Hedges and Conn. 2012. *Zootaxa* 3288: 1–244. Transfer from the genus *Mabuya*.

Marisora unimarginata: Hedges and Conn. 2012. *Zootaxa* 3288: 1–244. Transfer from the genus *Mabuya*.

Holcosus chaitzami: Harvey et al. 2012. *Zootaxa* 3459: 1–156. Transfer from the genus *Ameiva*.

Holcosus festivus: Harvey et al. 2012. *Zootaxa* 3459: 1–156. Transfer from the genus *Ameiva*.

Holcosus leptophrys: Harvey et al. 2012. *Zootaxa* 3459: 1–156. Transfer from the genus *Ameiva*.

Holcosus quadrilineatus: Harvey et al. 2012. *Zootaxa* 3459: 1–156. Transfer from the genus *Ameiva*.

Holcosus undulatus: Harvey et al. 2012. *Zootaxa* 3459: 1–156. Transfer from the genus *Ameiva*.

Epictia magnamaculata: Adalsteinnsson et al. 2009. *Zootaxa* 2244: 1–50. Resurrection from the synonymy of *E. goudotii*.

Trichellostoma macrolepis: Adalsteinnsson et al. 2009. *Zootaxa* 2244: 1–50. Transfer from the genus *Leptotyphlops*. Later established as the type species of a new leptotyphlopid genus *Trilepida* by Hedges (2011).

Amerotyphlops costaricensis: Hedges et al. 2014. *Caribbean Herpetology* 49: 1–61. Transfer from the genus *Typhlops*.

Amerotyphlops microstomus: Hedges et al. 2014. *Caribbean Herpetology* 49: 1–61. Transfer from the genus *Typhlops*.

Amerotyphlops stadelmani: Hedges et al. 2014. *Caribbean Herpetology* 49: 1–61. Transfer from the genus *Typhlops*.

Amerotyphlops tenuis: Hedges et al. 2014. *Caribbean Herpetology* 49: 1–61. Transfer from the genus *Typhlops*.

Amerotyphlops tycherus: Hedges et al. 2014. *Caribbean Herpetology* 49: 1–61. Transfer from the genus *Typhlops*.

Streicher et al. (2014) examined evolutionary relationships among some members of the *Craugastor rhodopis* species group and recognized four major clades, including one identified as *C. occidentalis*, which required its movement from the *C. mexicanus* species series to the *C. rhodopis* species group. A clade in eastern Mexico corresponds to *C. rhodopis* and one on both the Pacific and Atlantic versants of southeastern Mexico, Guatemala, and El Salvador to *C. loki*. Further, they identified a haplotype from Volcán San Martín in southern Veracruz, Mexico, which might correspond to a separate evolutionary lineage. The authors also indicated that, “a small group of specimens was reported from the northern department of Cortés in Honduras [that report appeared in McCranie and Wilson, 2002], but the actual occurrence of *C. loki* in Honduras is questionable given the abundance of the morphologically similar *C. chac*, *C. gollmeri*, and *C. laticeps*, in this region …” The authors left the identity of the Honduran material and the status of other populations in the *rhodopis* species group to future work.

In a broad-scale paper on blindsnake taxonomy, Hedges et al. (2014) transferred five Central American typhlopid species from *Typhlops* to a new genus, *Amerotyphlops*. This study, based on morphological and molecular data, supported the recognition of four subfamilies, of which three were described anew, and contains essentially geographically cohesive groups of genera and species. Recognition of the three new subfamilies restricts the remaining subfamily, the Typhlopinae, to genera and species in the New World. The authors recognized four genera, of which *Amerotyphlops*, *Antillotyphlops*, and *Cubatyphlops* were described as new. Interestingly, the first of these genera is composed of 14 species distributed “primarily on the mainland, ranging from eastern Mexico (Veracruz) to southern South America (Bolivia and Argentina), and includes a West Indian species, *A. tasymicris* in Grenada and the Grenadines” (Hedges et al. 2014: 44). Five of the 14 species are distributed in Central America (Appendix 2).

Torres et al. (2013) reported *Abronia lythrochila*, formerly a Mexican endemic, from northwestern Guatemala, thus adding this species to the Central American herpetofauna.

Griffin and Powell (2014) reported *Tropidodipsas fasciata*, formerly a Mexican endemic, from Guatemala, thus adding this species to the Central American herpetofauna.

Ecnomiohyla bailarina. The Golden-eyed Fringe-limbed Treefrog is known only from the type locality in extreme southwestern Panama near the border with Colombia (but, see Addendum), where it occurs in Premontane Wet Forest at an elevation of 750 m. We calculated its EVS as 20, placing it at the upper end of the high vulnerability category, but its IUCN status has not been determined. This individual is from the northern slope of the Jingurudó mountain range in the Comarca Emberá-Wounaan, in the Darién region. *Photo by Abel Batista.*

Heloderma charlesbogerti. The Motagua Valley Beaded Lizard is restricted to the Motagua Valley in eastern Guatemala, where it occurs in Lowland Arid and Premontane Dry forests at elevations from 300 to 900 m. We assessed its EVS as 18, placing it in the upper portion of the high vulnerability category, but its IUCN status has not been determined. This individual is from the Motagua River Valley in Guatemala. *Photo by Antonia Pachmann.*

Olson and David (2014) changed the spelling of the specific name of the single species of *Chelonoidis* occurring in Central America to *carbonarius*, given the ICZN requirement (ICZN 1999; Article 30,2.4) to treat the generic name as masculine since the original author (Fitzinger 1835) did not state it explicitly to be feminine.

Some other qualifications concerning the taxonomic status of certain species to which we adhere are found in the above Controversial Taxonomic Issues section.

Diversity and Endemism in the Central American Herpetofauna

Mesoamerica is one of the world's most important biodiversity reservoirs, and Central America contains a substantial component of that region's herpetofauna (Wilson and Johnson 2010). The Central American herpetofauna presently consists of 1,052 species (319 anurans, 159 salamanders, 15 caecilians, 3 crocodylians, 532 squamates, and 24 turtles; Table 1). Compared to the herpetofauna of Mexico, which currently consists of 1,252 species (239 anurans, 141 salamanders, 3 caecilians, 3 crocodylians, 818 squamates, and 48 turtles; J. D. Johnson, unpublished data), the number of species in Central America is significant given that the area of Mexico is about 3.75 times larger than that of Central America (www.cia.gov; accessed 14 December 2013). Compared to Mexico, Central America also is a haven for anurans, salamanders, and caecilians, as it contains 1.3 times more species. In contrast, however, Mexico contains 1.6 times more crocodylians, squamates, and turtles than Central America. Evidently, these differences are related to the environmental requirements for these two groups of vertebrates, and the variety of ecosystems in the two regions.

The 493 species amphibians in Central America are classified in 16 families and 69 genera (Table 1). The Hylidae contains the most genera (21); the remaining 15 families contain 1–8 genera. The Dendrobatidae and Plethodontidae contain eight genera each; the remaining anuran and caecilian families five or fewer (Table 1). The number of species per family ranges from one (Pipidae and Rhinophrynidae) to 159 (Plethodontidae). Three families (Craugastoridae, Hylidae, and Plethodontidae) contain close to or considerably more than 100 species each, and collectively total 358 (72.6%) of all the amphibian species. The remaining 13 families contain 1–39 species (the latter number is for the Bufonidae). In total, there are 13 families and 57 genera of anurans, one family and eight genera of salamanders, and two families and four genera of caecilians.

The 559 species of crocodylians, squamates, and turtles in Central America are classified in 42 families and 145 genera (Table 1). The Colubridae and Dipsadidae are the largest, with 24 and 35 genera, respectively; the remaining families contain 1–8 genera. Two families contain eight genera (Gymnophthalmidae and Viperidae), and the others contain five or fewer (Table 1). The number of species per family ranges from one (seven families) to 144 (Dipsadidae). Two families (Dactyloidae and Dipsadidae) contain close to or considerably more than 100 species (Table 1), collectively 239 (42.8%) of all the squamate species. The remaining 40 families contain 1–32 species (the latter number is for Viperidae). In total, there are two families and two genera of crocodylians, nine families and 14 genera of turtles, and 31 families and 129 genera of squamates.

The herpetofauna of Central America also is characterized by a high degree of endemism (Table 1). Of the 493 species of anurans, salamanders, and caecilians in

Table 1. Family composition and endemicity of the Central American herpetofauna.

Families	Genera	Species	Endemic Species	Percentage of Endemicity
Aromobatidae	2	3	2	66.7
Bufonidae	4	39	23	59.0
Centrolenidae	5	14	3	21.4
Craugastoridae	3	101	77	76.2
Dendrobatidae	8	19	12	63.2
Eleutherodactylidae	2	11	6	54.5
Hemiphractidae	2	3	0	0
Hylidae	21	98	53	54.1
Leptodactylidae	3	9	1	11.1
Microhylidae	4	9	1	11.1
Pipidae	1	1	1	100
Ranidae	1	11	5	45.5
Rhinophrynidae	1	1	0	0
Total Anurans	**57**	**319**	**184**	**57.5**
Plethodontidae	8	159	133	83.6
Total Salamanders	**8**	**159**	**133**	**83.6**
Caeciliidae	2	7	3	42.9
Dermophiidae	2	8	4	50.0
Total Caecilians	**4**	**15**	**7**	**46.7**
Total Amphibians	**69**	**493**	**324**	**65.7**
Alligatoridae	1	1	0	0
Crocodylidae	1	2	0	0
Total Crocodylians	**2**	**3**	**0**	**0**
Amphisbaenidae	1	2	0	0
Anguidae	5	28	22	78.6
Corytophanidae	3	9	0	0
Dactyloidae	3	95	67	70.5
Eublepharidae	1	2	0	0
Gymnophthalmidae	8	14	5	35.7
Helodermatidae	1	2	1	50.0
Hoplocercidae	2	2	0	0
Iguanidae	2	11	7	63.6
Mabuyidae	1	5	4	80.0
Phrynosomatidae	2	17	2	11.8
Phyllodactylidae	2	5	3	60.0
Polychrotidae	1	1	0	0
Scincidae	2	3	0	0
Sphaerodactylidae	4	19	10	52.6
Sphenomorphidae	1	4	1	25.0
Teiidae	4	12	4	33.3
Xantusiidae	1	4	1	25.0
Xenosauridae	1	1	0	0
Anomalepididae	3	3	1	33.3
Boidae	3	4	0	0
Charinidae	1	2	0	0

Table 1 (continued). Family composition and endemicity of the Central American herpetofauna.

Families	Genera	Species	Endemic Species	Percentage of Endemicity
Colubridae	24	74	26	35.1
Dipsadidae	35	144	78	54.2
Elapidae	2	18	8	44.4
Leptotyphlopidae	2	5	1	20.0
Loxocemidae	1	1	0	0
Natricidae	2	5	0	0
Sibynophiidae	1	2	0	0
Tropidophiidae	1	1	0	0
Typhlopidae	1	5	3	60.0
Viperidae	8	32	15	46.9
Total Squamates	**129**	**532**	**259**	**48.7**
Cheloniidae	4	5	0	0
Chelydridae	1	2	0	0
Dermatemydidae	1	1	0	0
Dermochelyidae	1	1	0	0
Emydidae	1	2	0	0
Geoemydidae	1	5	1	20.0
Kinosternidae	1	4	1	25.0
Staurotypidae	2	3	0	0
Testudinidae	1	1	0	0
Total Turtles	**14**	**24**	**2**	**8.3**
Total “Reptiles”	**145**	**559**	**261**	**46.7**
Total Herpetofauna	**214**	**1,052**	**585**	**55.6**

this region, 324 (65.7%) are endemic, and of the 559 species of crocodylians, squamates, and turtles, 261 (46.7%) are endemic. The percentage of endemicity for the entire herpetofauna is 55.6%. These figures are somewhat comparable to those for the Mexican herpetofauna (J.D. Johnson, unpublished data). Of the 383 Mexican amphibian species, 258 (67.4%) are endemic, and of the 869 species of crocodylians, squamates, and turtles, 499 (57.4%) are endemic. The percentage of endemicity for the entire herpetofauna is 60.5% (J.D. Johnson, unpublished data).

Among the Central American amphibians, the percentage of endemicity at the family level ranges from zero (Hemiphractidae and Rhinophrynidae) to 100 (Pipidae). Interestingly, each of these anuran families contains 1–3 species in Central America. The largest number of endemic species is in the family Plethodontidae (133); its percentage of endemicity is 83.6. The Bufonidae (23), Craugastoridae (77), and Hylidae (53) also contain sizable numbers of endemic species. Collectively, these four families contain 286 (88.3%) of all the amphibian endemic species.

Among the crocodylians, squamates, and turtles, the percentage of endemicity at the family level ranges from zero (in 21 families) to 80.0% (Mabuyidae). As with amphibians, the 21 families with no endemics contain relatively few species (nine or fewer). The largest number of endemic squamates is in the family Dipsadidae (78), with the next largest being the Dactyloidae (67). The next most sizable numbers of endemic species are in the families Colubridae (26) and Viperidae (15). Collectively, these four families contain 186 (71.8%) of all the squamate endemic species.

In summary, four amphibian and four squamate families contain the largest numbers of endemic species in Central America (472; 81.1%) of the 585 endemic species known from this region (Table 1). In total, these eight families contain 742 species, of which 63.6% are endemic to Central America (Table 1). With additional exploration and systematic research, the number and proportion of endemic species in Central America should continue to rise.

IUCN Red List Assessment of the Central American Herpetofauna

In response to the emerging picture of global amphibian population decline, the IUCN began a conservation assessment of the world’s amphibians (see Stuart et al. 2004). Consequently, in 2002, a workshop to assess the Mesoamerican amphibians was held at the La Selva Biological Station in Costa Rica, followed by one in Jalisco, Mexico, to assess the crocodylians, squamates,

Table 2. IUCN Red List categorizations for Central American herpetofaunal families.

Families	Number of Species	IUCN Red List categorizations							
		Extinct	Critically Endangered	Endangered	Vulnerable	Near Threatened	Least Concern	Data Deficient	Not Evaluated
Aromobatidae	3	—	—	—	—	—	1	—	2
Bufonidae	39	1	9	7	3	1	12	4	2
Centrolenidae	14	—	—	—	—	1	12	1	—
Craugastoridae	101	2	23	16	10	8	26	14	2
Dendrobatidae	19	—	—	3	1	1	8	5	1
Eleutherodactylidae	11	—	—	—	3	—	5	1	2
Hemiphractidae	3	—	—	1	—	1	1	—	—
Hylidae	98	—	33	14	5	5	35	3	3
Leptodactylidae	9	—	1	—	—	—	8	—	—
Microhylidae	9	—	—	—	1	—	8	—	—
Pipidae	1	—	—	1	—	—	—	—	—
Ranidae	11	—	—	—	3	1	6	—	1
Rhinophrynidae	1	—	—	—	—	—	1	—	—
Total Anurans	**319**	**3**	**66**	**42**	**26**	**18**	**123**	**28**	**13**
Plethodontidae	159	—	25	33	17	8	19	18	39
Total Salamanders	**159**	**—**	**25**	**33**	**17**	**8**	**19**	**18**	**39**
Caeciliidae	7	—	—	—	—	—	3	4	—
Dermophiidae	8	—	—	—	1	—	2	5	—
Total Caecilians	**15**	**—**	**—**	**—**	**1**	**—**	**5**	**9**	**—**
Total Amphibians	**493**	**3**	**91**	**75**	**44**	**26**	**147**	**55**	**52**
Alligatoridae	1	—	—	—	—	—	1	—	—
Crocodylidae	2	—	—	—	1	—	1	—	—
Total Crocodylians	**3**	**—**	**—**	**—**	**1**	**—**	**2**	**—**	**—**
Amphisbaenidae	2	—	—	—	—	—	1	—	1
Anguidae	28	—	2	8	2	2	6	5	3
Corytophanidae	9	—	—	—	—	—	5	—	4
Dactyloidae	95	—	—	3	1	—	4	3	84
Eublepharidae	2	—	—	—	—	—	2	—	—
Gymnophthalmidae	14	—	—	—	—	1	4	—	9
Helodermatidae	2	—	—	—	—	—	—	—	2
Hoplocercidae	2	—	—	—	—	—	—	—	2
Iguanidae	11	—	1	4	—	1	1	1	3
Mabuyidae	5	—	1	—	—	—	3	1	—
Phrynosomatidae	17	—	—	—	—	—	17	—	—
Phyllodactylidae	5	—	—	—	1	—	1	—	3
Polychrotidae	1	—	—	—	—	—	—	—	1
Scincidae	3	—	—	—	—	—	3	—	—
Sphaerodactylidae	19	—	—	—	—	—	10	—	9
Sphenomorphidae	4	—	—	—	—	—	2	1	1
Teiidae	12	—	—	—	—		6	1	5
Xantusiidae	4	—	—	—	—	1	3	—	—
Xenosauridae	1	—	—	—	1	—	—	—	—
Anomalepididae	3	—	—	—	—	—	—	2	1
Boidae	4	—	—	—	—	—	—	—	4

Table 2 (continued). IUCN Red List categorizations for Central American herpetofaunal families.

Families	Number of Species	IUCN Red List categorizations							
		Extinct	Critically Endangered	Endangered	Vulnerable	Near Threatened	Least Concern	Data Deficient	Not Evaluated
Charinidae	2	—	—	—	—	—	—	—	2
Colubridae	74	—	1	2	3	—	37	5	26
Dipsadidae	144	—	7	11	5	8	66	15	32
Elapidae	18	—	1	—	—	—	12	—	5
Leptotyphlopidae	5	—	—	—	—	—	1	—	4
Loxocemidae	1	—	—	—	—	—	1	—	—
Natricidae	5	—	—	—	—	—	5	—	—
Sibynophiidae	2	—	—	—	—	—	1	—	1
Tropidophiidae	1	—	—	—	—	—	—	—	1
Typhlopidae	5	—	—	—	1	—	3	—	1
Viperidae	32	—	—	2	1	1	12	1	15
Total Squamates	**532**	**—**	**13**	**30**	**15**	**14**	**206**	**35**	**219**
Cheloniidae	5	—	2	2	1	—	—	—	—
Chelydridae	2	—	—	—	1	—	—	—	1
Dermatemydidae	1	—	1	—	—	—	—	—	—
Dermochelyidae	1	—	1	—	—	—	—	—	—
Emydidae	2	—	—	—	—	—	—	—	2
Geoemydidae	5	—	—	—	—	3	—	—	2
Kinosternidae	4	—	—	—	1	1	—	—	2
Staurotypidae	3	—	—	—	—	3	—	—	—
Testudinidae	1	—	—	—	—	—	—	—	1
Total Turtles	**24**	**—**	**4**	**2**	**3**	**7**	**—**	**—**	**8**
Total "Reptiles"	**559**	**—**	**17**	**32**	**19**	**21**	**208**	**35**	**227**
Total Herpetofauna	**1,052**	**3**	**108**	**107**	**63**	**47**	**355**	**90**	**279**

and turtles of that country. Several years later, in 2012, a workshop to assess the squamates of Central America was held at Parque Nacional Palo Verde in Costa Rica. The results of the first two workshops appeared on the IUCN Red List website, but to date those for the third remain incomplete. Wilson et al. (2013a, b) presented an overview and conclusions of these assessments for the Mexican herpetofauna.

We accessed the IUCN website (www.iucnredlist.org) to summarize the present situation for Central American amphibians (Table 2). The data in this table are somewhat more complete than for crocodylians, squamates, and turtles, given that the Global Reptile Assessment still is underway. Nonetheless, of 493 species of Central American amphibians, 52 species (10.5%) have not been evaluated as of this writing, so we placed them in the NE (Not Evaluated) category. The remaining categories are: Extinct (EX, 3 [0.6%]); Critically Endangered (CR, 91 [18.5%]); Endangered (EN, 75 [15.2%]); Vulnerable (VU, 44 [8.9%]); Near Threatened (NT, 26 [5.3%]); Least Concern (LC, 147 [29.8%]); and Data Deficient (DD, 55 [11.2%]). A total of 210 species (42.6%), therefore, have been assessed in one of the three threat categories (CR, EN, or VU), which is slightly more than 10% higher than what was reported for these categories on a global scale (32.3%) by Stuart et al. (2010). If the EX and DD species are added to those in the threat categories, then 268 (54.4%) species are extinct, threatened with extinction, or too poorly known to allow for an assessment; these results are similar to those reported for the global situation (EX+CR+EN+VU+DD = 3,181 [55.4%]; Stuart et al. 2010). This percentage, however, is about 10 points lower than that reported for the Mexican amphibians (Wilson et al. 2013b).

The families Craugastoridae (49 of 101 species; 48.5%), Hylidae (52 of 98 species; 53.1%), and Plethodontidae (75 of 159 species; 47.2%) contain the greatest number and proportion of threatened species. For the salamanders, if the numbers of DD and NE species are added to those considered threatened (18+39+75 = 132), then 83.0% of the 159 Central American species are threatened, poorly known, or have not been evaluated. Collectively, the 358 species in the three largest families comprise 72.6% of the amphibian taxa in Central America, and the 176 threatened species in these families make up 83.8% of the 210 total. A similar proportion is seen among the Mexican amphibians (88.6% of 211 totals).

As startling as the statistics for amphibian population decline are on a global scale (Stuart et al. 2010), on a regional scale for Central America they are more alarming. According to the IUCN criteria, about four out of every 10 species of amphibians are judged as threatened, and more than one-half of those are threatened or too poorly known to allow for an assessment, which is the case for the most speciose families in the region. Two factors are expected to keep increasing the severity of this decline, even without considering the rate of accelerating environmental deterioration. The first is that new species will continue to be described, as indicated above in the discussion on taxonomic changes since the publication of Wilson et al. (2010). The other factor is that advancing molecular studies, especially on broadly distributed taxa, will continue to reveal the presence of new species. Both of these factors will increase the number of threatened taxa. As an example, Ruane et al. (2014) studied the molecular systematics of *Lampropeltis triangulum*, a species that for many decades was considered one of the world's most broadly distributed terrestrial snakes (Williams 1988). These authors recognized seven species in what previously was considered a single species-level taxon, and noted that additional species in this complex likely will be recognized in the future.

Critique of the IUCN Assessment

In conservation reassessments for the Mexican herpetofauna, we criticized the IUCN system of categorization and provided distinctions between this system and the EVS (Wilson et al. 2013a, b). Alvarado-Díaz et al. (2013) also criticized this system. The principal criticisms levied by these authors are as follows:

1. Using the IUCN system of conservation assessment is expensive and time-consuming. Stuart et al. (2010) provided a figure of $534.12 for the average cost of creating an IUCN threat assessment for a single species. If this figure were applied to the 1,052 species making up the Central American herpetofauna, the total expenditure would be $561,894.24. In comparison, costs for our EVS assessments were negligible because they were accomplished using the resources of the Internet and our own volunteered time. Creating the IUCN Global Amphibian Assessment, of which the results appeared in 2004 (Stuart et al. 2004) involved a number of years. For example, one of us (LDW) attended the Mesoamerican Amphibian Workshop undertaken at the La Selva Biological Station in Costa Rica in November 2002, so a period of close to two years elapsed before the global results were published (Stuart et al. 2004). Another example is that the complete results of the Central American Reptile Workshop, attended by two of us (JDJ and LDW), have not appeared two years and two months since this workshop was conducted at Palo Verde National Park in Costa Rica in May of 2012 (as of 1 March 2015). The delay primarily has been caused because evaluations for most of the anoles have not been completed, and because evaluations for a sizable number of species that occur in both Central America and South America will not be available until all of the relevant workshops for the latter region are completed. In contrast, we began working on the present paper in early October, 2013. We completed most of our EVS assessment of the Central American herpetofauna by the early portion of January, 2014, but the publication of this paper was delayed because we needed to wait until the entire results of the Palo Verde Workshop appeared at the IUCN Red List website (but see above). Accordingly, we consider it pertinent to quote the "important note" or proviso indicated on the Overview paper at the amphibians.org website, as follows: "Given the current quality control requirements needed for conservation assessments to be published on the IUCN Red List, and our very limited human resources, we are unable to process large numbers of assessments at this time. Country-level global reassessments may be possible if requests come with the funding and resources necessary to conduct such reassessments, or if the herpetological community of the country or region in question is willing to take over stewardship of its global assessments through its respective regional/national working group." Thus, the expense for such IUCN assessments has overwhelmed the ability of this organization to continue undertaking this work.

2. New herpetofaunal taxa are described more rapidly than the IUCN procedures can provide a conservation assessment. As noted in the previous section, 52 species of amphibians (13 anurans and 39 salamanders) remain unevaluated by the IUCN, which is 10.5% of the 493 species known from Central America as of this writing. Comparable figures are not available for the remainder of the herpetofauna, since the Global Reptile Assessment is ongoing, but we can state that 32 species of squamates (lizards and snakes) have been described since the publication of Wilson and Johnson (2010). This figure represents 6.0% of the 532 species of squamates now known from Central America. The data in Table 2 indicate that 227 species of crocodylians, squamates, and turtles (40.6% of the total of 559 species) have not been evaluated. Given the provisos indicated in the above paragraph and the consequences indicated, a much more rapid and cost-effective mode of conservation assessment is needed, not only for keeping up with the advances of systematic knowledge, but more importantly because of the increasing rate of environmental deterioration.

3. Once new herpetofaunal species are incorporated into the IUCN Red List, often they are placed in the Data Deficient category due to an expected lack of initial information on their population status. In particular, this situation occurs with taxa described from a single specimen and/or a single locality. Species in this category were termed "threat species in disguise" by Wilson et al. (2013b), because of the likelihood that such species, once evaluated, would fall into one of the three threat categories. One of our recommendations deals with this issue.

4. Typically, large numbers of taxa are assigned to the Least Concern (LC) category, described by Wilson et al. (2013b) as a "dumping ground" for species that might require "a more discerning look that would demonstrate that many of these species should be partitioned into IUCN categories other than LC," such as the three threat categories and the Near Threatened one. This opinion was expressed after the authors examined the relationship between the IUCN categorizations and the EVS assessments for Mexican amphibians, and is corroborated here by the assessment

Table 3. Environmental Vulnerability Scores for Central American herpetofaunal species, arranged by family. Shaded area to the left encompasses low vulnerability scores, and to the right high vulnerability scores.

Families	Number of species	Environmental Vulnerability Scores																	
		3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Aromabatidae	3	—	—	—	—	—	—	—	—	1	—	—	—	—	1	—	1	—	—
Bufonidae	39	1	—	—	1	1	2	3	1	3	3	8	9	4	2	1	—	—	—
Centrolenidae	14	—	—	—	—	—	1	1	2	2	4	1	—	1	2	—	—	—	—
Craugastoridae	101	—	—	—	—	—	—	1	—	1	6	2	6	15	35	17	18	—	—
Dendrobatidae	19	—	—	—	—	—	—	—	—	—	—	—	1	6	6	3	3	—	—
Eleutherodactylidae	11	—	—	—	—	—	—	—	—	1	1	—	—	3	1	2	3	—	—
Hemiphractidae	3	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—
Hylidae	98	1	2	—	—	3	4	2	6	9	11	18	18	8	1	2	4	3	6
Leptodactylidae	9	—	—	1	1	1	—	1	—	—	3	1	1	—	—	—	—	—	—
Microhylidae	9	—	1	—	—	—	2	—	1	1	3	—	1	—	—	—	—	—	—
Pipidae	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Ranidae	11	1	—	1	—	—	1	2	1	—	3	—	1	1	—	—	—	—	—
Rhinophrynidae	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Total Anurans	**319**	**3**	**3**	**2**	**2**	**5**	**11**	**10**	**11**	**18**	**34**	**30**	**37**	**39**	**50**	**26**	**29**	**3**	**6**
Total Anuran %	**—**	**0.9**	**0.9**	**0.6**	**0.6**	**1.6**	**3.4**	**3.1**	**3.4**	**5.6**	**10.7**	**9.4**	**11.6**	**12.2**	**15.7**	**8.2**	**9.1**	**0.9**	**1.9**
Plethodontidae	159	—	—	—	—	—	1	1	—	2	2	6	4	17	34	35	57	—	—
Total Salamanders	**159**	**—**	**—**	**—**	**—**	**—**	**1**	**1**	**—**	**2**	**2**	**6**	**4**	**17**	**34**	**35**	**57**	**—**	**—**
Total Salamander %	**—**	**—**	**—**	**—**	**—**	**—**	**0.6**	**0.6**	**—**	**1.3**	**1.3**	**3.8**	**2.5**	**10.7**	**21.4**	**22.0**	**35.8**	**—**	**—**
Caeciliidae	7	—	—	—	—	—	—	—	—	—	—	—	—	2	2	1	—	2	—
Dermophiidae	8	—	—	—	—	1	—	—	—	—	—	2	1	—	1	1	2	—	—
Total Caecilians	**15**	**—**	**—**	**—**	**—**	**1**	**—**	**—**	**—**	**—**	**—**	**2**	**1**	**2**	**3**	**2**	**2**	**2**	**—**
Total Caecilian %	**—**	**—**	**—**	**—**	**—**	**6.7**	**—**	**—**	**—**	**—**	**—**	**13.3**	**6.7**	**13.3**	**20.0**	**13.3**	**13.3**	**13.3**	**—**
Total Amphibians	**493**	**3**	**3**	**2**	**2**	**6**	**12**	**11**	**11**	**20**	**36**	**38**	**42**	**58**	**87**	**63**	**88**	**5**	**6**
Total Amphibian %	**—**	**0.6**	**0.6**	**0.4**	**0.4**	**1.2**	**2.4**	**2.2**	**2.2**	**4.1**	**7.3**	**7.7**	**8.5**	**11.8**	**17.6**	**12.8**	**17.8**	**1.0**	**1.2**
Alligatoridae	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Crocodylidae	2	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—
Total Crocodylians	**3**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**1**	**1**	**—**	**1**	**—**	**—**	**—**	**—**
Total Crocodylian %	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**33.3**	**33.3**	**—**	**33.3**	**—**	**—**	**—**	**—**
Amphisbaenidae	2	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—
Anguidae	28	—	—	—	—	—	1	—	—	—	—	1	2	7	9	3	5	—	—
Corytophanidae	9	—	—	—	—	1	—	2	1	2	—	2	—	1	—	—	—	—	—
Dactyloidae	95	—	—	—	—	2	2	4	1	1	4	12	11	23	13	22	—	—	—
Eublepharidae	2	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—

Table 3 (continued). Environmental Vulnerability Scores for Central American herpetofaunal species, arranged by family. Shaded area to the left encompasses low vulnerability scores, and to the right high vulnerability scores.

Families	Number of species	Environmental Vulnerability Scores																	
		3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Gymnophthalmidae	14	—	—	—	—	—	—	1	—	1	1	1	5	3	2	—	—	—	—
Helodermatidae	2	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—
Hoplocercidae	2	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—
Iguanidae	11	—	—	—	—	—	1	—	1	—	—	1	—	1	—	—	3	4	—
Mabuyidae	5	—	—	—	1	—	—	—	—	—	—	—	—	2	1	1	—	—	—
Phrynosomatidae	17	—	—	1	—	—	—	—	3	1	5	2	2	2	—	1	—	—	—
Phyllodactylidae	5	—	—	—	—	—	2	—	—	—	—	—	—	—	1	2	—	—	—
Polychrotidae	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Scincidae	3	—	—	—	—	—	—	—	—	—	1	1	1	—	—	—	—	—	—
Sphaerodactylidae	19	—	—	—	—	—	1	1	—	—	1	2	4	2	4	4	—	—	—
Sphenomorphidae	4	—	—	—	—	1	1	—	—	—	—	—	—	1	—	1	—	—	—
Teiidae	12	—	—	—	1	—	1	—	1	—	1	1	2	2	3	—	—	—	—
Xantusiidae	4	—	—	—	—	—	—	2	—	—	—	2	—	—	—	—	—	—	—
Xenosauridae	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Total Lizards	**236**	**—**	**—**	**1**	**2**	**5**	**9**	**11**	**7**	**6**	**15**	**26**	**29**	**45**	**33**	**34**	**9**	**4**	**—**
Anomalepididae	3	—	—	—	—	—	—	1	—	1	1	—	—	—	—	—	—	—	—
Boidae	4	—	—	—	—	—	2	—	—	1	—	1	—	—	—	—	—	—	—
Charinidae	2	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—
Colubridae	74	—	—	1	6	5	2	5	3	5	10	8	13	2	12	2	—	—	—
Dipsadidae	144	—	2	1	3	3	3	7	10	5	17	17	24	23	27	2	—	—	—
Elapidae	17	—	—	—	—	—	—	2	1	—	—	2	—	4	2	4	2	—	—
Leptotyphlopidae	5	—	—	2	—	—	—	—	1	—	2	—	—	—	—	—	—	—	—
Loxocemidae	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Natricidae	5	—	—	—	—	—	1	2	1	—	—	1	—	—	—	—	—	—	—
Sibynophiidae	2									1		1							
Tropidophiidae	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Typhlopidae	5	—	—	—	—	—	—	—	—	2	2	—	1	—	—	—	—	—	—
Viperidae	32	—	—	—	—	—	—	1	1	2	2	1	3	6	6	6	3	1	—
Total Snakes	**295**	**—**	**2**	**4**	**9**	**8**	**8**	**19**	**18**	**18**	**35**	**31**	**41**	**35**	**47**	**14**	**5**	**1**	**—**
Total Squamates	**531**	**—**	**2**	**5**	**11**	**13**	**17**	**30**	**25**	**24**	**50**	**57**	**70**	**80**	**80**	**48**	**14**	**5**	**—**
Total Squamate %	**—**	**—**	**0.4**	**0.9**	**2.1**	**2.4**	**3.2**	**5.6**	**4.7**	**4.5**	**9.4**	**10.7**	**13.2**	**15.1**	**15.1**	**9.0**	**2.6**	**0.9**	**—**
Chelydridae	2	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—
Dermatemydidae	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Emydidae	2	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—
Geoemydidae	5	—	—	—	—	—	1	—	—	—	1	1		1	1	—	—	—	—
Kinosternidae	4	—	—	—	—	—	2	—	—	—	—	—	1	—	1	—	—	—	—
Staurotypidae	3	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—
Testudinidae	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Total Turtles	**18**	**—**	**—**	**—**	**—**	**—**	**3**	**—**	**—**	**2**	**1**	**2**	**3**	**1**	**2**	**3**	**—**	**1**	**—**
Total Turtle %	**—**	**—**	**—**	**—**	**—**	**—**	**16.7**	**—**	**—**	**11.1**	**5.5**	**11.1**	**16.7**	**5.5**	**11.1**	**16.7**	**—**	**5.5**	**—**
Total “Reptiles”	**552**	**—**	**2**	**5**	**11**	**13**	**20**	**30**	**25**	**26**	**51**	**60**	**74**	**81**	**83**	**51**	**14**	**6**	**—**
Total “Reptile” %	**—**	**—**	**0.4**	**0.9**	**2.0**	**2.4**	**3.6**	**5.4**	**4.5**	**4.7**	**9.2**	**10.9**	**13.4**	**14.7**	**15.0**	**9.2**	**2.5**	**1.1**	**—**
Total Herpetofauna	**1,045**	**3**	**5**	**7**	**13**	**19**	**32**	**41**	**36**	**46**	**87**	**98**	**116**	**139**	**170**	**114**	**102**	**11**	**6**
Total Herpetofauna %	**—**	**0.3**	**0.5**	**0.7**	**1.2**	**1.8**	**3.1**	**3.9**	**3.4**	**4.4**	**8.3**	**9.4**	**11.1**	**13.3**	**16.3**	**10.9**	**9.8**	**1.1**	**0.6**

Imantodes phantasma. This blunt-headed treesnake is distributed in the Darién region of eastern Panama, where it occurs in Premontane Wet Forest at elevations from 1,000 to 1,100 m. We established its EVS as 16, placing in the middle portion of the high vulnerability category, and its IUCN status is Data Deficient. This individual is from the Serranía de Pirre, province of Darién, Panama. *Photo by Abel Batista.*

Isthmohyla zeteki. This treefrog is distributed from central Costa Rica to western Panama, where it occurs in Premontane Wet Forest and Rainforest on into Lower Montane Rainforest at elevations from 1,200 to 1,804 m. We evaluated its EVS as 13, placing it at the upper end of the middle vulnerability category, and its IUCN status is Critically Endangered. This individual is from the Cordillera de Tilarán, province of Alajuela, Costa Rica. *Photo by Brian Kubicki.*

Isthmohyla picadoi. This treefrog occurs in the Cordillera Central and Cordillera de Talamanca of Costa Rica and western Panama, where it occurs in Lower Montane and Montane rainforests at elevations from 1,920 to 2,770 m. We assessed its EVS as 19, placing it in the upper portion of the high vulnerability category, and its IUCN status is Near Threatened. This individual is from near Tres Colinas, Parque Internacional La Amistad, Cordillera de Talamanca, province of Puntarenas, Costa Rica. *Photo by Sean Michael Rovito.*

Kinosternon angustipons. The Narrow-bridged Mud Turtle is distributed along the Atlantic versant from southeastern Nicaragua to northwestern Panama, where it occurs in Tropical Moist Forest at elevations from near sea level to 260 m. We estimated its EVS as 16 in the middle portion of the high vulnerability category, and its IUCN status is Vulnerable. This individual is from the Río Papaturro, Los Guatuzos, department of Río San Juan, Nicaragua. *Photo by Javier Sunyer.*

for Central American species we provide in a following section.

Given our opinion about the nature of the IUCN system of conservation assessment, as in our assessments for the Mexican herpetofauna, we employ the EVS measure to conduct our own assessment of the conservation status of the Central American herpetofauna.

EVS for the Central American Herpetofauna

In our prior conservation reassessments of the members of the Mexican herpetofauna (Wilson et al. 2013a, b), we specified a number of advantages for using the EVS system. Based on the information in Wilson et al. (2013b:107), we summarize these advantages below.

1. “This measure can be applied as soon as a species is described, because the information necessary for its application generally is known at that point.” If the information is not entirely known (e.g., about amphibian reproductive mode), it can be estimated based on the phylogenetic relationships of the newly described species.

2. “The calculation of the EVS is an economical undertaking and does not require expensive, grant-supported workshops, such as those held in connection with the Global Reptile Assessment sponsored by the

IUCN." Given that any conservation assessment is only an estimate of an organism's status in nature, it will always remain subject to modification based on additions to our knowledge. As an extreme example, conservation biologists might reach a point where they feel justified to report that a certain species is extinct (i.e., the creature no longer is in existence). This theoretical definition of the term can be problematical, however, because it can be difficult or impossible to determine if any individuals of the species remain in nature. Thus, a practical definition of the term extinction can be adopted to mean that no individuals of the species have been found by anyone qualified to make such a determination. Interestingly, on 30 December 2013 the AmphibiaWeb site indicated that an anuran from Sri Lanka (*Pseudophilautus hypomelas*) that had been declared extinct was rediscovered (Wickramasinghe et al. 2013). The authors suggested that its status be changed to Critically Endangered "under the IUCN Red List Categories and Criteria because of the extent of occurrence (EOO) is less than 100 km^2, the area of occupancy (AOO) is less than 10 km^2, and is recorded from a single location. The habitat is under severe anthropogenic activities such as overexploitation of natural resources for tea cultivation, forest fragmentation, use of agrochemicals, soil erosion, inadequately planned constructions and illegal constructions, mini-hydro power plants, forest die back, and discharge of pollutants to the environment." This familiar litany of reasons for organismic endangerment also applies to environments in Central America, where similar reports have been published (Abarca et al. 2010).

3. "The EVS is predictive, because it provides a measure of succeptibility to anthropogenic pressure, and can pinpoint taxa in need of immediate attention and continuing scrutiny." We provide an example of two recently described species of the hylid genus *Ecnomiohyla*. Batista et al. (2014) described *E. bailarina* and *E. veraguensis* from southeastern and west-central Panama, respectively. The authors noted that, "the secretive habits of *Ecnomiohyla bailarina*, as with other *Ecnomiohyla* species, make it difficult to obtain an assessment of its population size. Considering that the status of the *E. bailarina* population is unknown, the data deficient (DD) criterion, according to the IUCN … seems appropriate for this species, until data on its population trend become available. Moreover, due to the fact that *E. bailarina* and *E. thysanota* occur in a region affected by social problems and political conflicts along the border between Panama and Colombia, it is unlikely that there will be sufficient opportunity to visit the region to assess population sizes." With respect to their other new species, Batista et al. (2014) indicated that, "since *Ecnomiohyla veraguensis* occurs along with relatively widely distributed species, it is not suspected to be endemic to the Cerro Negro surroundings [the vicinity of the type locality]. However, all species in the genus are known to be very susceptible to habitat degradation and thus most are listed under a threatened category … So it is very likely that *E. veraguensis* also will qualify for a threatened category as soon as additional data are available." These authors implied that this species should be given a Data Deficient status based on the same sort of reasoning used for *E. bailarina*. We reviewed the Batista et al. (2014) paper and determined the EVS for the two species based on the information provided in the original descriptions. As a result, the EVS for both species are the highest possible (Appendix 1), i.e., 20 (6+8+6), based on being known only from the type locality in a single vegetation formation and having presumably a reproductive mode like other species of *Ecnomiohyla* (i.e., with eggs and tadpoles in water-filled tree cavities). This EVS is the same as that for the recently described and famously endangered *Ecnomiohyla rabborum* (Appendix 1; Mendelson 2011). As a consequence of our ability to calculate EVS for both of the newest *Ecnomiohyla* species, we can bring attention to their plight and their conservation status to the point that they can be used as flagship species, along with *E. rabborum*, to publicize the issues surrounding the conservation of the Panamanian herpetofauna as a whole (also see Jaramillo et al. 2010).

4. "Finally, this measure is simple to calculate and does not 'penalize' species that are poorly known." In our opinion, this penalizing comes when a species is designated as Data Deficient, because it then enters into a conservation status limbo until and unless information is available that will allow for the application of another IUCN category to be applied (most likely one of the three threat categories). For this reason, as previously discussed, we consider the DD species as "threat species in disguise." Given the pace at which organismic endangerment proceeds and the survival chances for many species, obviously they cannot afford such delays.

We calculated the EVS scores for each of the 1,045 species of amphibians, crocodylians, squamates, and turtles in Central America to which it can be applied (see Appendix 1). We placed these data alongside those for the IUCN categorizations we obtained from the IUCN Red List website (www.iucnredlist.org) and used the designation NE for those species presently not evaluated by the IUCN.

Theoretically, the EVS scores can range from 3 to 20 for amphibians, crocodylians, squamates, and turtles. A score of 3 would be assigned to broadly distributed species both inside and outside of Central America, which occurs in eight or more forest formations, and, if an amphibian has both its eggs and tadpoles in large to small bodies of lentic or lotic water or, if a squamate, if a spe-

Lepidophyma reticulatum. This night lizard is distributed on the Pacific versant of Costa Rica and western Panama, where it occurs in Lowland Moist and Wet and Premontane Moist and Wet forests at elevations from 10 to 1,250 m. We estimated its EVS as 13, placing it at the upper end of the medium vulnerability category, and its IUCN status is Least Concern. This individual is from Portón, province of Chiriquí, Panama. *Photo by Abel Batista.*

Lithobates miadis. This leopard frog is endemic to Little Corn Island off the Caribbean coast of Nicaragua, whose area consists of only 3 km2; it occurs in Lowland Moist Forest and breeds in permanent ponds. We established its EVS as 15, placing it in the lower portion of the high vulnerability category, and its IUCN status is Vulnerable. This individual is from the Región Autónoma del Atlántico Sur. *Photo by Javier Sunyer.*

cies is fossorial and thus usually escapes human notice. The amphibian species receiving an EVS score of 3 are the ranid *Lithobates forreri*, the bufonid *Rhinella marina*, and the hylid *Smilisca baudinii* (Appendix 1). We did not assign this score to any crocodylian, squamate, or turtle. At the other extreme, an EVS score of 20 would be assigned to a species known only from the vicinity of its type locality, is restricted to a single forest formation, and, if an amphibian, has both its eggs and tadpoles in water-retaining arboreal bromeliads or water-filled tree cavities, or, if a crocodylian, squamate, or turtle is commercially or non-commercially exploited for hides, meat, eggs and/or the pet trade. We assigned an EVS score of 20 to six species of hylid anurans, including four in the genus *Ecnomiohyla*, one in *Isthmohyla*, and one in *Ptychohyla* (Appendix 1). As with the lowest possible score, no crocodylian, squamate, or turtle received the highest possible score. The remaining EVS scores ranged from 4 to 19. We provide a summary of the EVS scores for the Central American herpetofaunal species in Table 3. The EVS range falls into the following three categories: low (3–9), medium (10–13), and high (14–19).

The range and mean EVS scores for the major herpetofaunal groups are as follows: anurans = 3–20 (13.8); caecilians = 7–19 (15.4); and salamanders = 8–18 (16.5); crocodylians = 13–16 (14.3); lizards = 5–19 (14.0); snakes = 4–19 (12.8); and turtles = 8–19 (13.5). We found that on average among amphibians, salamanders are more susceptible to environmental deterioration, and anurans are less susceptible than caecilians; among the remainder of the herpetofauna, crocodylians are the most susceptible and snakes the least susceptible, with turtles and lizards falling in between. The average scores fell into the upper portion of the medium category (anurans, snakes, and turtles), and the lower portion of the high category (caecilians, salamanders, and lizards). We found the average EVS scores for all amphibian species as 14.7, a value near the lower end of the high range of vulnerability, and that for crocodylians, squamates, and turtles as 13.3, a value slightly above the upper end of the medium range of vulnerability. Based on these average EVS values, amphibians are somewhat more vulnerable to environmental degradation than the rest of the herpetofauna.

Our results show an EVS score of 16, near the middle portion of the high vulnerability category, in the highest percentage (15.6) of anuran species, and an EVS score of 18, near the upper end of the high vulnerability category, in the highest percentage (35.8) of the salamander species. For caecilians, we found the same percentage of species (13.3) with EVS values ranging from 13 to 19. When organized by EVS category, the lowest number of species of amphibians (39 [7.9%]) fell into the low category, an intermediate number (105 [21.3%]) into the medium category, and the highest number (349 [70.8%]) into the high category. These figures are more alarming than those reported for the Mexican amphibian fauna; Wilson et al. (2013b) noted that of the 378 total taxa, 50 (13.2%) fell into the low vulnerability category, 106 (28.0%) into the medium category, and 222 (58.7%) into the high category.

We discovered that the EVS scores for crocodylians are too few and too scattered to confirm a pattern. With squamates, however, we found EVS scores of 15 and 16, in the lower portion of the high vulnerability category, in the highest percentage (14.9%) of the species. Overall, the frequency of EVS values for all crocodylians, squamates, and turtles increased to peak at the value of 16, and decreased steeply thereafter. When organized by EVS category, as with amphibians we found that the lowest number of species (81 [14.7%]) fell into the low category, an intermediate number (162 [29.3%]) into the medium category, and the highest number (309 [56.0%]) into the high category. These statistics differ only slightly from those reported for Mexican crocodylians, squamates, and turtles by Wilson et al. (2013a), who indicated that of the 841 total taxa that could be scored, 99 (11.8%)

fell into the low vulnerability category, 272 (32.3%) into the medium category, and 470 (55.9%) into the high category.

For the total Central American herpetofauna, our results show 120 species (11.5%) with EVS scores in the low category of vulnerability, 267 (25.6%) in the medium category, and 658 (63.0%) in the high category. For Mexico, the comparable figures are 149 (12.2%), 378 (31.0%), and 692 (56.8%). Amazingly, we found more than six of every 10 species in Central America in the high category of vulnerability to environmental deterioration. This figure is more elevated than that for the Mexican herpetofauna, although in both regions more than one-half of the herpetofauna has been judged to have the highest level of vulnerability to environmental damage. This statistic has astounding implications for efforts to conserve this hugely significant herpetofauna.

Given that our EVS results show such a high percentage of the Central American herpetofauna in the high vulnerability category, this situation needs to be examined more closely. Thus, we indicate the EVS categorizations of low, medium, and high in the last column in Appendices 1 and 2. We summarized these categorizations and compared them to the scores for each of the three components that contribute to the total EVS, as well as the total EVS itself, and organized these data according to the herpetofaunal families and orders (Table 4).

As noted above, amphibians generally are more environmentally vulnerable than the remainder of the herpetofauna (percentage of high EVS 70.8% vs. 55.8%). The relatively high figure for amphibians primarily is due to the extremely high number of salamander species placed in the high vulnerability category (92.4%) compared to the situation among anurans (59.6%). All salamanders in Central America are categorized in the family Plethodontidae. According to the accounting at the AmphibiaWeb site (accessed 9 December 2014), this family consists of 444 species; thus, the 159 Central American species comprise 35.8% of the total. This figure also represents 60.9% of the 261 species known from Mesoamerica (www.mesoamericanherpetology.com; accessed 9 December 2014). The elevated vulnerability of Central American salamanders largely is due to the small geographic ranges and limited vegetational occurrence of most species (respective average component scores of 5.1 of 6 and 7.3 of 8; Table 4). All Central American plethodontids are direct developers, so the score for reproductive mode always is 4. The average total EVS score is 16.5, which is in the middle of the range of high vulnerability scores (14–20).

The next most vulnerable group of amphibians contains the caecilians, of which only 15 species occur in Central America. Typically, these amphibians are more broadly distributed, both geographically and vegetationally (average component scores of 3.9 and 6.8, respectively). Although their reproductive biology remains poorly understood, all species likely are direct developers or viviparous, and thus are allocated reproductive mode scores of 4 or 5.

Anurans generally are less environmentally vulnerable than caecilians or salamanders (average EVS of 13.7). This situation principally is due to the relatively fewer species with high scores for reproductive mode (average score 2.8 of 6). Otherwise, the other component scores for anurans are similar to those for caecilians (4.4 vs. 3.9 for geographic distribution and 6.7 vs. 6.8 for ecological distribution). Nonetheless, our assessment showed 59.6% of the 319 anuran species with high EVS scores.

Of the 319 anuran species, 238 (74.6%) are categorized in three families, the Bufonidae (39 species), Craugastoridae (101), and Hylidae (98). Generally, members of these families are more geographically widespread than the typical salamander (respective average geographic component scores of 4.4, 4.8, and 4.4 compared to that of 5.1 for salamanders). This situation also is the case with vegetational occurrence (6.6, 7.0, and 6.7 vs. 7.3). Typical bufonid and hylid anuran species lay eggs in standing or flowing water, whereas craugastorid species have direct development. Thus, the component for reproductive mode is lower for bufonids and hylids (1.3 and 2.0, respectively) than for craugastorids (4.0). Nonetheless, we found the species with the highest EVS scores, including the highest possible score, among the hylid anurans. We calculated a total score of 20 for six hylids (Appendix 1), four in the genus *Ecnomiohyla* (*E. bailarina*, *E. rabborum*, *E. thysanota*, and *E. veraguensis*), one in the genus *Isthmohyla* (*I. melacaena*), and one in the genus *Ptychohyla* (*P. dendrophasma*). Given a total score of 20, each of these species is known only from their respective type localities, from a single vegetation zone, and has a reproductive mode of either laying eggs in tree holes or in bromeliads (Appendix 1).

The reason why we assessed fewer crocodylians, squamates, and turtles in the high EVS category than amphibians primarily is due to their greater breadth in geographic and ecological distribution (respective average values of 4.0 vs. 4.6 and 6.1 vs. 6.9). Nevertheless, a slightly higher average score for degree of persecution is present in these creatures (3.6) than for reproductive mode in amphibians (3.2).

We found turtles and squamates slightly less vulnerable than crocodylians (13.5 and 13.3, respectively, vs. 14.3). Obviously, the patterns of vulnerability are skewed toward the squamates, since 96.2% of the Central American crocodylians, squamates, and turtles are squamates.

Most squamates are classified in the families Dactyloidae (95 species), Sphaerodactylidae (19), Colubridae (74), Dipsadidae (144), and Viperidae (32). Their total number (364) represents 68.4% of the 532 species for which an EVS can be calculated. We found the average EVS scores for these families, respectively, as follows: 14.4, 14.4, 11.9, 13.0, and 15.1. Only the values for the colubrids and dipsadids fell outside of the high value

Nothopsis rugosus. This unusual snake is distributed from northeastern Honduras to northwestern Colombia on the Atlantic versant, and on the Pacific versant from southwestern Costa Rica to northwestern Ecuador, where it occurs in Lowland Moist and Premontane Wet forests at elevations from near sea level to 900 m. We estimated its EVS as 10, placing it at the lower end of the medium vulnerability category, and its IUCN status is Least Concern. This individual is from the Serranía de San Blas, in Panama. *Photo by Abel Batista.*

Nototriton matama. The Matama Moss Salamander is known only from the type locality at the southeastern end of the Fila Matama, a ridge on the Atlantic slope of Cerro Chirripó in southeastern Costa Rica, where it occurs in Premontane Wet Forest at an elevation of 1,300 m. We calculated its EVS as 18, placing it in the upper portion of the high vulnerability category, but its IUCN status has not been determined. This individual is the holotype of the species. *Photo by Eduardo Boza Oviedo.*

Micrurus stewarti. This coralsnake is distributed in central Panama, where it occurs in Lowland Moist and Premontane Wet forests at elevations from 500 to 1,200 m. We gauged its EVS as 17, placing it in the middle portion of the high vulnerability category, and its IUCN status is Least Concern. This individual is from Donoso, province of Colón, Panama. *Photo by Abel Batista.*

Mastigodryas dorsalis. This racer is distributed from western Guatemala to north-central Nicaragua, where it occurs in Premontane Wet, Lower Montane Wet, and Lower Montane Moist forests at elevations from 635 to 2,200 m. We determined its EVS as14, placing it at the lower end of the high vulnerability category, and its IUCN status is Least Concern. This individual is from Cerro Kilambé, department of Jinotega, Nicaragua. *Photo by Javier Sunyer.*

range (14–20). The proportion of high EVS species fell below 50% only in colubrids (39.2%). In the other families, the percentage values were, respectively, 72.7, 73.7, 52.8, and 78.1. We did not assign a total EVS score of 20 to any crocodylian, squamate, or turtle, although we accorded a score of 19 to five species (four iguanids and one viperid; Appendix 2). The four iguanids all are members of the genus *Ctenosaura* (*C. bakeri*, *C. oedirhina*, *C. palearis*, and *C. quinquecarinata*). The single viperid is the recently described *Bothriechis guifarroi*.

In the case of amphibians and the remainder of the herpetofauna, the typical member is a species allocated to either the lower portion of the high vulnerability range (14.7) or slightly above the upper portion of the medium vulnerability category (13.3). Consequently, management plans for the general protection of the herpetofauna, and particularly the high vulnerability species, require development in all regions of Central America.

Comparison of IUCN Categorizations and EVS Values

Wilson et al. (2013a) stated that, "since the IUCN categorizations and EVS values both measure the degree of environmental threat impinging on a given species, a certain degree of correlation between the results of these two measures is expected." They also noted that, "Townsend and Wilson (2010) demonstrated this relationship with reference to the Honduran herpetofauna, by comparing the IUCN and EVS values for 362 species of amphibians and terrestrial reptiles in their table 4."

Table 4. Summary of Environmental Vulnerability Scores by component, total score, and category, arranged by family. The numbers in the Environmental Vulnerability Scores columns represent ranges followed by means in parentheses. Values for EVS categories are percentages. L = low vulnerability; M = medium vulnerability; H = high vulnerability.

Families	Environmental Vulnerability Scores				EVS Categories
	Geographic Distribution (range 1–6)	Ecological Distribution (range 1–8)	Reproductive Mode/Degree of Persecution (range 1–6)	Total Score (range 3–20)	
Aromobatidae (3)	1–6 (4.0)	6–8 (7.0)	4 (4.0)	11–18 (15.0)	L = 0.0, M = 33.3, H = 66.7
Bufonidae (39)	1–6 (4.4)	1–8 (6.6)	1–4 (1.3)	3–17 (12.2)	L = 20.5, M = 41.0, H = 38.5
Centrolenidae (14)	1–5 (2.3)	4–8 (6.6)	3 (3.0)	8–16 (11.1)	L = 14.3, M = 64.3, H = 21.4
Craugastoridae (101)	2–6 (4.8)	3–8 (7.0)	4 (4.0)	9–18 (15.8)	L = 1.0, M = 7.9, H = 91.1
Dendrobatidae (19)	4–6 (4.8)	6–8 (7.3)	4 (4.0)	14–18 (15.3)	L = 0.0, M = 0.0, H = 100
Eleutherodactylidae (11)	2–6 (4.5)	5–8 (7.2)	4 (4.0)	11–18 (15.6)	L = 0.0, M = 18.2, H = 81.8
Hemiphractidae (3)	3–4 (3.7)	7 (7.0)	5 (5.0)	15–16 (15.7)	L = 0.0, M = 0.0, H = 100
Hylidae (98)	1–6 (4.4)	1–8 (6.7)	1–6 (2.0)	3–20 (13.1)	L = 12.2, M = 44.9, H = 42.9
Leptodactylidae (9)	1–5 (2.7)	2–8 (5.2)	2 (2.0)	5–14 (10.0)	L = 44.4, M = 44.4, H = 11.2
Microhylidae (9)	2–5 (3.3)	1–8 (5.8)	1 (1.0)	4–14 (10.1)	L = 33.3, M = 55.6, H = 11.1
Pipidae (1)	4 (4.0)	8 (8.0)	5 (5.0)	17 (17.0)	L = 0.0, M = 0.0, H = 100
Ranidae (11)	1–6 (4.1)	1–8 (4.8)	1 (1.0)	3–15 (9.9)	L = 45.4, M = 36.4, 18.2
Rhinophrynidae (1)	2 (2.0)	5 (5.0)	1 (1.0)	8 (8.0)	L = 100, M = 0.0, H = 0.0
Total Anurans (319)	**1–6 (4.4)**	**1–8 (6.7)**	**1–6 (2.8)**	**3–20 (13.7)**	**L = 11.3, M = 29.2, H = 59.6**
Plethodontidae (159)	1–6 (5.1)	3–8 (7.3)	4 (4.0)	8–18 (16.5)	L = 1.3, M = 6.3, H = 92.4
Total Salamanders (159)	**1–6 (5.1)**	**3–8 (7.3)**	**4 (4.0)**	**8–18 (16.5)**	**L = 1.3, M = 6.3, H = 92.4**
Caeciliidae (7)	3–6 (4.4)	7–8 (7.9)	4–5 (4.4)	15–19 (16.7)	L = 0.0, M = 0.0, H = 100
Dermophiidae (8)	1–5 (3.4)	1–8 (5.9)	5 (5.0)	7–18 (14.3)	L = 12.5, M = 25.0, H = 62.5
Total Caecilians (15)	**1–6 (3.9)**	**1–8 (6.8)**	**4–5 (4.7)**	**7–19 (15.4)**	**L = 6.7, M = 13.3, H = 80.0**
Total Amphibians (493)	**1–6 (4.6)**	**1–8 (6.9)**	**1–6 (3.2)**	**3–20 (14.7)**	**L = 7.9, M = 21.3, H = 70.8**
Alligatoridae (1)	3 (3.0)	7 (7.0)	6 (6.0)	16 (16.0)	L = 0.0, M = 0.0, H = 100
Crocodylidae (2)	2–3 (2.5)	5 (5.0)	6 (6.0)	13–14 (13.5)	L = 0.0, M = 50.0, H = 50.0
Total Crocodylians (3)	**2–3 (2.7)**	**5–7 (5.7)**	**6 (6.0)**	**13–16 (14.3)**	**L = 0.0, M = 33.3, H = 66.7**

Table 4 (continued). Summary of Environmental Vulnerability Scores by component, total score, and category, arranged by family. The numbers in the Environmental Vulnerability Scores columns represent ranges followed by means in parentheses. Values for EVS categories are percentages. L = low vulnerability; M = medium vulnerability; H = high vulnerability.

Families	Environmental Vulnerability Scores				EVS Categories
	Geographic Distribution (range 1–6)	Ecological Distribution (range 1–8)	Reproductive Mode/Degree of Persecution (range 1–6)	Total Score (range 3–20)	
Amphisbaenidae (2)	3 (3.0)	7–8 (7.5)	1 (1.0)	11–12 (11.5)	L = 0.0, M = 100, H = 0.0
Anguidae (28)	2–6 (4.9)	3–8 (7.2)	3–4 (3.6)	8–18 (15.7)	L = 3.6, M = 3.6, H = 92.8
Corytophanidae (9)	1–5 (3.0)	3–7 (4.9)	3 (3.0)	7–15 (10.9)	L = 33.3, M = 55.6, H = 11.1
Dactyloidae (95)	1–6 (4.7)	2–8 (6.7)	3 (3.0)	7–17 (14.4)	L = 8.4, M = 18.9, H = 72.7
Eublepharidae (2)	3–5 (4.0)	3–5 (4.0)	4 (4.0)	10–14 (12.0)	L = 0.0, M = 50.0, H = 50.0
Gymnophthalmidae (14)	2–5 (4.0)	3–8 (7.0)	2–3 (2.7)	9–16 (13.7)	L = 7.1, M = 21.5, H = 71.4
Helodermatidae (2)	3–5 (4.0)	6–8 (7.0)	5 (5.0)	14–18 (16.0)	L = 0.0, M = 0.0, H = 100
Hoplocercidae (2)	3–4 (3.5)	7–8 (7.5)	3 (3.0)	13–15 (14.0)	L = 0.0, M = 50.0, H = 50.0
Iguanidae (11)	1–5 (4.0)	3–8 (6.5)	3–6 (5.7)	10–19 (16.3)	L = 0.0, M = 27.3, H = 72.7
Mabuyidae (5)	1–6 (4.4)	2–8 (6.4)	3 (3.0)	6–17 (13.8)	L = 20.0, M = 0.0, H = 80.0
Phrynosomatidae (17)	1–5 (3.6)	1–8 (5.0)	3 (3.0)	5–15 (11.6)	L = 11.8m M = 64.7, H = 23.5
Phyllodactylidae (5)	1–6 (3.8)	4–8 (6.4)	3 (3.0)	8–17 (13.2)	L = 40.0, M = 0.0, H = 60.0
Polychrotidae (1)	1 (1.0)	8 (8.0)	3 (3.0)	12 (12.0)	L = 0.0, M = 100, H = 0.0
Scincidae (3)	4–5 (4.3)	5–6 (5.7)	3 (3.0)	12–14 (13.0)	L = 0.0, M = 66.7, H = 33.3
Sphaerodactylidae (19)	1–6 (4.3)	3–8 (7.1)	3 (3.0)	8–17 (14.4)	L = 10.5, M = 15.8, H = 73.7
Sphenomorphidae (4)	2–6 (4.0)	2–8 (4.8)	3 (3.0)	7–17 (11.8)	L = 50.0, M = 0.0, H = 50.0
Teiidae (12)	1–5 (3.6)	2–8 (6.3)	3 (3.0)	6–16 (12.9)	L = 16.7, M = 25.0, H = 58.3
Xantusiidae (4)	2–5 (3.5)	4–7 (5.5)	2 (2.0)	9–13 (11.0)	L = 50.0, M = 50.0, H = 0.0
Xenosauridae (1)	3 (3.0)	1 (1.0)	3 (3.0)	7 (7.0)	L = 100, M = 0.0, H = 0.0
Anomalepididae (3)	2–5 (3.3)	5–8 (6.3)	1 (1.0	9–12 (10.7)	L = 33.3, M = 66.7, H = 0.0
Boidae (4)	1–3 (1.5)	1–8 (5.5)	2–6 (3.0)	8–13 (10.0)	L = 50.0, M = 50.0, H = 0.0
Charinidae (2)	2–4 (3.0)	5–6 (5.5)	2 (2.0)	9–12 (10.5)	L = 50.0, M = 50.0, H = 0.0
Colubridae (74)	1–6 (3.6)	1–8 (5.1)	2–5 (3.2)	5–17 (11.9)	L = 25.7m M = 35.1, H = 39.2

Table 4 (continued). Summary of Environmental Vulnerability Scores by component, total score, and category, arranged by family. The numbers in the Environmental Vulnerability Scores columns represent ranges followed by means in parentheses. Values for EVS categories are percentages. L = low vulnerability; M = medium vulnerability; H = high vulnerability.

Families	Environmental Vulnerability Scores				EVS Categories
	Geographic Distribution (range 1–6)	Ecological Distribution (range 1–8)	Reproductive Mode/Degree of Persecution (range 1–6)	Total Score (range 3–20)	
Dipsadidae (144)	1–6 (4.1)	1–8 (6.2)	2–5 (4.0)	4–17 (13.0)	L = 13.9, M = 33.3, H = 52.8
Elapidae (17)	2–5 (4.0)	1–8 (5.7)	5 (5.0)	9–18 (14.7)	L = 11.8, M = 17.6, H = 70.6
Leptotyphlopidae (5)	3–5 (3.6)	1-8 (4.2)	1 (1.0)	5–12 (8.8)	L = 40.0, M = 60.0, H = 0.0
Loxocemidae (1)	1 (1.0)	5 (5.0)	4 (4.0)	11 (11.0)	L = 0.0, M = 100, H = 0.0
Natricidae (5)	1–4 (2.8)	1–5 (3.4)	2–4 (3.6)	8–13 (9.8)	L = 60.0, M = 40.0, H = 0.0
Sibynophiidae (2)	1 (1.0)	5–7 (6.0)	5 (5.0)	11–13 (12.0)	L = 0.0, M = 100, H = 0.0
Tropidophiidae (1)	3 (3.0)	5 (5.0)	3 (3.0)	11 (11.0)	L = 0.0, M = 100, H = 0.0
Typhlopidae (5)	4–5 (4.6)	5–8 (6.4)	1 (1.0)	11–14 (12.0)	L = 0.0, M = 80.0, H = 20.0
Viperidae (32)	1–6 (4.0)	2–8 (6.0)	5 (5.0)	9–19 (15.1)	L = 3.1, M = 18.8, H = 78.1
Total Squamates (531)	**1–6 (4.1)**	**1–8 (6.1)**	**1–6 (3.5)**	**4–19 (13.3)**	**L = 14.7, M = 29.6, H = 55.7**
Chelydridae (2)	1–4 (2.5)	4–7 (5.5)	6 (6.0)	11–17 (14.0)	L = 0.0, M = 50.0, H = 50.0
Dermatemydidae (1)	4 (4.0)	7 (7.0)	6 (6.0)	17 (17.0)	L = 0.0, M = 0.0, H = 100
Emydidae (2)	1–5 (3.0)	4–8 (6.0)	6 (6.0)	11–19 (15.0)	L = 0.0, M = 50.0, H = 50.0
Geoemydidae (5)	1–5 (3.2)	4–8 (6.6)	3 (3.0)	8–16 (12.8)	L = 20.0, M = 40.0, H = 40.0
Kinosternidae (4)	1–5 (2.8)	4–8 (5.8)	3 (3.0)	8–16 (11.5)	L = 50.0, M = 0.0, H = 50.0
Staurotypidae (3)	4 (4.0)	4–8 (6.7)	3 (3.0)	13–14 (13.7)	L = 0.0, M = 33.3, H = 66.7
Testudinidae (1)	3 (3.0)	8 (8.0)	6 (6.0)	17 (17.0)	L = 0.0, M = 0.0, H = 100
Total Turtles (18)	**1–5 (3.2)**	**4–8 (6.3)**	**3–6 (4.0)**	**8–19 (13.5)**	**L = 16.7, M = 27.8, H = 55.5**
Total "Reptiles" (552)	**1–6 (4.0)**	**1–8 (6.1)**	**1–6 (3.6)**	**4–19 (13.3)**	**L = 14.7, M = 29.5, H = 55.8**
Total Herpetofauna (1045)	**1–6 (4.3)**	**1–8 (6.5)**	**1–6 (3.4)**	**3–20 (14.0)**	**L = 11.5, M = 25.6, H = 62.9**

As Wilson et al. (2013a, b) developed for the Mexican herpetofauna, we constructed a pair of tables (Tables 5 and 6) to judge whether such a correspondence exists between these two measures of conservation status for the Central American herpetofauna. The results for the Mexican and Central American amphibian faunas are comparable to a point, but not otherwise. With respect to the IUCN categorizaitons, the absolute numbers for the three threat categories and the NT category are similar to one another (Central American values indicated first; CR = 91 vs. 88, EN = 75 vs. 79, VU = 44 vs. 44, NT = 26 vs. 21), even though 114 more amphibian species occur in Central America than in Mexico (493 vs. 379). Interestingly, the values for the LC, DD, and NE categories are not similar between the two regions, especially with respect to the latter two (LC = 147 vs. 91, DD = 55 vs. 38, NE = 52 vs. 17). Apparently, a correlation exists between the greater number of amphibian species in Central America and those in Mexico, and the number of species relegated to the LC, DD, and NE categories in the two regions. Of the 493 Central American amphibian species, 236 (47.9%) have been categorized as CR, EN, VU, and NT. In Mexico, 232 (61.4%) of these species have been assessed in these categories. In Central America, however, a significantly larger percentage of the species have been assessed in the LC, DD, and NE categories (254 [51.5%]) than in Mexico (146 [38.6%]). Note that the two percentage figures for Central America do not add up to 100, because three species in this region have been judged as extinct (Appendix 1). Why such a relatively large percentage of DD + NE species (21.7%) is present in Central American amphibians compared to those in Mexico (14.6%) is not evident, but it means that more than one in every five species in Central America has not been evaluated or is too poorly known to allow for an evaluation. This situation provided us with a special impetus to conduct an EVS analysis on these creatures.

Like Wilson et al. (2013b) did for the Mexican amphibians, we determined the mean EVS for each of the IUCN columns in Table 5, including the NE species and the total species. The results are as follows: CR (91 spp.) = 15.4 (range 7–20); EN (75 spp.) = 15.3 (9–18); VU (44 spp.) = 14.8 (7–18); NT (26 spp.) = 14.9 (8–20); LC (147 spp.) = 8.0 (3–17); DD (55 spp.) = 16.8 (13–20); NE (52 spp.) = 17.3 (8–20); and total (493 spp.) = 14.7 (3–20). Some interesting resemblances are evident between these data and those for the Mexican amphibians (Wilson et al. 2013b). As with the Mexican species, the mean EVS value decreases steadily (though not as dramatically) from the CR category (15.4) through the EN (15.3), and VU (14.8) categories, with the value for the NT species (14.9) almost the same as that for the VU species. A precipitous drop also is evident from the VU and NT values to those for the LC species (8.0), more so than for the Mexican amphibians. Although this decrease was expected, as for the Mexican amphibians we did not anticipate the size of the mean value for the DD species in Central America (16.8), which is almost the highest mean value for these categories. Thus, this value is substantially higher than that for any of the threat species. Even more surprising is that the mean value for the NE species is even higher (17.3) than that for the DD species. The value for the DD species supports our stated opinion about these species; apparently the NE group also is comprised of such species. As expected, the EVS values for almost all the DD (54 of 55 [98.2%]) and the NE species (51 of 52 [98.1%]) fell into the high vulnerability category, including the average total value (14.7). These additional reasons provide a compelling argument for conducting a reassessment of the Central American herpetofauna based on the EVS measure.

A revealing statistic is that the average EVS value for each IUCN category, except for the LC, fell into the high vulnerability category. With the LC category, of the 38 amphibian species with EVS values in the low vulnerability category, 30 (78.9%) have been placed in this IUCN category; however, 51 (34.7%) of the LC species fell into the medium category, with the remaining 66 (44.9%) species into the high category. Thus, as with our work on the Mexican herpetofauna, these data support our opinion that the LC category is applied too broadly in IUCN assessments to be of significant value in conservation planning.

As with Table 5, the data in Table 6 illustrate the relationship between the IUCN ratings and EVS values for the 552 Central American crocodylians, squamates, and turtles. These data can be compared to those for these creatures in Mexico (see Wilson et al. 2013a). With reference to the IUCN categorizations, the absolute numbers for the three threat categories and the NT category for the two regions are not as similar to one another for the crocodylians, squamates, and turtles as they are for the amphibians (Central American values listed first; CR = 14 vs. 6, EN = 30 vs. 36, VU = 18 vs. 44, NT = 21 vs. 26). The figures for Central America total 83, compared to 112 for Mexico. The total figures for the two regions, however, comprise reasonably close percentages of the respective total non-amphibian herpetofaunas (i.e., 83 of 552 [15.0%] vs. 112 of 841 [13.3%]). We believe, however, that once the IUCN categorizations are available for Central American anoles that the ranks of the three threat categories and the NT category will be augmented, similar to when the categorizations are published for the species in Central and South America. With respect to the remainder of the IUCN categorizations, however, the total relative figures are comparable for Central America and Mexico. The comparable absolute figures for the two regions, respectively, are as follows: LC = 208 vs. 422, DD = 35 vs. 118, NE = 226 vs. 189. For Central America, the three absolute values total 469 species (85.0% of the total of 552); for Mexico, the comparable figures are 729 and 86.7%.

Equivalent to the approach in Wilson et al. (2013a) for Mexican crocodylians, squamates, and turtles, we ascertained the mean EVS scores for each of the IUCN columns in Table 6, including the NE species and the total species. The results are as follows: CR (14 spp.) = 16.6 (15–19); EN (30 spp.) = 15.9 (13–19); VU (18 spp.) = 15.0 (7–18); NT (21 spp.) = 14.3 (12–16); LC (208 spp.) = 12.3 (4–18); DD (35 spp.) = 15.6 (11–18); NE (226 spp.) = 13.2 (4–19). In common with Mexican crocodylians, squamates, and turtles (Wilson et al. 2013a), a corresponding increase in average EVS scores is evident with ascending degrees of threat, from LC through CR. Similar to the situation with Mexican crocodylians,

Table 5. Comparison of Environmental Vulnerability Scores (EVS) and IUCN categorizations for Central American amphibians. Shaded area at the top encompasses low vulnerability scores, and that at the bottom high vulnerability scores.

EVS	IUCN categories								Totals
	Extinct	Critically Endangered	Endangered	Vulnerable	Near Threatened	Least Concern	Data Deficient	Not Evaluated	
3	—	—	—	—	—	3	—	—	3
4	—	—	—	—	—	3	—	—	3
5	—	—	—	—	—	2	—	—	2
6	—	—	—	—	—	2	—	—	2
7	—	1	—	1	—	4	—	—	6
8	—	—	—	1	1	9	—	1	12
9	—	1	1	1	—	8	—	—	11
10	—	2	2	1	—	6	—	—	11
11	—	2	—	4	—	14	—	—	20
12	—	5	6	3	5	17	—	—	36
13	—	14	4	2	2	14	1	1	38
14	—	9	8	3	2	17	4	—	43
15	2	11	8	6	4	19	7	1	58
16	—	7	24	7	7	25	10	5	85
17	—	12	18	5	1	4	11	12	63
18	1	23	4	10	2	—	19	30	89
19	—	2	—	—	1	—	2	—	5
20	—	2	—	—	1	—	1	2	6
Totals	**3**	**91**	**75**	**44**	**26**	**147**	**55**	**52**	**493**

Table 6. Comparison of Environmental Vulnerability Scores (EVS) and IUCN categorizations for Central American crocodylians, squamates, and turtles. Shaded area at the top encompasses low vulnerability scores, and that at the bottom high vulnerability scores.

EVS	IUCN categories							Totals
	Critically Endangered	Endangered	Vulnerable	Near Threatened	Least Concern	Data Deficient	Not Evaluated	
3	—	—	—	—	—	—	—	—
4	—	—	—	—	1	—	1	2
5	—	—	—	—	1	—	4	5
6	—	—	—	—	6	—	5	11
7	—	—	1	—	7	—	6	14
8	—	—	—	—	9	—	10	19
9	—	—	—	—	17	—	12	29
10	—	—	—	—	15	—	11	26
11	—	—	—	—	13	2	12	27
12	—	—	—	1	33	1	17	52
13	—	3	—	4	28	1	24	60
14	—	4	6	6	27	1	30	74
15	1	5	2	7	25	6	34	80
16	8	7	5	3	18	17	26	84
17	1	5	3	—	6	4	30	49
18	3	4	1	—	2	3	1	14
19	1	2	—	—	—	—	3	6
20	—	—	—	—	—	—	—	—
Totals	**14**	**30**	**18**	**21**	**208**	**35**	**226**	**552**

squamates, and turtles, the average EVS scores for the DD species (15.6) is closest to that for the VU species (15.5), which also suggests that if and when these species are better known, they likely will be judged as VU, EN, or CR. The amount of decrease in average EVS scores for Central American crocodylians, squamates, and turtles from the NT to the LC categories (14.3 to 12.3) is comparable to the same groups in Mexico (12.9 to 10.5), although those for Central America are higher. The NE species constitute the largest component of the Central American crocodylian, squamate, and turtle fauna (226 species [40.9%] of the total). The average EVS score for these species is closest to that for the LC species (13.2 vs. 12.3), the second largest group (208 species). The ranges in their EVS values are similar to one another (4–19 for NE species, 4–18 for LC species). Eventually, the large number of NE species likely will join the large number of LC species when the IUCN categorizations have been determined for the former group. If so, then the combined 226 NE and 208 LC species would comprise 434 species (78.6% of the Central American crocodylian, squamate, and turtle fauna). If this eventually occurs, it would constitute a travesty of conservation effort, allowing for a serious degradation of the significance of this fauna.

Similar to the situation with Central American amphibians, most of the average EVS values we assessed for the crocodylians, squamates, and turtles, except for those in the LC and NE categories, fell into the high vulnerability category. The LC and NE averages, however, fell into the upper portion of the medium vulnerability category (12.3 and 13.2, respectively). Interestingly, the ranges of EVS values for the LC and NE species are similar (4–18 and 4–19, respectively). Both of these ranges are close to the total possible EVS range of 3–20. The EVS values, however, were not evenly distributed among the three vulnerability categories in either case. With the LC category, 41 of the 208 species (19.7%) fell into the low vulnerability grouping, 89 (42.8%) into the medium category, and 78 (37.5%) into the high category. With regard to the NE category, the comparable values are 38 (16.8%), 64 (28.3%), and 122 (54.9%). As with the Central American amphibians, the LC category appears too broadly applied to a large a group of species to be of meaningful conservation value for decision-making. Given the large number of species that remain unevaluated, many of these species likely will be allocated to the LC category, thus inflating the lack of utility of this category to reasonably reflect the conservation status of the species involved.

We harbor no illusions that the EVS measure will come to replace the IUCN system of categorization of conservation status and do not necessarily desire for this change to happen, but we maintain that the IUCN system has serious disadvantages when compared with the EVS measure. For the purposes of this analysis, if we divide the IUCN categories into three groups so they can be compared with the three EVS categories, and determine the absolute and relative numbers of species occupying each, the results are germane to our conclusions.

The three groupings of the IUCN categories are as follows: EX+CR+EN+VU; NT+LC; and DD+NE. Summing the numbers of species from tables 5 and 6 in each of these groupings for amphibians and the remainder of the herpetofauna provides a set of absolute values for the entire herpetofauna, in respective order as follows: 275 species (26.3%); 402 (38.5%); and 368 (35.2%). For the three EVS groupings, from high through medium to low, the results are as follows: 656 (62.8%); 270 (25.8%); and 119 (11.4%). The three IUCN groups and the three EVS groupings are not entirely comparable; nonetheless, the first IUCN grouping (EX+CR+EN+VU), i.e., the threat categories plus the extinct one, can be compared to the high vulnerability EVS grouping. Only 275 species (26.3%) of the total are allocated to the IUCN grouping, whereas 656 species (62.8%) are placed in the EVS grouping. The second IUCN grouping (NT+LC) is grossly comparable to the low vulnerability EVS grouping; the respective values are: 402 (38.5%) and 119 (11.4%). The third IUCN grouping is not comparable to any of the EVS groupings, since all the species can be evaluated using the latter, whereas a substantial proportion (367 species [35.2%]) of the former remain unevaluated. Even with the discrepancies between the IUCN and EVS systems, the use of the latter identifies a substantially larger absolute and relative number of species in need of serious conservation attention (275 [26.3%] vs. 656 [62.8%], respectively) and a substantially smaller absolute and relative number of species least needing this attention (402 [38.5%] vs. 119 [11.4%], respectively). These highly divergent results have profound consequences in efforts to conserve the highly significant Central American herpetofauna. The IUCN evaluation implies that this is a much simpler task to accomplish than the EVS evaluation. Such a conservation effort presently is a huge undertaking, which will grow increasingly in extent into the forseeable future.

Comparison of EVS Results for Central America and Mexico

We demonstrated that a large proportion of the Central American herpetofauna is highly vulnerable to environmental deterioration, more so than for the Mexican herpetofauna. To examine this situation in more detail, we constructed Table 7, in which the absolute and relative distribution of EVS values is indicated for the major herpetofaunal groups. For ease of understanding, we collapsed these data (Table 8) into the three categories of vulnerability generally recognized for the EVS measure, i.e., low, medium, and high.

Perusal of the data in Table 8 indicates that the general pattern for amphibians is for the numbers and percentages to increase from the low through the medium to the high categories. This pattern is evident in both regions

Table 7. Comparison of Environmental Vulnerability Scores and Percentages for the Central American and Mexican herpetofauna, arranged by major groups. Shaded area to the left encompasses low vulnerability scores, and to the right high vulnerability scores. CA = Central American. Data for Central American taxa are from Table 3, and for Mexican taxa from Wilson et al. (2013a, b).

Major groups	**Number of species**	**Environmental Vulnerability Scores**																	
		3	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
CA Anurans	319	3	3	2	2	5	11	10	11	18	34	30	37	39	50	26	29	3	6
Percentages	—	**0.9**	**0.9**	**0.6**	**0.6**	**1.6**	**3.4**	**3.1**	**3.4**	**5.6**	**10.7**	**9.4**	**11.6**	**12.2**	**15.7**	**8.2**	**9.1**	**0.9**	**1.9**
Mexican Anurans	237	4	3	3	4	9	12	14	13	20	25	29	36	30	8	14	12	1	—
Percentages	—	**1.7**	**1.3**	**1.3**	**1.7**	**3.8**	**5.1**	**5.9**	**5.4**	**8.4**	**10.5**	**12.2**	**15.2**	**12.7**	**3.4**	**5.9**	**5.1**	**8.4**	**—**
CA Salamanders	159	—	—	—	—	—	1	1	—	2	2	6	4	17	34	35	57	—	—
Percentages	—	**—**	**—**	**—**	**—**	**—**	**0.6**	**0.6**	**—**	**1.3**	**1.3**	**3.8**	**2.5**	**10.7**	**21.4**	**22.0**	**35.8**	**—**	**—**
Mexican Salamanders	139	—	—	—	—	—	—	1	2	2	6	7	13	23	13	36	36	—	—
Percentages	—	**—**	**—**	**—**	**—**	**—**	**—**	**0.7**	**1.4**	**1.4**	**4.3**	**5.0**	**9.4**	**16.6**	**9.4**	**25.9**	**25.9**	**—**	**—**
CA Caecilians	15	—	—	—	—	1	—	—	—	—	—	2	2	2	2	2	2	2	—
Percentages	—	**—**	**—**	**—**	**—**	**6.7**	**—**	**—**	**—**	**—**	**—**	**13.3**	**13.3**	**13.3**	**13.3**	**13.3**	**13.3**	**13.3**	**—**
Mexican Caecilians	3	—	—	—	—	—	—	—	—	1	1	—	—	—	1	—	—	—	—
Percentages	—	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**33.3**	**33.3**	**—**	**—**	**—**	**33.3**	**—**	**—**	**—**	**—**
CA Amphibians	493	3	3	2	2	6	12	11	11	20	36	38	42	58	87	63	88	5	6
Percentages	—	**0.6**	**0.6**	**0.4**	**0.4**	**1.2**	**2.4**	**2.2**	**2.2**	**4.1**	**7.3**	**7.7**	**8.5**	**11.8**	**17.6**	**12.8**	**17.8**	**1.0**	**1.2**
Mexican Amphibians	379	4	3	3	4	9	12	15	15	23	32	36	49	53	22	50	48	1	—
Percentages	—	**1.1**	**0.8**	**0.8**	**1.1**	**2.4**	**3.2**	**4.0**	**4.0**	**6.1**	**8.4**	**9.5**	**12.9**	**14.0**	**5.8**	**13.2**	**12.7**	**0.3**	**—**
CA Crocodylians	3	—	—	—	—	—	—	—	—	—	—	1	1	—	1	—	—	—	—
Percentages	—	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**33.3**	**33.3**	**—**	**33.3**	**—**	**—**	**—**	**—**
Mexican Crocodylians	3	—	—	—	—	—	—	—	—	—	—	1	1	—	1	—	—	—	—
Percentages	—	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**33.3**	**33.3**	**—**	**33.3**	**—**	**—**	**—**	**—**
CA Lizards	236	—	—	1	2	5	9	11	7	6	15	26	29	45	33	34	9	4	—
Percentages	—	**—**	**—**	**0.4**	**0.8**	**2.1**	**3.8**	**4.7**	**3.0**	**2.5**	**6.4**	**11.0**	**12.3**	**19.1**	**14.0**	**14.4**	**3.8**	**1.7**	
Mexican Lizards	413	—	—	1	3	6	11	13	14	28	39	49	54	67	78	38	10	2	—
Percentages	—	**—**	**—**	**0.2**	**0.7**	**1.5**	**2.7**	**3.1**	**3.4**	**6.8**	**9.4**	**11.9**	**13.1**	**16.2**	**18.9**	**9.2**	**2.4**	**0.5**	**—**
CA Snakes	295	—	2	4	9	8	8	19	18	18	35	31	41	35	47	14	5	1	—
Percentages	—	**—**	**0.7**	**1.4**	**3.1**	**2.7**	**2.7**	**6.4**	**6.1**	**6.1**	**11.9**	**10.5**	**13.9**	**11.9**	**15.9**	**4.7**	**1.7**	**0.3**	**—**
Mexican Snakes	383	1	1	7	10	9	19	17	30	25	31	47	52	50	44	24	9	7	—
Percentages	—	**0.3**	**0.3**	**1.8**	**2.6**	**2.3**	**5.0**	**4.4**	**7.8**	**6.5**	**8.1**	**12.3**	**13.6**	**13.1**	**11.5**	**6.3**	**2.3**	**1.8**	**—**
CA Turtles	18	—	—	—	—	—	3	—	—	2	1	2	3	1	2	3	—	1	—
Percentages	—	**—**	**—**	**—**	**—**	**—**	**16.7**	**—**	**—**	**11.1**	**5.5**	**11.1**	**16.7**	**5.5**	**11.1**	**16.7**	**—**	**5.5**	**—**
Mexican Turtles	42	—	—	—	—	—	1	—	3	1	1	3	8	6	4	3	5	6	1
Percentages	—	**—**	**—**	**—**	**—**	**—**	**2.4**	**—**	**7.1**	**2.4**	**2.4**	**7.1**	**19.0**	**14.3**	**9.5**	**7.1**	**11.9**	**14.3**	**2.4**
CA “Reptiles”	552	—	2	5	11	13	20	30	25	26	51	60	74	81	83	51	14	6	—
Percentages	—	**—**	**0.4**	**0.9**	**2.0**	**2.4**	**3.6**	**5.4**	**4.5**	**4.7**	**9.2**	**10.9**	**13.4**	**14.7**	**15.0**	**9.2**	**2.5**	**1.1**	**—**
Mexican “Reptiles”	841	1	1	8	13	15	31	30	47	54	71	100	115	123	127	65	24	15	1
Percentages	—	**0.1**	**0.1**	**1.0**	**1.5**	**1.8**	**3.7**	**3.6**	**5.6**	**6.4**	**8.4**	**11.9**	**13.7**	**14.6**	**15.1**	**7.7**	**2.9**	**1.8**	**0.1**

(Central America and Mexico), and in each of the major groups (anurans, caecilians, and salamanders). The relationship of the numbers and percentages changes, however, between the two regions and among the three major groups. Among the anurans, proportionately more taxa were assigned to the high category in Central America (59.5%) than in Mexico (42.6%). Among the salamanders, the same situation is evident (92.4% vs. 87.1%). This relationship is not evident among the caecilians, since there is only one of three Mexican caecilians, including the recently reported *Gymnopis syntrema* with an assessed score falling into the high category. Overall, more taxa were assessed in the high category in Central America than Mexico (70.8% vs. 58.8%, respectively). In both Central America and Mexico, the group of amphibians exhibiting the greatest vulnerability to environmental damage were the salamanders, with about nine of every 10 species assessed in the high category. A ma-

Table 8. Summary comparison of EVS category values and percentages from Table 6 for the Central American and Mexican herpetofauna, arranged by major groups.

Major groups	Number of species	EVS Categories		
		Low	Medium	High
CA Anurans	319	36	93	190
Percentages	—	**11.3**	**29.2**	**59.5**
Mexican Anurans	237	49	87	101
Percentages	—	**20.7**	**36.7**	**42.6**
CA Salamanders	159	2	10	147
Percentages	—	**1.3**	**6.3**	**92.4**
Mexican Salamanders	139	1	17	121
Percentages	—	**0.7**	**12.2**	**87.1**
CA Caecilians	15	1	2	12
Percentages	—	**6.7**	**13.3**	**80.0**
Mexican Caecilians	3	—	2	1
Percentages	—	—	**66.7**	**33.3**
CA Amphibians	493	39	105	349
Percentages	—	**7.9**	**21.3**	**70.8**
Mexican Amphibians	379	50	106	223
Percentages	—	**13.2**	**28.0**	**58.8**
CA Crocodylians	3	—	1	2
Percentages	—	—	**33.3**	**66.7**
Mexican Crocodylians	3	—	1	2
Percentages	—	—	**33.3**	**66.7**
CA Lizards	236	28	54	154
Percentages	—	**11.9**	**22.9**	**65.2**
Mexican Lizards	413	34	130	249
Percentages	—	**8.2**	**31.5**	**60.3**
CA Snakes	295	50	102	143
Percentages	—	**16.9**	**34.6**	**48.5**
Mexican Snakes	383	64	133	186
Percentages	—	**16.7**	**34.7**	**48.6**
CA Turtles	18	3	5	10
Percentages	—	**16.7**	**27.8**	**55.5**
Mexican Turtles	42	1	8	33
Percentages	—	**2.4**	**19.0**	**78.6**
CA “Reptiles”	552	81	162	309
Percentages	—	**14.7**	**29.3**	**56.0**
Mexican “Reptiles”	841	99	272	470
Percentages	—	**11.8**	**32.3**	**55.9**

jor distinction is evident between the salamanders and the anurans, given that about four of every 10 species of anurans in Mexico and about six of every 10 species in Central America were assessed in the high category. In both Central America and Mexico (thus, all of Mesoamerica) salamanders are of most crucial conservation concern.

The same general pattern we found among the amphibians also is evident among the remainder of the herpetofauna, i.e., an increase in the numbers and percentages from low through medium to high in both regions and within each group. Again, as with the amphibians, some distinctions can be made among the proportions of taxa falling into the three categories of vulnerability. Among the turtles, a greater proportion fell into the high category in Mexico than in Central America (78.6% vs. 55.5%). Among the lizards, however, the proportions falling into the three categories are similar to one another in Cen-

Nototriton lignicola. This salamander is endemic to mountains in north-central Honduras, where it occurs in Lower Montane Wet Forest at elevations from 1,760 to 2,000 m. We determined its EVS as 18, placing it in the upper portion of the high vulnerability category, and its IUCN status is Critically Endangered. This individual is from Cataguana, Parque Nacional Montaña de Yoro, department of Yoro. *Photo by Josiah H. Townsend.*

tral America and Mexico, respectively (low: 11.9 vs. 8.2; medium: 22.9 vs. 31.5; high: 65.2 vs. 60.3). Interestingly, among the snakes, the proportions were almost the same in Central America and Mexico (low: 16.9 vs.16.7; medium: 34.6 vs. 34.7; high: 48.5 vs. 48.6). Considering the two larger species groups, lizards and snakes, lizards generally were more vulnerable to environmental damage than snakes in both Central America and Mexico (65.2% and 60.3% for lizards and 48.5% and 48.6% for snakes, respectively). Nonetheless, just as with amphibians, more than one-half of the combined Central American and Mexican crocodylians, squamates, and turtles fell into the high category of vulnerability (56.0% and 55.9%, respectively), which is of major conservation concern.

Discussion

Biodiversity conservation requires one of the greatest efforts for crisis intervention ever undertaken by humanity. As we stated in the Introduction, the fundamental significance of this effort generally goes unappreciated by humanity at large. Thus, the attempt to salvage planet Earth as a haven for life essentially falls to the interest of an extremely small number of professional conservation biologists and a somewhat larger group of committed non-professional environmentalists. In essence, this tiny group of people is pitted against the remainder of humanity, collectively termed the "planetary killer" by Wilson (2002), which, knowingly or unknowingly, has cooperated to create the sixth mass extinction episode in Earth's history (Wake and Vredenburg 2008).

No matter what the actual number of people devoted to conserving biodiversity is, it pales in significance when compared to the number of humans who collectively represent the reason why biodiversity decline exists. At the time of this writing (4:20 PM on 10 December 2014), the global human population was estimated as 7,210,491,630 (www.census.gov). This constantly increasing figure is the most important statistic in attempting to determine the impact of humanity on the natural world. According to the Population Reference Bureau World (PRB) 2013 Population Data Sheet (available at www.prb.org), the current rate of natural increase is 1.2 (i.e., crude birth rate – crude death rate / 10). Thus, the current doubling time of the global population is 58.3 years. In other words, the current world population indicated above will double to 14,420,098,326 by early April, 2073, assuming that the growth rate remains constant. Nonetheless, the growth rate has been declining since peaking in the period from 1962 to 1963 and is projected to fall to zero in about 2080; thus, the total human population might peak at about 10.3 billion (Population growth, Wikipedia, en.wikipedia.org; accessed 9 January 2014). The actual pattern of growth will depend on the extent of family planning on the growth rate. The 2013 Population Data Sheet projects that the mid-2050 global population will be 9.727 billion, and that the greatest amount of growth (1.3 billion) will come in Sub-Saharan Africa. This figure exceeds the growth expected in Asia, the population giant. By the year 2050, Nigeria will surpass the United States to become the world's third most populous nation, after India and China (which will switch positions to become the largest and second most populous nations, respectively). In contrast, by 2050 the populations of North America and Europe are projected to remain at their current levels (at 0.4 and 0.7 billion, respectively).

Given this projected pattern of growth, what consequences can we expect? With respect to human impact on planetary biodiversity, we can expect that "nearly all future population growth will be in the world's less developed countries" (PRB 2012 Population Data Sheet: 5). The current population level in the less developed countries is 4.7 times greater than that of the more developed

Nototriton mime. This moss salamander is known only from the type locality, Cerro de Ulloa on the border of the departments of Colón and Olancho in north-central Honduras, where it occurs in Lower Montane Wet Forest at an elevation of 1,705 m. We evaluated its EVS as 18, placing it in the upper portion of the high vulnerability category, but its IUCN status has not been determined. This individual is from the type locality. *Photo by Josiah H. Townsend.*

Nototriton stuarti. Stuart's Moss Salamander is known only from the type locality, Montañas del Mico in extreme eastern Guatemala, where it occurs in Premontane Wet Forest at an elevation of 744 m. We assessed its EVS as 18, placing it in the upper portion of the high vulnerability category, and its IUCN status is Data Deficient. *Photo by Sean Michael Rovito.*

Oedipina nica. This worm salamander is known only from three isolated localities in north-central Nicaragua, where it occurs in Lower Montane Wet Forest at elevations from 1,360 to 1,660 m. We gauged its EVS as 17, placing it in the middle portion of the high vulnerability category, but its IUCN status has not been determined. This individual is from Finca Monimbo, department of Matagalpa. *Photo by Javier Sunyer.*

Oedipina carablanca. This worm salamander is known only from the vicinity of the type locality in east-central Costa Rica, where it occurs in Lowland Moist Forest at elevations from 60 to 260 m. We established its EVS as 18, placing it in the upper portion of the high vulnerability category, and its IUCN status is Endangered. This individual is from Pocora, 15 km NW Siquirres, province of Limón. *Photo by Brian Kubicki.*

ones (PRB 2012 Population Data Sheet). Based on the population projection in this same data sheet, the level will rise to 6.2 in the year 2050. This increasing disparity is expected to continue into the foreseeable future, again assuming that growth rates remain constant. The more developed countries are all of those in Europe and North America (i.e., Canada and the United States), as well as Australia, Japan, and New Zealand. The less developed ones comprise the world's remaining countries. The remarkable disparity in growth patterns between the more and less developed countries also is evident by comparing the rates of natural increase between the two regions. For the more developed countries, the figure is 0.1%, and for the less developed ones 1.4%. Thus, the growth rate for the less developed region is 14 times greater than that for the more developed area.

Because this paper deals with the Central American herpetofauna, we will examine the population growth trends in this region. The mid-2013 population for the seven Central American nations is 45.2 million (PRB 2013 Population Data Sheet: 8). The rate of natural increase ranges from a low of 1.2 in Costa Rica and El Salvador to 2.6 in Guatemala; the latter figure is 2.2 times greater than that of the former. Thus, the doubling time in Costa Rica and El Salvador is 58.3 years, the same as for the entire globe. That for Guatemala, however, is 26.9 years, which is slightly more than for Nigeria (25.0 years); as noted above, Nigeria is projected to become the world's third most populous nation by 2050. The average rate of natural increase for all of Central America is 1.8, which provides a doubling time of 38.9 years. Assuming no change in the average growth rate, the population of Central America would double to 90.4 million by about 2052. The growth rate for the region is predicted to decrease, however, so the PRB 2013 Population Data Sheet provides an estimate of 74 million by 2050. Nonetheless, this figure is about 29 million more than the mid-2013 figure, a 64.2% size increase.

The decrease in growth rate is relatively good news, but largely will depend on the rate of increase in the use of contraceptives and the consequential frequency of decrease of the total fertility rate. The current average percentage rate for the use of all types of contraceptives by married women ages 15–49 is 65.9% (PRB Population Data Sheet 2013). This statistic, however, does not consider the use of contraceptives by unmarried women or women outside of the usual reproductive age range, or the failure rate of contraceptive use by women or the use of contraceptives by men. Assuming that the rate of natural increase will decrease in the next 36 years to allow for a population of 73.5 million by the year 2050, this growth pattern will measurably increase the impact of population pressure on the remaining natural areas in Central America. The current average density of human population in the region is 103.1 people per km^2, and this figure should grow to 167.7 in the intervening 36 years. The rate of deforestation can be expected to be roughly comparable to that of the addition of people to the population. Deforestation, therefore, can be predicted to continue, especially given the income disparity in the region. The average percentage comprising the poorest one-fifth of the population is 3.7, and the wealthiest one-fifth 55.3. These figures exceed those for the entire world, which are 6.7 and 45.8, respectively (PRB Population Data Sheet 2013).

Our examination of the average figures for population growth and related factors tell only a portion of the story. The average figures hide rather sizable disparities in these statistics on a country level. When we examined these statistics on a country basis, it became evident that Guatemala is faced with the most serious problems and Belize the least. Of the 45.2 million people currently inhabiting Central America, 15.4 million (34.1%) live in Guatemala; the next most populous country is Honduras, with 8.6 million (19.0%); and the least populated country is Belize with 0.3 million (0.7%). Any reduction in the human population growth rate in Central America would be highly desirable in terms of biodiversity conservation, but will the projected decrease in growth rate be sufficient to allow for the continued protection of this biodiversity?

The most significant reason for biodiversity decline generally is conceded as habitat destruction, fragmentation, and degradation (Raven and Berg 2004; Vitt and Caldwell 2009). This premise is easy to understand, because the word habitat is defined as “the local environment in which an organism, population, or species lives” (Raven and Berg 2004). Living organisms derive the resources to support their lives and their efforts at reproduction from their habitats. The relationship between an organism and its habitat has evolved over time, and thus is an outcome of the evolutionary process. Anthropogenic damage to habitats reduces the capability of the resident organisms to survive and reproduce in their natural homes. The extent of such damage is evident in the following statement in Vitt and Caldwell (2009): “Humans have modified the environment everywhere.” They further noted that “such a comment may seem to be an exaggeration, but it is not an overstatement … Globally, our activities have resulted in a rising average annual temperature and in a rise in ultraviolet radiation at the earth’s surface. These climatic effects are only one facet of our environmental alteration, which ranges from global climatic change to the local loss of a marsh or a patch of forest.”

Habitat alteration proceeds at a rate commensurate with the following three principal factors: 1) an increase in the number of people inhabiting the Earth; 2) an increase in standards of living; and 3) the level of technological advantage enjoyed by these people. These three factors have a combined environmental effect that is described by the formula I = PAT, in which I stands for “human impact,” P for “population,” A for “affluence,” and T for “technology” (Chertow 2000). This formula describes how our growing population, affluence, and technology contribute to our increasing environmental impact. It also predicts that the increase in any one of these factors, or in any combination, can increase the amount of environmental impact felt not only by us, but also by the biosphere at large. This formula also predicts that environmental impact can increase as a consequence of rising affluence and technological capability, most evident in the more developed countries, just as it does with increasing population numbers, most evident in the less developed countries. Thus, environmental impact arises from all outcomes of the human experiment on our planet. Nonetheless, not all technological advances are undesirable (Chertow 2000). What is undesirable is humanity’s willingness to augment the undesirable aspects of such technology, i.e., planned obsolescence, lack of recycling of resources, accumulation of pollutants, and so forth.

The human experiment has been an effort, ostensibly successful, to move away from being under the control of the environmental limiting factors that impinge on all organisms. In human terms, this has meant attempting to improve the standards of living of human beings. No matter how desirable this effort might be, however, it has resulted in the creation of an unsustainable society, of which the defects and the consequences are becoming increasingly apparent over time. Perusal of the data on income distribution in the PRB 2013 Population Data Sheet is informative in this regard. Improvements to standards of living have been more beneficial to the wealthy than the poor, both at the global and individual levels. Currently, the distinction in the gross national income in purchasing power parity (GNI PPP) between the more developed and less developed sectors is startling; in the former it is $35,800 and in the latter $6,600, a disparity of 5.4 times between the two. The PRB data also indicate

Oedipina koehleri. This worm salamander is limited in distribution to three isolated montane regions in northern Nicaragua, where it occurs in Premontane Moist and Premontane Wet forests at elevations from about 600 to 945 m. We estimated its EVS as 16, placing it in the middle portion of the high vulnerability category, but its IUCN status has not been assessed. This individual is from the Reserva Natural Cerro Musún, department of Matagalpa. *Photo by Javier Sunyer.*

Rhinobothryum bovallii. This arboreal false coralsnake occurs from southeastern Honduras to northwestern Venezuela and northwestern Ecuador, where it occurs in Lowland Moist and Wet forests at elevations from near sea level to 550 m. We calculated its EVS as 16, placing it in the middle portion of the high vulnerability category, and its IUCN status is Least Concern. This individual is from Guayacán, Costa Rica. *Photo by Tobias Eisenberg.*

Rhinoclemmys funerea. The Black River Turtle is distributed from the Río Coco on the border between Honduras and Nicaragua southward to central Panama, where it occurs in Lowland Moist Forest at elevations from near sea level to 600 m. We established its EVS as 16, placing it in the middle portion of the high vulnerability category, and its IUCN status is Near Threatened. This individual is from the Río Puerto Viejo, Sarapiqui, province of Alajuela, Costa Rica. *Photo by Alejandro Solórzano.*

Oscaecilia osae. This caecilian is endemic to the Golfo Dulce region of southwestern Costa Rica, where it occurs in Lowland Moist Forest at elevations from near sea level to 40 m. We calculated its EVS as 19, placing it in the upper portion of the high vulnerability category, and its IUCN status is Data Deficient. This individual is from La Gamba, province of Puntarenas. *Photo by Peter Weish.*

that the percentage growth of the gross domestic product (GDP) has been decreasing both in the more developed and less developed portions of the world. In the more developed nations, the percentage dropped from 6.3 during the period of 2000–2006 to 1.9 during 2007–2011. In the less developed nations, the drop was from 10.2 to 7.8.

As unnerving as these statistics are, living in the more developed portion of the world does not confer insulation from economic disparity. The percent share of income between the poorest one-fifth and the richest one-fifth in the less developed and more developed regions of the world essentially is the same (6.7 and 46.3 in the former, 6.7 and 43.4 in the latter). This economic reality is relevant in the United States, where the PRB report (p. 4) concludes that "the rich get richer and the poor get poorer," a common way to characterize this disparity. Moreover, "despite having one of the world's highest standards of living, the gap between the income share of the wealthiest and poorest households in the United States is one of the widest among industrialized countries" and has increased over time. In 1967, the richest one-fifth controlled 43.6 percent of household income, compared to 4.0 percent for the poorest one-fifth. In 2011, the poorest one-fifth of households received only 3.2 percent of total national household income, while the wealthiest one-fifth received 51.1 percent. This inequality is expected to continue to grow and the economy of the United Sates will continue to suffer, even though this country's economy is discussed widely on a daily basis. So, the affluence factor in the I = PAT formula looks a bit shaky.

Since Earth presents a finite quantity of area for the human population to occupy, the density of this population will continue to increase with time. Actually, the amount of habitable land will continue to decrease with time, as a predicted consequence of global warming (Intergovernmental Panel on Climate Change [IPCC] Approved Climate Change Summary for Policymakers: 27 September 2013). Currently, the average density of the population in the less developed world is 71 people per square kilometer, which is 2.6 times greater than that in the more developed world (27/km^2). The increasing movement of people from rural to urban areas across the globe worsens this overall pattern. As noted in the PRB report, "in 1950, 117 million people lived in the top 30 [metropolitan areas] but that number rose to 426 million by 2011. In 1950, 19 of the top 30 ["mega-cities"] were in industrialized countries. By 2011, that number had shrunk to eight. In 1950, Delhi was not even in the top 30 but it is now second behind only Tokyo. Such phenomenal growth usually is due to rural-urban migration, as migrants seek a better life in cities. Unfortunately, the better life being sought often proves illusory, inasmuch as rural areas are those that provide the resources necessary to support life in both rural and urban areas. The economic investment necessary to support people in urban settings increases the impact on the resource base in rural regions. As these unsustainable practices continue environmental degradation mounts, and the impact on the remaining natural areas increases commensurately.

These features of human social evolution portend disaster for the maintenance of biodiversity. Economic primacy, especially in the more developed world, and uncontrolled population growth, especially in the less developed world, combines to create an unsustainable society for humanity (Raven and Berg 2004). Unsustainability increases the environmental pressure on organismic populations. Increasing environmental pressure promotes increasing endangerment of the other members of the living world. Thus, the job for conservation biologists grows more diffcult with the passing of time. Consequently, the time lost to inaction becomes increasingly important.

Perhaps the most unfortunate aspect of attempts at conserving biodiversity is that the most biodiverse areas overlap those that support the most rapidly growing human populations. As posted at the Conservational International website (www.conservation.org/hotspots), "the world's most remarkable places are also the most threatened." The most biodiverse areas of the planet have been termed "biodiversity hotspots." Thirty-four such areas are recognized (www.conservation.org/hotspots). Four of these areas, as recognized by Conservation International, lie in North and Central America. Almost all of two of these areas, however, lie in what we define as Mesoamerica, i.e., Mexico and Central America (Wilson and Johnson, 2010). These two are termed the Madrean Pine-Oak Woodlands and Mesoamerica; the latter name a different usage of the term than that of Wilson and Johnson (2010). The former encompasses the main mountain chains in Mexico and isolated islands in Baja California, and the southern United States (actually the southwestern United States in southeastern Arizona, southwestern New Mexico, and southwestern Texas). Apart from the northernmost portions lying in the southwestern United States, the remainder of this hotspot lies in Mexico. The other hotspot includes the lowland and premontane areas from northern Sinaloa on the Pacific versant and the Gulf coastal plain as far north as Tampico, Tamaulipas, on the Atlantic versant south to eastern Panama. This hotspot encompasses essentially all of Central America. Although the Mesoamerican forests, as defined by Conservation International, constitute the third largest hotspot in the world, the original extent of 1,130,019 km^2 has been reduced to 226,004 km^2 (to 20.0% of the original). Of the original extent, only 142,103 km^2 (12.6%) are protected, with only 63,902 km^2 (5.7%) afforded higher levels of protection. We presume that the relative figures for the entire hotspot also apply to its portion in Central America.

Ultimately, answering all the questions about biodiversity conservation will depend on finding fundamental answers to the questions about why biodiversity decline occurs. Until we uncover why humans represent such a great threat to the rest of the planet's organisms, i.e., why they have assembled themselves into unsustainable societies of one sort or another, we will have no hope of devising lasting solutions to this problem. Even though we do not intend to explore this subject in depth, at least we can offer what we consider some important comments indicating the seriousness of biodiversity decline.

1. If, as Wake and Vredenburg (2008) reported "we are entering or in the midst of the sixth great mass extinction," and that "intense human pressure, both direct and indirect, is having profound effects on natural environments," then our species is predicted to be responsible for a mass extinction episode that will be equivalent in impact to those that have preceded it. Scientists have documented that "in each of the five events" generally thought to have occurred during Earth's history, "there was a profound loss of biodiversity during a relatively short period" (Wake and Vredenburg 2008). "The most recent mass extinction was at the Cretaceous-Tertiary boundary (~65 Mya); 16% of the families, 47% of the genera of marine organisms, and 18% of the vertebrate families were lost. Most notable was the disappearance of nonavian dinosaurs; causes continue to be debated (Wake and Vreden-

Sphaerodactylus homolepis. This gecko is distributed from extreme southeastern Nicaragua to north-central Panama, where it occurs in Lowland Moist and Wet forests at elevations from near sea level to 600 m. We established its EVS as 16, placing in the middle portion of the high vulnerability category, and its IUCN status is Least Concern. This individual is from the province of Bocas del Toro, Panama. *Photo by Adam G. Clause.*

burg 2008). Given that whole genera and families of organisms, including vertebrates, disappeared during this most recent event, then a central question for humanity is whether the progenitor of the sixth mass extinction episode will survive its own malevolent creation.

2. Organisms persist on our planet because sufficient quantities of resources exist over time to support their populations. These resources arise from the atmosphere, hydrosphere, and lithosphere, as well as from the sphere of life. The three abiotic spheres interact among themselves and with the biosphere, and these interactions allow life to exist and persist on our planet. These statements are very simple and can be confirmed by a cursory examination of any ecology or environmental science textbook; however, humanity proceeds as though its collective actions are exempt from these fundamental rules of survival.

3. Natural science is one of the principal intellectual undertakings of the human species (Wilson 1998). What we know about the natural world is the result of the application of scientific methodology to the endless questions that arise from our boundless curiosity. The design of science and its use is the result of the way in which rationality operates. We generally consider that humans are the best exemplars of the rational being. Only a few other creatures (e.g., cetaceans) are thought to have the mental ability to compare favorably with our rational capacity. No other organism, however, has the benefit of our brain design coupled with bipedal posture and an opposable thumb on a five-fingered hand. Interestingly, finding an operational definition of rationality is elusive; the effort commonly results in the construction of circular definitions (i.e., definitions that do not actually define, but eventually lead back to the word one is attempting to define). Irrespectively, rationality is a function of our nervous system that allows for the connection of cause to effect from the past through the present to the future. It allows us to understand the consequences of our actions. Strangely, rationality also allows us to "ignore" the consequences of our actions. Thus, the use of scientific methodology, which is one outcome of rationality, can allow us to ask and answer questions about the natural world, within limits, but whether the answers lead to ap-

propriate actions depends on a number of other factors, such as can be understood from the viewing of any day's events in the human world.

4. Scientific advance depends on the use of scientific methodology to generate tangible and sometimes reproducible evidence to falsify hypotheses in order to support philosophies. In turn, assembling such evidence depends upon the functioning of our sensory structures, as assisted by scientific instrumentation. Other sorts of systems exist, however, that do not depend on structuring ideas based on evidence. Many people use these types of belief systems in the conduct of their lives (Ehrlich and Ehrlich 1996). To illustrate our meaning, we will use the example of evolution. As any biologist knows, the theory of evolution is the central concept of modern-day biology; examination of any modern-day university-level biology textbook will confirm this statement (e.g., Reese et al. 2013). Broad-based disciplines such as environmental science and conservation biology have the same conceptual foundation. Among the general public, however, the reality of the evolutionary process often is thought to be a matter of opinion. The word "opinion" is defined as "a belief or conclusion held with confidence but not substantiated by positive knowledge or proof" (American Heritage Dictionary, 3rd edition). A recent report (30 December 2013) of the Pew Research Center (www.pewresearch.org; accessed 2 January 2014) entitled "Public's Views on Human Evolution" is based on telephone interviews conducted from 21 March to 8 April 2013 among a national sample of 1,983 adults (age 18 and older) living in all 50 U.S. states. The question asked of the respondents was whether "humans and other living things have existed in their present form since the beginning of time, or humans and other living things have evolved over time." Thirty-three percent of the respondents agreed with the former statement and 60 percent with the latter. The greatest divergence from the results for all adults was evidenced among white evangelical Protestants (64 vs. 27%), which also was the largest group to think that evolution has been guided by a supreme being (36 vs. 36%), and Republicans (43 vs. 48%). Since the Pew Research Center's survey questions ask for yes or no responses, the basis for the variation in the responses was not explored, although it seems unlikely that it has to do with the scientific examination of the evidence for the theory of evolution through natural selection.

5. Climate change is another issue subject to the vagaries of public opinion. This term refers to the phenomenon of the anthropogenic alteration of global climatic patterns. In the sense of this definition, climate change is an environmental superproblem, in the sense of Bright (2000). Wilson and McCranie (2004) reflected that Bright "uses this term to describe environmental synergisms resulting from the interaction of two or more environmental problems, so that their combined effect is greater than the sum of their individual effects. These problems represent an environmental worst-case scenario—the point when environmental problems become so serious that they produce unanticipated results, the successful resolution of which threatens to slip forever from the grasp of humanity." This global superproblem has been studied by the Intergovernmental Panel of Climate Change (IPCC), which released its latest report in September of 2013. The panel produced an "approved summary for policymakers," which includes several conclusions of great importance. The most significant conclusion is as follows (p. 3): "Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millenia. The atmosphere and ocean have warmed, the amounts of snow and ice have diminished, sea level has risen, and the concentrations of greenhouse gases have increased." With respect to the atmosphere, the report concluded that, "each of the last three decades has been successively warmer at the Earth's surface than any preceding decade since 1850. In the Northern Hemisphere, 1983–2012 was likely the warmest 30-year period of the last 1,400 years (medium confidence)." Concerning the ocean, the report concluded that, "ocean warming dominates the increase in energy stored in the climate system, accounting for more than 90% of the energy accumulated between 1971 and 2010 (high confidence). It is virtually certain that the upper ocean (0–700 m) warmed from 1971 to 2010." The IPCC report summary also indicated that with regard to the cryosphere "over the last two decades, the Greenland and antarctic ice sheets have been losing mass, glaciers have continued to shrink almost worldwide, and Arctic sea ice and Northern Hemisphere spring snow cover have continued to decrease in extent (high confidence)." As a consequence of this diminution of ice and snow at the polar regions, "the rate of sea level rise since the mid-19th century has been larger than the mean rate during previous two millennia (high confidence). Over the period of 1901–2010, global mean sea level rose by 0.19 [0.17 to 0.21] m." Finally, the report indicated that, "the atmospheric concentrations of carbon dioxide (CO_2), methane, and nitrous oxide have increased to levels unprecedented in at least the last 800,000 years. CO_2 concentrations have increased by 40% since pre-industrial times, primarily from fossil

Tantilla vermiformis. This centipede snake is distributed from El Salvador to northwestern Costa Rica, where it occurs in Lowland Dry Forest at elevations from near sea level to 520 m. We evaluated its EVS as 14, placing it at the lower end of the high vulnerability category, and its IUCN status is Least Concern. This juvenile individual is from Volcán Masaya, Nicaragua. *Photo by José Gabriel Martínez-Fonseca.*

fuel emissions and secondarily from net land use change emissions. The ocean has absorbed about 30% of the emitted anthropogenic carbon dioxide, causing ocean acidification." Taken in their entirety, these conclusions about the anthropogenic impact on the global climate system are extremely frightening and portend future environmental changes that will have worldwide effects of hugely significant consequence. These conclusions also point very clearly to the way in which the lithosphere, the home of humanity, interacts with the atmosphere and how the atmosphere interacts with the hydrosphere and, in turn, the lithosphere. Thus, climate change is a best-case example of how an environmental superproblem evolves. In light of the general high confidence levels for the summary statements in the IPCC report, we examined the results of a Pew Research Center report published 5 November 2013 (available at www.pewresearch.org) and entitled "Climate Change: Key Data Points from Pew Research," which concluded that "the American public routinely ranks dealing with global warming low on its list of priorities for the president and Congress. This year, it ranked at the bottom of the 21 tested." Of the people surveyed in January of 2013, just 28% indicated that dealing with global warming is a top priority. This statistic contrasts most markedly with strengthening the economy, which was identified as a top priority by 86% of the survey respondents. Even dealing with "moral breakdown" at 40% beat out global warming as a top priority. Interestingly, people in the United States, who collectively are major contributors to global climate change, fell behind people in most other countries in recognizing global climate change as a major threat. Beyond all this opinion, some people opine that global warming is "just not happening." Another view of the significance of global climate change is provided in the report of the World Economic Forum entitled "Outlook on the Global Agenda 2014" (2013). One portion of this report identifies the Top Trends of 2014. Interestingly, "inaction on climate change" is on the list, but only at spot number five and after "rising societal tensions in the Middle East and North Africa," "widening income disparities," "persistent structural unemployment," and "intensifying cyber threats." Addressing issues of biodiversity decline, however, does not appear on the list. Given the glacial pace at which scientific research results are transformed into governmental policy and, beyond that, into sufficiently comprehensive plans of action that are put into effect, the question obviously arises as to whether humanity, even with its vaunted rational capacity, has the wherewithal to deal with the gargantuan problems of its own creation, especially since those problems increase in severity at a rate commensurate with the exponential growth of human population. As always, however, time will tell.

6. Given that all of humanity is faced with environmental superproblems, exemplified by global climate change, and that these problems originate in planetary spheres remote from human control, the question arises as to what effect these superproblems will have on efforts to conserve organismic populations in particular, and the structure and function of the biosphere in general. The biosphere, the entire compendium of life on Earth, exists at the interface of the three abiotic spheres based on the retrieval of resources from them. Inasmuch as the three abiotic spheres and their interrelationships evolve over time, the biosphere generally persists over time by also evolving to adapt to these environmental changes. The adaptability of organisms depends on the process of evolution according to natural selection, which obviously is a powerful enough force to allow life on Earth to survive several mass extinction episodes that date back to as far as ≈439 Mya (Wake and Vredenburg 2008). All of these past episodes have been geological in nature. As noted by Wake and Vredenburg (2008), "many scientists think that we are just now entering a profound spasm of extinction and that one of its main causes is global climate change … Furthermore, both global climate change and many other factors (e.g., habitat destruction and modification) responsible for extinction events are directly related to activities of humans." Thus, perhaps the major question facing humanity now and in the future is what portion of the biosphere will disappear into the extinction void, and if ultimately humans will join these other unfortunate creatures.

7. Presently we do not know the answers to these fundamental questions, but we are beginning to understand the extent of the impact on selected groups of organisms, especially the best known. Most zoologists work on vertebrate animals and we three are among them. As herpetologists working in one of Earth's most significant biodiversity hotspots (Mesoamerica), and attempting to assess the conservation status of the herpetofaunal species resident in this hotspot, we offer some ideas about how the sixth mass extinction episode will impact these creatures. We bring to this subject some 102 person-years of experience, as judged by the date of publication of the first scientific paper for each of us. All three of us were involved in the production of the 2010 volume entitled *Conservation of Mesoamerican Amphibians and Reptiles*, and last year we coauthored two papers in the Special Mexico Issue of the journal Amphibian & Reptile Conservation entitled "A conservation reassessment of the reptiles of Mexico based on the EVS measure" and "A conservation reassessment of the amphibians of Mexico based on the EVS measure." Other herpetologists also have weighed in on these questions, most importantly Gibbons et al. (2000), Wake and Vredenburg (2008), Stuart et al. (2010), and Böhm et al. (2013). The Gibbons et al. (2000) study was written in part to document that crocodylians, squamates, and turtles are undergoing population declines similar in scope on a global scale "to those experienced by amphibians in terms of taxonomic breadth, geographic scope, and severity." Böhm et al. (2013) presented "the first-ever global analysis of extinction risk in reptiles, based on a random representative sample of 1,500 species (16% of all currently known species)" and concluded that, "nearly one in five reptilian species [is] threatened with extinction, with another one in five species classed as Data Deficient." They further concluded that, "conservation actions specifically need to mitigate the effects of human-induced habitat loss and harvesting, which are the predominant threats to reptiles." The Stuart et al. (2010) paper reiterated the Global Amphibian Assessment analysis presented in the Stuart et al. (2004) study and concluded that "a plethora of threats impact amphibian species globally, with habitat loss and degradation being the principal threat followed by pollution. Disease is a less significant threat on a global scale, but can bring about rapid population declines leading to extinction. Deforestation is a significant threat to amphibian population stability, inasmuch as the vast majority of species depend on forest for their survival. A sizable number also depends on flowing and still freshwater habitats, largely due to their biphasic lifestyle. If the observed declines are not quickly understood and reversed, hundreds of species of amphibians will face extinction within the next few decades." Finally, Wake and Vredenburg (2008) attempted to answer the question "Are we in the midst of the sixth mass extinction?" using amphibians as a test group. These authors concluded in the most sweeping way of any of these four papers that "multiple factors acting synergistically are contributing to the loss of amphibians. But we can be sure that behind all of these activities is one weedy species, *Homo sapiens*, which has unwittingly achieved the ability to directly affect its own fate and that of most of the other species on this planet. It is an intelligent species that potentially has the capability of exercising necessary controls on the direction, speed, and intensity of factors related to the extinction crisis.

Education and changes of political direction take time that we do not have, and political leadership to date has been ineffective largely because of so many competing, short-term demands. *A primary message from the amphibians, other organisms, and environments, such as the oceans, is that little time remains to stave off mass extinction, if it is possible at all*" (emphasis ours). Using the conclusions of Wake and Vredenburg (2008) as a starting point, we provide our conclusions and recommendations on the conservation status of the Central American herpetofauna.

Conclusions and Recommendations

One or more of us previously have provided sets of conclusions and recommendations for addressing the issues of conservation of the Mesoamerican herpetofauna (Wilson and Townsend 2010; Wilson et al. 2013a, b). We used this information as a partial framework and starting point for our conclusions and recommendations concerning the conservation of the Central American herpetofauna.

1. Biodiversity decline is an environmental problem of global dimensions, comparable to the more commonly publicized problem of climate change. Both of these environmental superproblems exist because of human action and inaction, exacerbated by humanity's anthropocentric focus.

2. Our work deals with the scientific study of the herpetofauna, of which all groups are prominent components of terrestrial ecosystems in temperate and tropical regions across the globe. Only crocodylians, squamates, and turtles have made relatively limited inroads into marine habitats. Some of our earlier work dealt with the conservation status of the herpetofauna of Mexico; in this study, we are concerned with the herpetofauna of Central America.

3. Central America is a major component of Mesoamerica, the other component consisting of Mexico. Together, these two regions contribute to and extend beyond the limits of the third largest of the 34 biodiversity hotspots identified by Conservation International. The herpetofauna of Central America is of major significance and presently consists of 493 amphibians and 559 crocodylians, squamates, and turtles, for a total of 1,052 species. Our knowledge of the dimensions of this herpetofauna will continue to augment with time. In the interim between 31 December 2008 and the present, 92 species have been added to this herpetofauna, an increase of 9.7% percent over the number considered in Wilson and Johnson (2010). Presently, there are more amphibians in Central America than in Mexico (493 vs. 383), and more crocodylians, squamates, and turtles collectively in Mexico than in Central America (869 vs. 559). Although more amphibians, crocodylians, squamates, and turtles occur in Mexico than in Central America (1,252 vs. 1,052), Mexico is about three and three-quarters the size of Central America, indicating significantly greater herpetofaunal numbers per unit area in Central America than in Mexico.

4. Herpetofaunal endemism also is significant in Central America. Of the 493 amphibians known from the region, 324 (65.7%) are endemic. Of the 559 reptiles found there, 261 (46.7%) are endemic. The entire herpetofauna is characterized by an endemicity of 55.6%. These figures are fairly comparable to those for Mexico. Amphibian endemism is only slightly higher in Mexico than in Central America (67.4 vs. 65.7%). Endemism of the remainder of the herpetofauna is about 11 percentage points higher in Mexico than in Central America (57.4 vs. 46.7%). Endemism for the total herpetofauna is only a few percentage points higher in Mexico than in Central America (60.4% vs. 55.6%). Thus, more than one-half of the Central American herpetofauna is endemic to the region, compared to six of every 10 species in Mexico.

5. The IUCN employs the most commonly used means of conservation status assessment. The implementation of this system, however, is expensive, time-consuming, slow to respond to systematic advances, and likely to resort to the Data Deficient category when assessing taxa described from single specimens and/or single localities, and to the Least Concern category as a kind of conservation "dumping ground" for species that deserve a more careful examination.

6. Given the problems we see with the use of the IUCN system of categorizaitons, we employed a revised Environmental Vulnerability Score (EVS) measure that allowed us to address the deficiencies of the IUCN system and to provide a conservation assessment for all of the species now known to comprise the Central America herpetofauna. The EVS values can range from 3–20 and are placed in three categories: low (3–9); medium (10–13); and high (14–20). Our calculations indicate that the EVS values for amphibians are categorized as follows: low (39 species of 493 [7.9%]); medium (105 [21.3%]); and high (349 [70.8%]). For the crocodylians, squamates, and turtles, the values are: low (81 of 552 [14.7%]); medium (162 [29.3%]); and high (309 [56.0%]). For the entire herpetofauna, the values are: low (119 of 1,045 [11.4%]); medium (267 [25.6%]); and high (658 [63.0%]). Thus,

Ungaliophis panamensis. This small arboreal boa is found on the Atlantic versant from southeastern Nicaragua to northwestern Colombia, and on the Pacific versant from northwestern Costa Rica to western Panama, where it occurs in Lowland Moist and Wet, Premontane Wet, and Lower Montane Wet forests at elevations from near sea level to 2,100 m. We gauged its EVS as 12, placing it in the upper portion of the medium vulnerability category, but its IUCN status has not been determined. This individual is from the Río Indio Lodge located in the Indio Maiz Biological Reserve, department of Río San Juan, in southeastern Nicaragua. *Photo by Javier Sunyer.*

our analysis indicates that more than six of every 10 herpetofaunal species are highly vulnerable to environmental damage from anthropogenic causes.

7. In 2013, we conducted a similar study of the Mexican herpetofauna. When comparing our results for Central America and Mexico, a greater proportion of amphibians in Central America fell into the high vulnerability category than in Mexico (70.8% vs. 58.8%). In both regions, salamanders are the most vulnerable when compared to anurans and caecilians. Among the rest of the herpetofauna, however, we found about the same proportion in the high vulnerability category in Central America (56.0%) as in Mexico (55.9%). Considering the two highest species groups (lizards and snakes), in both Mexico and Central America lizards are more vulnerable to environmental damage than snakes.

8. Given the length of time it takes for an IUCN assessment to appear at the Red List website after a new species is described and the expense involved to produce such an assessment, we recommend that the original describers provide at least an estimate of the conservation status of the taxon in question in the original description. In addition, since this task might be difficult to undertake, given the deficiencies of the IUCN system we have identified here and elsewhere, we also recommend that the original describers calculate an Environmental Vulnerability Score to provide an additional assessment of the conservation status for the species being described.

9. Assessments of the conservation status of any group of organisms essentially remain academic exercises, unless sufficient attention is provided to the imperatives underlying the threats to biodiversity created by humanity. Humanity lives unsustainably on planet Earth. The pressure placed on limited resources by an exponentially growing human population creates this reality. Humans are cosmopolitan animals that become more so with the passage of time. The approach is the same wherever one finds humans, as essentially it is a unidirectional track from point A (what humans want) to point B (what humans obtain), with the minimal amount of possible diversion between the two points. Unidirectionality, however, is not a feature of the structure and function of Earth.

Rather, this planet, especially the portion of most concern to humanity, consists of four primary spheres that intertwine among themselves to create an environment in which humanity can exist. All of these spheres, the atomsphere, hydrosphere, lithosphere, and biosphere provide resources to our species, without which its survival is impossible. One way of looking at this matter is that humanity, in return for life support and from its perch on Earth's surface, favors these spheres with a plethora of environmental problems that retrace the same pathways as exist in the natural world to make the resources for life support available to humans. As an example, burning forests and fossil fuels pumps CO_2 into the atmosphere and this pollutant causes its temperature to rise and creates global warming, which in turn produces climate change that impacts the planet's solid and liquid surfaces. Burning forests to make way for agriculture also degrades habitats for the world's creatures, especially those that live on land, creating biodiversity decline.

10. More than two decades ago on 18 November 1992, the Union of Concerned Scientists issued the World Scientists' Warning to Humanity (www.ucsusa.org). To date, this statement has been signed by "some 1,700 of the world's leading scientists, including the majority of Nobel laureates in the sciences" (www.ucsusa.org/about/1992-world-scientists.html; accessed 2 February 2014). The one-paragraph introduction to the statement is cogently powerful. "Human beings and the natural world are on a collision course. Human activities inflict harsh and often irreversible damage on the environment and on critical resources. If not checked, many of our current practices put at serious risk the future that we wish for human society and the plant and animal kingdoms, and may so alter the living world that it will be unable to sustain life in the manner that we know [emphasis ours]. Fundamental changes are urgent if we are to avoid the collision our present course will bring about." For all intents and purposes, we have lost the intervening two decades to inaction and further encroachment.

11. The warning to humanity contained a simple and elegant statement of "what we must do." This statement consists of "five inextricably linked areas that must be addressed simultaneously," as follows:

    "**We must bring environmentally damaging activities under control to restore and protect the integrity of the earth's systems we depend on.** We must, for example, move away from fossil fuels to more benign, inexhaustible energy sources to cut greenhouse gas emissions and the pollution of our air and water. Priority must be given to the development of energy sources matched to Third World needs—small-scale and relatively easy to implement."

    "**We must manage resources crucial to human welfare more effectively.** We must give high priority to efficient use of energy, water, and other materials, including expansion of conservation and recycling."

    "**We must stabilize population.** This will be possible only if all nations recognize that it requires improved social and economic conditions, and the adoption of effective, voluntary family planning."

    "**We must reduce and eliminate poverty.**"

    "**We must ensure sexual equality, and guarantee women control over their own reproductive decisions.**"

12. Only within the context of simultaneously addressing the above-indicated "inextricably linked" social imperatives can we sensibly discuss "what we must do" to safeguard organismic populations, including those of the herpetofauna of Central America. So, our most significant recommendation is to address these imperatives in the shortest time possible.

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Addendum (changes past conclusion of analyses)

We chose a cut-off date of 1 March 2015 for which to discontinue revising the hundreds to thousands of numbers and calculations dealing with the 1,052 herpetofaunal species in this paper. After this date, we continued adding pertinent taxa and publications in this addendum, as follows:

(1) *Hyalinobatrachium dianae*. Kubicki et al. (2015) described this new species of glassfrog from the lowland and premontane forests of Caribbean Costa Rica, which is known from the provinces of Heredia and Limón at elevations from 400 to 900 m. Its EVS can be calculated as 5+7+3=15.

(2) *Gerrhonotus liocephalus*. Morales et al. (2015) reported this alligator lizard, formerly limited in distribution to Mexico and Texas in the United States, from Guatemala, thus adding this species to the Central American herpetofauna. Its EVS remains as 2+1+3=6.

(3) *Ecnomiohyla bailarina*. Kubicki and Salazar (2015) reported this fringe-limbed treefrog, formally known only from the type locality in Panama, from the Caribbean foothills of southeastern Costa Rica. As a consequence, its EVS needs to be recalcuated as 5+7+6=18.

(4) *Holcosus* spp. Meza-Lázaro and Nieto Montes de Oca (2015) revised the species *Holcosus undulatus* and elevated nine former subspecies to species level in Mesoamerica, including five taxa in Central America (*H. hartwegi*, *H. miadis*, *H. parvus*, *H. pulcher*, and *H. thomasi*). As a consequence, the ranges of these elevated taxa naturally are smaller and the resulting EVS will be higher than that calculated in Appendix 2 for the former *H. undulatus*.

(5) *Bradytriton silus*. Since its description in 1983, this plethodontid salamander species, the single member of its genus, has been considered endemic to Guatemala and, therefore, to Central America. Recently, however, a specimen was collected by a field crew associated with Sean Rovito at San Francisco Jimbal in northern Chiapas, which constitutes the first record for this species in Mexico (Bouzid et al. 2015). Thus, *B. silus* no longer is a Central American endemic.

Jerry D. Johnson is Professor of Biological Sciences at The University of Texas at El Paso, and has extensive experience investigating the herpetofauna of Mesoamerica, especially in Mexico. Presently, he is the Director of the 40,000 acre "Indio Mountians Research Station" located in the Chihuahuan Desert near the Mexican border. Jerry is a co-editor of the recently published *Conservation of Mesoamerican Amphibians and Reptiles*, is Mesoamerica/Caribbean section editor for Geographic Distribution segment of *Herpetological Review*, and is an Associate Editor and Co-chair of the Taxonomic Board for the Journal *Mesoamerican Herpetology*. Johnson has authored or co-authored 100 peer-reviewed papers, including two 2010 articles, "Geographic distribution and conservation of the herpetofauna of southeastern Mexico" and "Distributional patterns of the herpetofauna of Mesoamerica, a biodiversity hotspot," as well as two 2013 articles in the Special Mexican Edition of *Amphibian & Reptile Conservation* entitled, "A conservation reassessment of the reptiles of Mexico based on the EVS measure, and "A conservation reassessment of the amphibians of Mexico based on the EVS measure." He was also Co-editor for the books *Middle American Herpetology: A Bibliographic Checklist* and *Mesoamerican Herpetology: Systematics, Zoogeography, and Conservation*.

Vicente Mata-Silva is a herpetologist interested in ecology, conservation, geographic distribution, and the monitoring of amphibians and reptiles in Mexico and the southwestern United States. His bachelor's thesis at the Universidad Nacional Autónoma de México (UNAM) compared herpetofaunal richness in Puebla, México, in habitats with different degrees of human-related disturbance. Vicente's master thesis focused primarily on the diet of two syntopic whiptail lizard species, one unisexual and the other bisexual, in the Trans-Pecos region of the Chihuanhuan Desert. His dissertation was on the ecology of the rock rattlesnake, *Crotalus lepidus*, in the northern Chihuahuan Desert. To date, Vicente has authored or co-authored over 60 peer-reviewed scientific publications. Currently, he is a research fellow and lecturer at the University of Texas at El Paso, where his work focuses on the ecology of rattlesnake populations in a Chihuahuan Desert habitat; he also is a Distribution Notes Section Editor for the journal *Mesoamerican Herpetology*.

Larry David Wilson is a herpetologist with lengthy experience in Mesoamerica, totaling six and one-half collective years (combined over the past 49). Larry is the senior editor of *Conservation of Mesoamerican Amphibians and Reptiles* (2010) and the co-author of seven of its chapters. He is retired from 35 years of service as a professor of biology at Miami-Dade College in Miami, Florida. Larry is the author or co-author of over 315 peer-reviewed papers and books on herpetology, including the 2004 *Amphibian & Reptile Conservation* paper entitled "The conservation status of the herpetofauna of Honduras" and the two 2013 papers entitled "A conservation reassessment of the amphibians of Mexico based on the EVS measure" and "A conservation reassessment of the reptiles of Mexico based on the EVS measure." His other books include *The Snakes of Honduras* (1985), *Middle American Herpetology* (1988), *The Amphibians of Honduras* (2002), *Amphibians & Reptiles of the Bay Islands and Cayos Cochinos, Honduras* (2005), *The Amphibians and Reptiles of the Honduran Mosquitia* (2006), and *Guide to the Amphibians & Reptiles of Cusuco National Park, Honduras* (2008). For 33 years he served as the Snake Section Editor for the *Catalogue of American Amphibians and Reptiles*. Over his career to date, he has authored or co-authored the descriptions of 70 currently recognized herpetofaunal species and six species have been named in his honor, including the anuran *Craugastor lauraster* and the snakes *Cerrophidion wilsoni*, *Myriopholis wilsoni*, and *Oxybelis wilsoni*.

Appendix 1. Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	IUCN rating	Environmental Vulnerability Score				EVS Category
		Geographic Distribution	Ecological Distribution	Reproductive Mode	Total Score	
Order Anura (319 species)						
Family Aromobatidae (3 species)						
Allobates talamancae	LC	1	6	4	11	M
Anomaloglossus astralogaster*	NE	6	8	4?	18	H
Anomaloglossus isthminus*	NE	5	7	4?	16	H
Family Bufonidae (39 species)						
Atelopus certus*	EN	5	8	1	14	H
Atelopus chiriquiensis*	CR	5	8	1	14	H
Atelopus chirripoensis*	CR	6	8	1?	15	H
Atelopus glyphus	CR	4	8	1	13	M
Atelopus limosus*	EN	5	8	1	14	H
Atelopus senex*	CR	5	7	1	13	M
Atelopus varius*	CR	5	5	1	11	M
Atelopus zeteki*	CR	5	7	1	13	M
Incilius aucoinae*	LC	5	8	1	14	H
Incilius aurarius	NE	4	8	1	13	M
Incilius bocourti	LC	4	6	1	11	M
Incilius campbelli	NT	4	7	1	12	M
Incilius canaliferus	LC	4	3	1	8	L
Incilius chompipe*	VU	5	7	1?	13	M
Incilius coccifer	LC	3	5	1	9	L
Incilius coniferus	LC	1	6	1	8	L
Incilius epioticus*	LC	5	7	4?	16	H
Incilius fastidiosus*	CR	5	7	1	13	M
Incilius guanacaste*	DD	5	8	4?	17	M
Incilius holdridgei*	CR	5	8	1	14	H
Incilius ibarrai*	EN	5	7	1	13	M
Incilius karenlipsae*	NE	6	8	1?	15	H
Incilius leucomyos*	EN	5	6	1	12	M
Incilius luetkenii	LC	3	3	1	7	L
Incilius macrocristatus	VU	4	6	1	11	M
Incilius melanochlorus*	VU	5	6	1	12	M
Incilius periglenes*	EX	6	8	1	15	H
Incilius peripatetes*	CR	5	8	1?	14	H
Incilius porteri*	DD	5	8	1?	14	H
Incilius signifer*	LC	5	8	1?	14	H
Incilius tacanensis	EN	4	4	1	9	L
Incilius tutelarius	EN	4	5	1	10	M
Incilius valliceps	LC	3	2	1	6	L
Rhaebo haematiticus	LC	1	7	1	9	L
Rhinella acrolopha	DD	4	8	4?	16	H

Appendix 1 (continued). Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	IUCN rating	Environmental Vulnerability Score				EVS Category
		Geographic Distribution	Ecological Distribution	Reproductive Mode	Total Score	
Rhinella alata	DD	4	7	4?	15	H
*Rhinella centralis**	LC	5	8	1	14	H
*Rhinella chrysophora**	EN	5	7	1	13	M
Rhinella marina	LC	1	1	1	3	L
Family Centrolenidae (14 species)						
Cochranella euknemos	LC	1?	6	3	10	M
*Cochranella granulosa**	LC	5	7	3	15	H
Espadarana prosoblepon	LC	1?	5	3	9	L
Hyalinobatrachium aureoguttatum	NT	3	7	3	13	M
Hyalinobatrachium chirripoi	LC	2	7	3	12	M
Hyalinobatrachium colymbiphyllum	LC	1?	6	3	10	M
Hyalinobatrachium fleischmanni	LC	1?	4	3	8	L
*Hyalinobatrachium talamancae**	LC	5	8	3	16	H
Hyalinobatrachium valerioi	LC	1?	7	3	11	M
*Hyalinobatrachium vireovittatum**	DD	5	8	3	16	H
Sachatamia albomaculata	LC	2	7	3	12	M
Sachatamia ilex	LC	2?	7	3?	12	M
Teratohyla pulverata	LC	2?	7	3	12	M
Teratohyla spinosa	LC	1?	7	3	11	M
Family Craugastoridae (101 species)						
*Craugastor adamastus**	DD	6	8	4	18	H
Craugastor alfredi	VU	2	5	4	11	M
Craugastor amniscola	DD	4	6	4	14	H
*Craugastor anciano**	CR	5	7	4	16	H
*Craugastor andi**	CR	5	8	4	17	H
*Craugastor angelicus**	CR	5	6	4	15	H
*Craugastor aphanus**	VU	5	8	4	17	H
*Craugastor aurilegulus**	EN	5	6	4	15	H
*Craugastor azueroensis**	EN	5	7	4	16	H
*Craugastor bocourti**	VU	5	7	4	16	H
*Craugastor bransfordii**	LC	5	4	4	13	M
Craugastor brocchi	VU	4	6	4	14	H
*Craugastor campbelli**	DD	5?	7	4	16	H
*Craugastor catalinae**	CR	5	8	4	17	H
*Craugastor chac**	NT	5	7	4	16	H
*Craugastor charadra**	EN	5	6	4	15	H
*Craugastor chingopetaca**	DD	6	8	4	18	H
*Craugastor chrysozetetes**	EX	6	8	4	18	H
*Craugastor coffeus**	CR	6	8	4	18	H
Craugastor crassidigitus	LC	2	6	4	12	M
*Craugastor cruzi**	CR	6	8	4	18	H

Appendix 1 (continued). Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	IUCN rating	Environmental Vulnerability Score				EVS Category
		Geographic Distribution	Ecological Distribution	Reproductive Mode	Total Score	
*Craugastor cuaquero**	DD	6	8	4	18	H
*Craugastor cyanochthebius**	NT	6	8	4	18	H
*Craugastor daryi**	EN	5	8	4	17	H
*Craugastor emcelae**	CR	5	8	4	17	H
*Craugastor emleni**	CR	5	6	4	15	H
*Craugastor epochthidius**	CR	5	7	4	16	H
*Craugastor escoces**	EX	5	6	4	15	H
*Craugastor evanesco**	NE	5	8	4	17	H
*Craugastor fecundus**	CR	5	7	4	16	H
Craugastor fitzingeri	LC	2	6	4	12	M
*Craugastor fleischmanni**	CR	5	7	4	16	H
*Craugastor gollmeri**	LC	5	7	4	16	H
Craugastor greggi	CR	4	7	4	15	H
*Craugastor gulosus**	EN	5	8	4	17	H
*Craugastor inachus**	EN	5	8	4	17	H
*Craugastor jota**	DD	6	8	4	18	H
*Craugastor laevissimus**	EN	5	3	4	12	M
Craugastor laticeps	NT	4	4	4	12	M
*Craugastor lauraster**	EN	5	7	4	16	H
Craugastor lineatus	CR	4	7	4	15	H
Craugastor loki	LC	4	4	4	12	M
Craugastor longirostris	LC	3	7	4	14	H
Craugastor matudai	VU	4	7	4	15	H
*Craugastor megacephalus**	LC	5	7	4	16	H
*Craugastor melanostictus**	LC	5	7	4	16	H
*Craugastor merendonensis**	CR	6	8	4	18	H
*Craugastor milesi**	CR	5	7	4	16	H
*Craugastor mimus**	LC	5	7	4	16	H
*Craugastor monnichorum**	DD	5	7	4	16	H
*Craugastor myllomyllon**	DD	6	8	4	18	H
*Craugastor nefrens**	DD	6	8	4	18	H
*Craugastor noblei**	LC	5	7	4	16	H
*Craugastor obesus**	EN	5	8	4	17	H
*Craugastor olanchano**	CR	6	8	4	18	H
*Craugastor omoaensis**	CR	6	8	4	18	H
Craugastor opimus	LC	4	7	4	15	H
Craugastor palenque	DD	4	7	4	15	H
*Craugastor pechorum**	EN	5	7	4	16	H
*Craugastor persimilis**	VU	5	7	4	16	H
*Craugastor phasma**	DD	6	8	4	18	H
*Craugastor podiciferus**	NT	5	6	4	15	H

Appendix 1 (continued). Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	IUCN rating	Environmental Vulnerability Score				EVS Category
		Geographic Distribution	Ecological Distribution	Reproductive Mode	Total Score	
*Craugastor polyptychus**	LC	5	8	4	17	H
*Craugastor psephosypharus**	VU	5	7	4	16	H
*Craugastor punctariolus**	EN	5	7	4	16	H
Craugastor pygmaeus	VU	2	3	4	9	L
Craugastor raniformis	LC	4	7	4	15	H
*Craugastor ranoides**	CR	5	6	4	15	H
*Craugastor rayo**	DD	5	7	4	16	H
*Craugastor rhyacobatrachus**	EN	5	7	4	16	H
*Craugastor rivulus**	VU	5	8	4	17	H
*Craugastor rostralis**	NT	5	7	4	16	H
*Craugastor rugosus**	LC	5	7	4	16	H
Craugastor rupinius	LC	4	5	4	13	H
*Craugastor sabrinus**	EN	5	7	4	16	H
*Craugastor saltuarius**	CR	6	8	4	18	H
*Craugastor sandersoni**	EN	5	7	4	16	H
*Craugastor stadelmani**	CR	5	7	4	16	H
*Craugastor stejnegerianus**	LC	5	5	4	14	H
Craugastor stuarti	EN	4	7	4	15	H
*Craugastor tabasarae**	CR	5	8	4	17	H
*Craugastor talamancae**	LC	5	8	4	17	H
*Craugastor taurus**	CR	5	8	4	17	H
*Craugastor trachydermus**	CR	6	8	4	18	H
*Craugastor underwoodi**	LC	5	7	4	16	H
*Craugastor xucanebi**	VU	5	7	4	16	H
Pristimantis achatinus	LC	3	7	4	14	H
*Pristimantis adnus**	NE	6	8	4	18	H
*Pristimantis altae**	NT	5	7	4	16	H
*Pristimantis caryophyllaceus**	NT	5	6	4	15	H
*Pristimantis cerasinus**	LC	5	7	4	16	H
Pristimantis cruentus	LC	4	6	4	14	H
Pristimantis gaigeae	LC	4	8	4	16	H
Pristimantis moro	LC	4	8	4	16	H
*Pristimantis museosus**	EN	5	8	4	17	H
*Pristimantis pardalis**	NT	5	8	4	17	H
*Pristimantis pirrensis**	DD	6	8	4	18	H
Pristimantis ridens	LC	2	6	4	12	M
Pristimantis taeniatus	LC	4	8	4	16	H
Strabomantis bufoniformis	LC	4	8	4	16	H
*Strabomantis laticorpus**	DD	5	8	4	17	H
Family Dendrobatidae (19 species)						
*Ameerega maculata**	DD	6	8	4?	18	H

Appendix 1 (continued). Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	IUCN rating	Environmental Vulnerability Score				EVS Category
		Geographic Distribution	Ecological Distribution	Reproductive Mode	Total Score	
*Andinobates claudiae**	DD	6	8	4	18	H
Andinobates fulguritus	LC	4	7	4	15	H
*Andinobates geminisae**	NE	6	8	4	18	H
Andinobates minutus	LC	4	7	4	15	H
*Colostethus latinasus**	DD	5	6	4	15	H
Colostethus panamensis	LC	4	7	4	15	H
Colostethus pratti	LC	4	7	4	15	H
Dendrobates auratus	LC	4	7	4	15	H
Hyloxalus chocoensis	DD	4	8	4	16	H
*Oophaga arborea**	EN	5	7	4	16	H
*Oophaga granulifera**	VU	5	8	4	17	H
*Oophaga pumilio**	LC	5	7	4	16	H
*Oophaga speciosa**	EN	5	7	4	16	H
*Oophaga vicentei**	DD	5	7	4	16	H
*Phyllobates lugubris**	LC	5	8	4	17	H
*Phyllobates vittatus**	EN	5	8	4	17	H
*Silverstoneia flotator**	LC	5	7	4	16	H
Silverstoneia nubicola	NT	4	6	4	14	H
Family Eleutherodactylidae (11 species)						
*Diasporus citrinobapheus**	NE	5	8	4	17	H
*Diasporus diastema**	LC	5	6	4	15	H
*Diasporus hylaeformis**	LC	5	8	4	17	H
*Diasporus igneus**	NE	6	8	4	18	H
Diasporus quidditus	LC	4	8	4	16	H
*Diasporus tigrillo**	DD	6	8	4	18	H
*Diasporus ventrimaculatus**	VU	6	8	4	18	H
Diasporus vocator	LC	4	7	4	15	H
Eleutherodactylus leprus	VU	2	6	4	12	M
Eleutherodactylus pipilans	LC	2	5	4	11	M
Eleutherodactylus rubrimaculatus	VU	4	7	4	15	H
Family Hemiphractidae (3 species)						
Gastrotheca cornuta	EN	4	7	5	16	H
Gastrotheca nicefori	LC	3	7	5	15	H
Hemiphractus fasciatus	NT	4	7	5	16	H
Family Hylidae (98 species)						
*Agalychnis annae**	EN	5	7	3	15	H
Agalychnis callidryas	LC	3	5	3	11	M
Agalychnis lemur	CR	2	7	3	12	M
Agalychnis litodryas	VU	4	8	3	15	H
Agalychnis moreletii	CR	1	3	3	7	L
*Agalychnis saltator**	LC	5	6	3	14	H

Appendix 1 (continued). Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	**IUCN rating**	**Environmental Vulnerability Score**				**EVS Category**
		Geographic Distribution	**Ecological Distribution**	**Reproductive Mode**	**Total Score**	
Agalychnis spurrelli	LC	4	7	3	14	H
Anotheca spinosa	LC	3	6	6	15	H
Bromeliohyla bromeliacia	EN	4	7	6	17	H
Cruziohyla calcarifer	LC	4	8	3	15	H
Dendropsophus ebraccatus	LC	3	6	3	12	M
Dendropsophus microcephalus	LC	3	3	1	7	L
Dendropsophus phlebodes	LC	3	7	1	11	M
Dendropsophus robertmertensi	LC	4	4	1	9	L
Dendropsophus subocularis	LC	4	8	1	13	M
*Duellmanohyla lythrodes**	EN	5	8	1	14	H
*Duellmanohyla rufioculis**	LC	5	8	1	14	H
*Duellmanohyla salvavida**	CR	5	7	1	13	M
Duellmanohyla schmidtorum	VU	4	3	1	8	L
*Duellmanohyla soralia**	CR	5	6	1	12	M
*Duellmanohyla uranochroa**	EN	5	6	1	12	M
*Ecnomiohyla bailarina**	NE	6	8	6?	20	H
Ecnomiohyla fimbrimembra	CR	6	7	6	19	H
*Ecnomiohyla miliaria**	VU	5	7	6	18	H
*Ecnomiohyla minera**	EN	5	7	6	18	H
*Ecnomiohyla rabborum**	CR	6	8	6	20	H
*Ecnomiohyla salvaje**	CR	5	8	6	19	H
*Ecnomiohyla sukia**	NE	5	7	6	18	H
*Ecnomiohyla thysanota**	DD	6	8	6?	20	H
*Ecnomiohyla veraguensis**	NE	6	8	6?	20	H
*Exerodonta catracha**	EN	5	8	1	14	H
*Exerodonta perkinsi**	CR	6	8	1	15	H
*Hyla bocourti**	CR	5	8	1	14	H
Hyla walkeri	VU	4	6	1	11	M
Hyloscirtus colymba	CR	4	8	1	13	M
Hyloscirtus palmeri	LC	4	8	1	13	M
Hypsiboas boans	LC	3	8	1	12	M
Hypsiboas crepitans	LC	3	8	1	12	M
Hypsiboas pugnax	LC	4	8	1	13	M
Hypsiboas rosenbergi	LC	4	8	1	13	M
*Hypsiboas rufitelus**	LC	5	8	1	14	H
*Isthmohyla angustilineata**	CR	5	7	1	13	M
*Isthmohyla calypsa**	CR	5	8	3	16	H
*Isthmohyla debilis**	CR	5	8	1	14	H
*Isthmohyla graceae**	CR	5	7	1	13	M
*Isthmohyla infucata**	DD	5	8	1	14	H
*Isthmohyla insolita**	CR	6	8	3	17	H

Appendix 1 (continued). Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	IUCN rating	Environmental Vulnerability Score				EVS Category
		Geographic Distribution	Ecological Distribution	Reproductive Mode	Total Score	
*Isthmohyla lancasteri**	LC	5	8	1	14	H
*Isthmohyla melacaena**	NT	6	8	6	20	H
*Isthmohyla picadoi**	NT	5	8	6	19	H
*Isthmohyla pictipes**	EN	5	8	1	14	H
*Isthmohyla pseudopuma**	LC	5	7	1	13	M
*Isthmohyla rivularis**	CR	5	7	1	13	M
*Isthmohyla tica**	CR	5	7	1	13	M
*Isthmohyla xanthosticta**	DD	6	8	1	15	H
*Isthmohyla zeteki**	NT	5	7	6	18	H
Phyllomedusa venusta	LC	4	8	1	13	M
Plectrohyla acanthodes	CR	4	7	1	12	M
Plectrohyla avia	CR	4	8	1	13	M
*Plectrohyla chrysopleura**	CR	5	7	1	13	M
*Plectrohyla dasypus**	CR	6	7	1	14	H
*Plectrohyla exquisita**	CR	6	8	1	15	H
*Plectrohyla glandulosa**	EN	5	6	1	12	M
Plectrohyla guatemalensis	CR	4	4	1	9	L
Plectrohyla hartwegi	CR	4	5	1	10	M
Plectrohyla ixil	CR	4	7	1	12	M
Plectrohyla matudai	VU	4	6	1	11	M
*Plectrohyla pokomchi**	CR	5	7	1	13	M
*Plectrohyla psiloderma**	EN	5	8	1	14	H
*Plectrohyla quecchi**	CR	5	7	1	13	M
Plectrohyla sagorum	EN	4	5	1	10	M
*Plectrohyla tecunumani**	CR	5	8	1	14	H
*Plectrohyla teuchestes**	CR	6	8	1	15	H
*Ptychohyla dendrophasma**	CR	6	8	6?	20	H
Ptychohyla euthysanota	NT	4	3	1	8	L
*Ptychohyla hypomykter**	CR	5	4	1	10	M
*Ptychohyla legleri**	EN	5	8	1	14	H
Ptychohyla macrotympanum	CR	4	6	1	11	M
*Ptychohyla panchoi**	EN	5	7	1	13	M
*Ptychohyla salvadorensis**	EN	5	6	1	12	M
*Ptychohyla sanctaecrucis**	CR	6	7	1	14	H
*Ptychohyla spinipollex**	EN	5	6	1	12	M
*Scinax altae**	LC	5	8	1	14	H
Scinax boulengeri	LC	4	6	1	11	M
*Scinax elaeochroa**	LC	5	7	1	13	M
Scinax rostrata	LC	3	7	1	11	M
Scinax rubra	LC	3	7	1	11	M
Scinax staufferi	LC	2	1	1	4	L

Appendix 1 (continued). Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	IUCN rating	Environmental Vulnerability Score				EVS Category
		Geographic Distribution	Ecological Distribution	Reproductive Mode	Total Score	
Smilisca baudinii	LC	1	1	1	3	L
Smilisca cyanosticta	NT	4	7	1	12	M
Smilisca phaeota	LC	4	6	1	11	M
*Smilisca puma**	LC	5	8	1	14	H
Smilisca sila	LC	4	5	1	10	M
Smilisca sordida	LC	2	5	1	8	L
Tlalocohyla loquax	LC	3	3	1	7	L
Tlalocohyla picta	LC	2	5	1	8	L
Trachycephalus typhonius	LC	1	2	1	4	L
Triprion petasatus	LC	4	5	1	10	M
Family Leptodactylidae (9 species)						
Engystomops pustulosus	LC	3	2	2	7	L
Leptodactylus fragilis	LC	1	2	2	5	L
Leptodactylus fuscus	LC	3	7	2	12	M
Leptodactylus insularum	LC	3	7	2	12	M
Leptodactylus melanonotus	LC	1	3	2	6	L
Leptodactylus poecilochilus	LC	4	6	2	12	M
Leptodactylus savagei	LC	2	5	2	9	L
*Leptodactylus silvanimbus**	CR	5	7	2	14	H
Pleurodema brachyops	LC	3	8	2	13	M
Family Microhylidae (9 species)						
Ctenophryne aterrima	LC	4	7	1	12	M
Elachistocleis ovalis	LC	3	7	1	11	M
Elachistocleis panamensis	LC	4	7	1	12	M
Elachistocleis pearsei	LC	3	8	1	12	M
Gastrophryne elegans	LC	2	5	1	8	L
Hypopachus barberi	VU	4	5	1	10	M
*Hypopachus pictiventris**	LC	5	8	1	14	H
Hypopachus ustus	LC	3	4	1	8	L
Hypopachus variolosus	LC	2	1	1	4	L
Family Pipidae (1 species)						
*Pipa myersi**	EN	4	8	5	17	H
Family Ranidae (11 species)						
Lithobates brownorum	NE	4	3	1	8	L
Lithobates forreri	LC	1	1	1	3	L
*Lithobates juliani**	NT	5	6	1	12	M
Lithobates macroglossa	VU	4	7	1	12	M
Lithobates maculatus	LC	3	1	1	5	L
*Lithobates miadis**	VU	6	8	1	15	H
Lithobates pipiens complex	LC	4	4	1	9	L
*Lithobates taylori**	LC	5	6	1	12	M

Appendix 1 (continued). Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	IUCN rating	Environmental Vulnerability Score				EVS Category
		Geographic Distribution	Ecological Distribution	Reproductive Mode	Total Score	
Lithobates vaillanti	LC	3	5	1	9	L
*Lithobates vibicarius**	VU	5	8	1	14	H
*Lithobates warszewitschii**	LC	5	4	1	10	M
Family Rhinophrynidae (1 species)						
Rhinophrynus dorsalis	LC	2	5	1	8	L
Order Caudata (159 species)						
Family Plethodontidae (159 species)						
*Bolitoglossa alvaradoi**	EN	5	7	4	16	H
*Bolitoglossa anthracina**	DD	6	8	4	18	H
*Bolitoglossa aureogularis**	NE	6	8	4	18	H
Bolitoglossa biseriata	LC	1	8	4	13	M
*Bolitoglossa bramei**	DD	5	8	4	17	H
*Bolitoglossa carri**	CR	6	8	4	18	H
*Bolitoglossa cataguana**	NE	6	8	4	18	H
*Bolitoglossa celaque**	EN	5	8	4	17	H
*Bolitoglossa centenorum**	NE	6	8	4	18	H
*Bolitoglossa cerroensis**	LC	5	7	4	16	H
Bolitoglossa chucantiensis	NE	6	8	4	18	H
*Bolitoglossa colonnea**	LC	5	7	4	16	H
*Bolitoglossa compacta**	EN	5	8	4	17	H
*Bolitoglossa conanti**	EN	5	7	4	16	H
*Bolitoglossa copia**	DD	6	8	4	18	H
*Bolitoglossa cuchumatana**	NT	5	5	4	14	H
*Bolitoglossa cuna**	DD	5	8	4	17	H
*Bolitoglossa daryorum**	NE	5	8	4	17	H
*Bolitoglossa decora**	CR	6	8	4	18	H
*Bolitoglossa diaphora**	CR	6	8	4	18	H
*Bolitoglossa diminuta**	VU	6	8	4	18	H
*Bolitoglossa dofleini**	NT	5	6	4	15	H
*Bolitoglossa dunni**	EN	5	7	4	16	H
Bolitoglossa engelhardti	EN	4	7	4	15	H
*Bolitoglossa epimela**	DD	5	8	4	17	H
*Bolitoglossa eremia**	NE	6	8	4	18	H
Bolitoglossa flavimembris	EN	4	7	4	15	H
Bolitoglossa flaviventris	EN	4	5	4	13	M
Bolitoglossa franklini	EN	4	6	4	14	H
*Bolitoglossa gomezi**	DD	5	7	4	16	H
*Bolitoglossa gracilis**	VU	6	8	4	18	H
Bolitoglossa hartwegi	NT	4	4	4	12	M
*Bolitoglossa heiroreias**	EN	5	8	4	17	H
*Bolitoglossa helmrichi**	NT	5	7	4	16	H

Appendix 1 (continued). Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	IUCN rating	Environmental Vulnerability Score				EVS Category
		Geographic Distribution	Ecological Distribution	Reproductive Mode	Total Score	
*Bolitoglossa huehuetenanguensis**	NE	6	8	4	18	H
*Bolitoglossa indio**	DD	5	8	4	17	H
*Bolitoglossa insularis**	VU	6	8	4	18	H
*Bolitoglossa jacksoni**	DD	6	8	4	18	H
*Bolitoglossa jugivagans**	NE	6	8	4	18	H
*Bolitoglossa kamuk**	NE	6	8	4	18	H
*Bolitoglossa kaqchikelorum**	NE	5	8	4	17	H
*Bolitoglossa la**	NE	5	8	4	17	H
*Bolitoglossa lignicolor**	VU	5	7	4	16	H
Bolitoglossa lincolni	NT	4	5	4	13	M
*Bolitoglossa longissima**	CR	6	8	4	18	H
*Bolitoglossa magnifica**	EN	5	7	4	16	H
*Bolitoglossa marmorea**	EN	5	8	4	17	H
Bolitoglossa medemi	VU	4	7	4	15	H
*Bolitoglossa meliana**	EN	5	7	4	16	H
Bolitoglossa mexicana	LC	1	3	4	8	L
*Bolitoglossa minutula**	EN	5	8	4	17	H
*Bolitoglossa mombachoensis**	VU	5	8	4	17	H
*Bolitoglossa morio**	LC	5	4	4	13	M
Bolitoglossa mulleri	VU	2	7	4	13	M
*Bolitoglossa nigrescens**	EN	5	7	4	16	H
*Bolitoglossa ninadormida**	NE	6	8	4	18	H
*Bolitoglossa nussbaumi**	NE	6	8	4	18	H
*Bolitoglossa nympha**	NE	5	7	4	16	H
*Bolitoglossa obscura**	VU	6	8	4	18	H
Bolitoglossa occidentalis	LC	4	3	4	11	M
*Bolitoglossa odonnelli**	EN	5	7	4	16	H
*Bolitoglossa omniumsanctorum**	NE	5	7	4	16	H
*Bolitoglossa oresbia**	CR	5	8	4	17	H
*Bolitoglossa pacaya**	NE	5	8	4	17	H
*Bolitoglossa pesrubra**	VU	5	6	4	15	H
Bolitoglossa phalarosoma	DD	4	8	4	16	H
*Bolitoglossa porrasorum**	EN	5	7	4	16	H
*Bolitoglossa psephena**	NE	6	8	4	18	H
*Bolitoglossa pygmaea**	NE	5	8	4	17	H
*Bolitoglossa robinsoni**	NE	5	7	4	16	H
*Bolitoglossa robusta**	LC	5	7	4	16	H
Bolitoglossa rostrata	VU	4	6	4	14	H
Bolitoglossa rufescens	LC	1	4	4	9	L
*Bolitoglossa salvinii**	EN	5	7	4	16	H
*Bolitoglossa schizodactyla**	LC	5	6	4	15	H

Appendix 1 (continued). Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	IUCN rating	Environmental Vulnerability Score				EVS Category
		Geographic Distribution	Ecological Distribution	Reproductive Mode	Total Score	
*Bolitoglossa sombra**	VU	5	7	4	16	H
*Bolitoglossa sooyorum**	EN	5	7	4	16	H
*Bolitoglossa splendida**	NE	6	8	4	18	H
*Bolitoglossa striatula**	LC	5	7	4	16	H
Bolitoglossa stuarti	DD	4	7	4	15	H
*Bolitoglossa subpalmata**	EN	5	6	4	15	H
*Bolitoglossa suchitanensis**	DD	6	8	4	18	H
*Bolitoglossa synoria**	CR	5	8	4	17	H
*Bolitoglossa taylori**	DD	5	8	4	17	H
*Bolitoglossa tenebrosa**	NE	5	8	4	17	H
*Bolitoglossa tica**	EN	5	8	4	17	H
*Bolitoglossa tzultacaj**	NE	6	8	4	18	H
*Bolitoglossa xibalba**	NE	5	8	4	17	H
Bolitoglossa yucatana	LC	4	7	4	15	H
*Bolitoglossa zacapensis**	NE	6	8	4	18	H
*Bradytriton silus**	CR	6	8	4	18	H
*Cryptotriton monzoni**	CR	6	8	4	18	H
*Cryptotriton nasalis**	EN	6	8	4	18	H
Cryptotriton necopinus	NE	6	8	4	18	H
*Cryptotriton sierraminensis**	DD	5	8	4	17	H
*Cryptotriton veraepacis**	CR	5	8	4	17	H
*Dendrotriton bromeliacius**	CR	5	8	4	17	H
*Dendrotriton chujorum**	CR	6	8	4	18	H
*Dendrotriton cuchumatanus**	CR	6	8	4	18	H
*Dendrotriton kekchiorum**	EN	6	8	4	18	H
*Dendrotriton rabbi**	CR	5	8	4	17	H
*Dendrotriton sanctibarbarus**	VU	6	8	4	18	H
*Nototriton abscondens**	LC	5	7	4	16	H
*Nototriton barbouri**	EN	5	7	4	16	H
*Nototriton brodiei**	CR	5	8	4	17	H
*Nototriton gamezi**	VU	6	8	4	18	H
*Nototriton guanacaste**	VU	5	8	4	17	H
*Nototriton lignicola**	CR	6	8	4	18	H
*Nototriton limnospectator**	EN	5	8	4	17	H
*Nototriton major**	CR	6	8	4	18	H
*Nototriton matama**	NE	6	8	4	18	H
*Nototriton mime**	NE	6	8	4	18	H
*Nototriton picadoi**	NT	5	7	4	16	H
*Nototriton picucha**	NE	6	8	4	18	H
*Nototriton richardi**	NT	5	7	4	16	H
*Nototriton saslaya**	VU	6	8	4	18	H

Appendix 1 (continued). Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	IUCN rating	Environmental Vulnerability Score				EVS Category
		Geographic Distribution	Ecological Distribution	Reproductive Mode	Total Score	
*Nototriton stuarti**	DD	6	8	4	18	H
*Nototriton tapanti**	VU	6	8	4	18	H
*Nototriton tomamorum**	NE	6	8	4	18	H
Nyctanolis pernix	EN	4	7	4	15	H
*Oedipina alfaroi**	VU	5	7	4	16	H
*Oedipina alleni**	LC	5	7	4	16	H
*Oedipina altura**	CR	6	8	4	18	H
*Oedipina carablanca**	EN	6	8	4	18	H
*Oedipina chortiorum**	NE	6	8	4	18	H
*Oedipina collaris**	DD	5	8	4	17	H
Oedipina complex	LC	1	6	4	11	M
*Oedipina cyclocauda**	LC	5	6	4	15	H
Oedipina elongata	LC	2	7	4	13	M
*Oedipina fortunensis**	NE	6	8	4	18	H
*Oedipina gephyra**	EN	5	8	4	17	H
*Oedipina gracilis**	EN	5	7	4	16	H
*Oedipina grandis**	EN	5	8	4	17	H
*Oedipina ignea**	DD	5	6	4	15	H
*Oedipina kasios**	NE	5	7	4	16	H
*Oedipina koehleri**	NE	5	7	4	16	H
*Oedipina leptopoda**	NE	5	8	4	17	H
*Oedipina maritima**	CR	6	8	4	18	H
*Oedipina motaguae**	NE	6	8	4	18	H
*Oedipina nica**	NE	5	8	4	17	H
*Oedipina nimaso**	NE	6	8	4	18	H
*Oedipina pacificensis**	LC	5	7	4	16	H
Oedipina parvipes	LC	4	7	4	15	H
*Oedipina paucidentata**	CR	6	8	4	18	H
*Oedipina petiola**	NE	6	8	4	18	H
*Oedipina poelzi**	EN	5	7	4	16	H
*Oedipina pseudouniformis**	EN	5	7	4	16	H
*Oedipina quadra**	NE	5	8	4	17	H
*Oedipina savagei**	DD	6	8	4	18	H
*Oedipina stenopodia**	EN	5	8	4	17	H
*Oedipina stuarti**	DD	5	6	4	15	H
*Oedipina taylori**	LC	5	5	4	14	H
*Oedipina tomasi**	CR	6	8	4	18	H
*Oedipina tzutujilorum**	NE	6	8	4	18	H
*Oedipina uniformis**	NT	5	6	4	15	H
Pseudoeurycea brunnata	CR	4	7	4	15	H
*Pseudoeurycea exspectata**	CR	6	8	4	18	H
Pseudoeurycea goebeli	CR	4	7	4	15	H
Pseudoeurycea rex	CR	4	4	4	12	M

Appendix 1 (continued). Comparison of the IUCN Ratings from the Red List website (updated to 10 August 2014) and Environmental Vulnerability Scores for 493 Central American amphibians. See text for explanations of the IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America. ? = reproductive mode estimated based on phylogenetic relationships.

Species	IUCN rating	Environmental Vulnerability Score				EVS Category
		Geographic Distribution	Ecological Distribution	Reproductive Mode	Total Score	
Order Gymnophiona (15 species)						
Family Caeciliiidae (7 species)						
Caecilia isthmica	DD	4	8	4?	16	H
Caecilia leucocephala	LC	3	8	4?	15	H
Caecilia nigricans	LC	3	8	4?	15	H
*Caecilia volcani**	DD	5	8	4?	17	H
*Oscaecilia elongata**	DD	6	8	5	19	H
Oscaecilia ochrocephala	LC	4	7	5	16	H
*Oscaecilia osae**	DD	6	8	5?	19	H
Family Dermophiidae (8 species)						
*Dermophis costaricensis**	DD	5	8	5	18	H
Dermophis glandulosus	DD	2	6	5?	13	M
*Dermophis gracilior**	DD	5	8	5	18	H
Dermophis mexicanus	VU	1	1	5	7	L
*Dermophis occidentalis**	DD	5	7	5	17	H
Dermophis parviceps	LC	2	6	5?	13	M
*Gymnopis multiplicata**	LC	5	4	5	14	H
Gymnopis syntrema	DD	4	7	5	16	H

Appendix 2. Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
Order Crocodylia (3 species)						
Family Alligatoridae (1 species)						
Caiman crocodilus	LC	3	7	6	16	H
Family Crocodylidae (2 species)						
Crocodylus acutus	VU	3	5	6	14	H
Crocodylus moreletii	LC	2	5	6	13	M
Order Squamata (532 species)						
Family Amphisbaenidae (2 species)						
Amphisbaena fuliginosa	LC	3	7	1	11	M
Amphisbaena spurrelli	NE	3	8	1	12	M
Family Anguidae (28 species)						
*Abronia anzuetoi**	VU	6	8	4	18	H
*Abronia aurita**	EN	5	7	4	16	H
*Abronia campbelli**	CR	6	8	4	18	H
*Abronia fimbriata**	NE	5	7	4	16	H

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
*Abronia frosti**	CR	6	8	4	18	H
*Abronia gaiophantasma**	EN	5	7	4	16	H
Abronia lythrochila	LC	4	7	4	15	H
Abronia matudai	EN	4	7	4	15	H
*Abronia meledona**	EN	6	8	4	18	H
*Abronia montecristoi**	EN	5	8	4	17	H
Abronia ochoterenai	DD	4	8	4	16	H
*Abronia salvadorensis**	EN	5	8	4	17	H
*Abronia vasconcelosii**	VU	5	7	4	16	H
*Celestus adercus**	DD	6	8	3	17	H
*Celestus atitlanensis**	NE	5	7	3	15	H
*Celestus bivittatus**	EN	5	7	3	15	H
*Celestus cyanochloris**	LC	5	6	3	14	H
*Celestus hylaius**	NT	5	8	3	16	H
*Celestus montanus**	EN	5	7	3	15	H
*Celestus orobius**	DD	5	8	3	16	H
Celestus rozellae	LC	4	6	3	13	M
*Celestus scansorius**	NT	5	7	3	15	H
*Coloptychon rhombifer**	DD	5	8	3	16	H
*Diploglossus bilobatus**	LC	5	7	4	16	H
Diploglossus monotropis	NE	4	7	4	15	H
*Diploglossus montisilvestris**	DD	6	8	4	18	H
*Mesaspis monticola**	LC	5	6	3	14	H
Mesaspis moreletii	LC	2	3	3	8	L
Family Corytophanidae (9 species)						
Basiliscus basiliscus	NE	4	4	3	11	M
Basiliscus galeritus	NE	3	7	3	13	M
Basiliscus plumifrons	LC	5	7	3	15	H
Basiliscus vittatus	NE	1	3	3	7	L
Corytophanes cristatus	NE	2	5	3	10	M
Corytophanes hernandesii	LC	4	6	3	13	M
Corytophanes percarinatus	LC	4	4	3	11	M
Laemanctus longipes	LC	1	5	3	9	L
Laemanctus serratus	LC	3	3	3	9	L
Family Dactyloidae (95 species)						
Anolis allisoni	NE	3	7	3	13	M
*Dactyloa casildae**	NE	5	8	3	16	H
Dactyloa chloris	NE	3	8	3	14	H
Dactyloa chocorum	NE	4	8	3	15	H
Dactyloa frenata	NE	4	7	3	14	H
*Dactyloa ginaelisae**	NE	5	4	3	12	M

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
*Dactyloa ibanezi**	NE	5	7	3	15	H
*Dactyloa insignis**	NE	5	6	3	14	H
*Dactyloa kunayalae**	NE	5	7	3	15	H
Dactyloa latifrons	NE	3	7	3	13	M
*Dactyloa microtus**	NE	5	7	3	15	H
Norops alocomyos	NE	5	8	3	16	H
*Norops altae**	LC	5	7	3	15	H
*Norops amplisquamosus**	EN	6	8	3	17	H
*Norops apletophallus**	NE	5	7	3	15	H
*Norops aquaticus**	NE	5	7	3	15	H
Norops auratus	NE	3	7	3	13	M
Norops beckeri	NE	3	6	3	12	M
*Norops benedikti**	NE	5	8	3	16	H
*Norops bicaorum**	NE	6	8	3	17	H
Norops biporcatus	NE	2	4	3	9	L
*Norops campbelli**	NE	6	8	3	17	H
Norops capito	NE	2	6	3	11	M
*Norops carpenteri**	LC	5	8	3	16	H
*Norops charlesmyersi**	NE	5	8	3	16	H
*Norops cobanensis**	NE	5	5	3	13	M
Norops crassulus	NE	2	4	3	9	L
Norops cristifer	DD	4	6	3	13	M
*Norops cryptolimifrons**	NE	5	8	3	16	H
*Norops cupreus**	NE	5	5	3	13	M
*Norops cusuco**	EN	6	8	3	17	H
*Norops datzorum**	NE	5	7	3	15	H
Norops dollfusianus	NE	4	6	3	13	M
*Norops fortunensis**	DD	6	8	3	17	H
*Norops fungosus**	NE	5	7	3	15	H
Norops fuscoauratus	NE	3	7	3	13	M
Norops gaigei	NE	4	7	3	14	H
*Norops gruuo**	NE	6	8	3	17	H
*Norops haguei**	NE	6	8	3	17	H
*Norops heteropholidotus**	NE	5	8	3	16	H
*Norops humilis**	NE	5	6	3	14	H
*Norops intermedius**	NE	5	6	3	14	H
*Norops johnmeyeri**	NE	5	8	3	16	H
*Norops kemptoni**	NE	5	7	3	15	H
*Norops kreutzi**	NE	6	8	3	17	H
Norops laeviventris	NE	2	3	3	8	L
Norops leditzigorum	NE	5	7	3	15	H

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
Norops lemurinus	NE	2	2	3	7	L
*Norops limifrons**	NE	5	7	3	15	H
*Norops lionotus**	LC	5	6	3	14	H
*Norops loveridgei**	EN	5	6	3	14	H
*Norops macrophallus**	NE	5	7	3	15	H
*Norops magnaphallus**	NE	6	8	3	17	H
*Norops marsupialis**	NE	5	8	3	16	H
Norops matudai	NE	4	6	3	13	M
*Norops monteverde**	NE	6	8	3	17	H
*Norops morazani**	NE	6	8	3	17	H
*Norops muralla**	VU	6	8	3	17	H
*Norops ocelloscapularis**	NE	5	7	3	15	H
*Norops osa**	NE	5	8	3	16	H
*Norops pachypus**	LC	5	7	3	15	H
*Norops pentaprion**	NE	5	4	3	12	M
Norops petersii	NE	2	4	3	9	L
*Norops pijolensis**	NE	6	7	3	16	H
Norops poecilopus	NE	4	7	3	14	H
*Norops polylepis**	NE	5	7	3	15	H
*Norops pseudokemptoni**	NE	6	8	3	17	H
*Norops pseudopachypus**	NE	6	8	3	17	H
*Norops purpurgularis**	NE	5	8	3	16	H
*Norops quaggulus**	NE	5	7	3	15	H
*Norops roatanensis**	NE	6	8	3	17	H
Norops rodriguezii	NE	4	3	3	10	M
*Norops rubribarbaris**	NE	6	8	3	17	H
Norops sagrei	NE	3	7	3	13	M
*Norops salvini**	NE	5	7	3	15	H
Norops sericeus	NE	2	3	3	8	L
Norops serranoi	NE	4	5	3	12	M
*Norops sminthus**	DD	5	7	3	15	H
*Norops tenorioensis**	NE	6	8	3	17	H
*Norops townsendi**	NE	6	8	3	17	H
*Norops triumphalis**	NE	6	8	3	17	H
Norops tropidogaster	NE	3	7	3	13	M
*Norops tropidolepis**	NE	5	7	3	15	H
Norops tropidonotus	NE	4	2	3	9	L
Norops uniformis	NE	4	6	3	13	M
Norops unilobatus	NE	1	3	3	7	L
*Norops utilensis**	NE	6	8	3	17	H
*Norops villai**	NE	6	8	3	17	H

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
Norops vittigerus	NE	4	7	3	14	H
*Norops wampuensis**	NE	6	8	3	17	H
*Norops wellbornae**	NE	5	7	3	15	H
*Norops wermuthi**	NE	5	8	3	16	H
*Norops woodi**	NE	5	6	3	14	H
*Norops yoroensis**	NE	5	7	3	15	H
*Norops zeus**	NE	5	7	3	15	H
Family Eublepharidae (2 species)						
Coleonyx elegans	LC	3	3	4	10	M
Coleonyx mitratus	LC	5	5	4	14	H
Family Gymnophthalmidae (14 species)						
*Anadia ocellata**	NE	5	8	3	16	H
Anadia vittata	NE	4	7	3	14	H
*Bachia blairi**	NT	5	8	2	15	H
Bachia pallidiceps	NE	4	8	2	14	H
Cercosaura vertebralis	NE	3	7	3	13	M
Echinosaura palmeri	NE	3	7	2	12	M
*Echinosaura panamensis**	LC	5	7	2	14	H
Gymnophthalmus speciosus	NE	3	3	3	9	L
Leposoma rugiceps	LC	4	8	3	15	H
Leposoma southi	NE	4	7	3	14	H
*Potamites apodemus**	LC	5	7	3	15	H
Ptychoglossus festae	NE	4	7	3	14	H
*Ptychoglossus myersi**	LC	5	8	3	16	H
Ptychoglossus plicatus	NE	2	6	3	11	M
Family Helodermatidae (2 species)						
Heloderma alvarezi	NE	3	6	5	14	H
*Heloderma charlesbogerti**	NE	5	8	5	18	H
Family Hoplocercidae (2 species)						
Enyalioides heterolepis	NE	3	7	3	13	M
Morunasaurus groi	NE	4	8	3	15	H
Family Iguanidae (11 species)						
Ctenosaura acanthura	NE	3	4	6	13	M
Ctenosaura alfredschmidti	NT	4	8	3	15	H
*Ctenosaura bakeri**	CR	5	8	6	19	H
*Ctenosaura flavidorsalis**	EN	5	7	6	18	H
*Ctenosaura melanosterna**	EN	5	7	6	18	H
*Ctenosaura oedirhina**	EN	5	8	6	19	H
*Ctenosaura palearis**	EN	5	8	6	19	H
*Ctenosaura praeocularis**	DD	5	7	6	18	H
*Ctenosaura quinquecarinata**	NE	5	8	6	19	H

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
Ctenosaura similis	LC	1	4	6	11	M
Iguana iguana	NE	1	3	6	10	M
Family Mabuyidae (5 species)						
*Marisora alliacea**	LC	5	7	3	15	H
Marisora brachypoda	LC	1	2	3	6	L
*Marisora magnacornae**	DD	6	8	3	17	H
*Marisora roatanae**	CR	5	8	3	16	H
*Marisora unimarginata**	LC	5	7	3	15	H
Family Phrynosomatidae (17 species)						
Phrynosoma asio	LC	3	6	3	12	M
Sceloporus acanthinus	LC	4	7	3	14	H
Sceloporus carinatus	LC	4	5	3	12	M
Sceloporus chrysostictus	LC	4	6	3	13	M
Sceloporus internasalis	LC	4	4	3	11	M
*Sceloporus lunaei**	LC	5	7	3	15	H
Sceloporus lundelli	LC	4	7	3	14	H
*Sceloporus malachiticus**	LC	5	2	3	10	M
Sceloporus melanorhinus	LC	3	4	3	10	M
Sceloporus prezygus	LC	4	8	3	15	H
Sceloporus serrifer	LC	3	1	3	7	L
Sceloporus siniferus	LC	3	6	3	12	M
Sceloporus smaragdinus	LC	4	5	3	12	M
Sceloporus squamosus	LC	2	5	3	10	M
Sceloporus taeniocnemis	LC	4	5	3	12	M
Sceloporus teapensis	LC	4	6	3	13	M
Sceloporus variabilis	LC	1	1	3	5	L
Family Phyllodactylidae (5 species)						
*Phyllodactylus insularis**	VU	6	8	3	17	H
*Phyllodactylus palmeus**	NE	5	8	3	16	H
*Phyllodactylus paralepis**	NE	6	8	3	17	H
Phyllodactylus tuberculosus	LC	1	4	3	8	L
Thecadactylus rapicauda	NE	1	4	3	8	L
Family Polychrotidae (1 species)						
Polychrus gutturosus	NE	1	8	3	12	M
Family Scincidae (3 species)						
Mesoscincus managuae	LC	5	6	3	14	H
Mesoscincus schwartzei	LC	4	6	3	13	M
Plestiodon sumichrasti	LC	4	5	3	12	M
Family Sphaerodactylidae (19 species)						
Aristelliger georgeensis	NE	3	7	3	13	M
Aristelliger praesignis	NE	3	8	3	14	H

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
Gonatodes albogularis	NE	1	5	3	9	L
Lepidoblepharis sanctaemartae	LC	4	7	3	14	H
Lepidoblepharis xanthostigma	LC	4	6	3	13	M
*Sphaerodactylus alphus**	NE	6	8	3	17	H
Sphaerodactylus continentalis	NE	2	3	3	8	L
*Sphaerodactylus dunni**	LC	5	7	3	15	H
Sphaerodactylus glaucus	LC	4	5	3	12	M
*Sphaerodactylus graptolaemus**	LC	5	8	3	16	H
*Sphaerodactylus guanaje**	NE	6	8	3	17	H
*Sphaerodactylus homolepis**	LC	5	8	3	16	H
*Sphaerodactylus leonardovaldesi**	NE	5	8	3	16	H
Sphaerodactylus lineolatus	NE	4	7	3	14	H
*Sphaerodactylus millepunctatus**	LC	5	7	3	15	H
Sphaerodactylus notatus	LC	3	8	3	14	H
*Sphaerodactylus pacificus**	LC	6	8	3	17	H
*Sphaerodactylus poindexteri**	NE	6	8	3	17	H
*Sphaerodactylus rosaurae**	LC	5	8	3	16	H
Family Sphenomorphidae (4 species)						
Scincella assatus	LC	3	2	3	8	L
Scincella cherriei	LC	2	2	3	7	L
Scincella incerta	NE	5	7	3	15	H
*Scincella rara**	DD	6	8	3	17	H
Family Teiidae (12 species)						
Ameiva praesignis	NE	3	8	3	14	H
Aspidoscelis angusticeps	LC	4	6	3	13	M
Aspidoscelis deppii	LC	1	4	3	8	L
Aspidoscelis maslini	LC	4	8	3	15	H
Aspidoscelis motaguae	LC	4	5	3	12	M
*Cnemidophorus duellmani**	NE	5	8	3	16	H
*Cnemidophorus ruatanus**	NE	5	7	3	15	H
Holcosus chaitzami	DD	4	7	3	14	H
Holcosus festivus	NE	2	5	3	10	M
*Holcosus leptophrys**	NE	5	8	3	16	H
*Holcosus quadrilineatus**	LC	5	8	3	16	H
Holcosus undulatus	LC	1	2	3	6	L
Family Xantusiidae (4 species)						
Lepidophyma flavimaculatum	LC	2	5	2	9	L
Lepidophyma mayae	NT	4	7	2	13	M
*Lepidophyma reticulatum**	LC	5	6	2	13	M
Lepidophyma smithii	LC	3	4	2	9	L

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
Family Xenosauridae (1 species)						
Xenosaurus grandis	VU	3	1	3	7	L
Family Anomalepididae (3 species)						
Anomalepis mexicanus	DD	2	8	1	11	M
*Helminthophis frontalis**	DD	5	6	1	12	M
Liotyphlops albirostris	NE	3	5	1	9	L
Family Boidae (4 species)						
Boa imperator	NE	1	1	6	8	L
Corallus annulatus	NE	1	8	2	11	M
Corallus ruschenbergerii	NE	3	8	2	13	M
Epicrates maurus	NE	1	5	2	8	L
Family Charinidae (2 species)						
Ungaliophis continentalis	NE	2	5	2	9	L
Ungaliophis panamensis	NE	4	6	2	12	M
Family Colubridae (74 species)						
Chironius exoletus	NE	3	5	4	12	M
Chironius flavopictus	DD	4	7	4	15	H
Chironius grandisquamis	NE	1	6	4	11	M
Coluber constrictor	LC	3	6	3	12	M
Dendrophidion apharocybe	NE	5	7	4	16	H
*Dendrophidion crybelum**	NE	5	8	4	17	H
Dendrophidion clarkii	NE	4	6	4	14	H
*Dendrophidion paucicarinatum**	LC	5	7	4	16	H
Dendrophidion percarinatum	NE	1	6	4	11	M
*Dendrophidion rufiterminorum**	NE	5	7	4	16	H
Dendrophidion vinitor	LC	3	7	3	13	M
Drymarchon melanurus	LC	1	1	4	6	L
Drymobius chloroticus	LC	1	3	4	8	L
Drymobius margaritiferus	NE	1	1	4	6	L
*Drymobius melanotropis**	LC	5	7	4	16	H
Drymobius rhombifer	LC	3	7	4	14	H
Ficimia publia	LC	4	3	2	9	L
Lampropeltis abnorma	NE	1	3	5	9	L
Lampropeltis micropholis	NE	4	1	5	10	M
*Leptodrymus pulcherrimus**	LC	5	4	4	13	M
Leptophis ahaetulla	NE	3	3	4	10	M
Leptophis depressirostris	NE	3	7	4	14	H
Leptophis mexicanus	LC	1	1	4	6	L
Leptophis modestus	VU	3	7	4	14	H
*Leptophis nebulosus**	LC	5	5	4	14	H
Leptophis riveti	NE	3	7	4	14	H
Masticophis mentovarius	NE	1	1	4	6	L
*Mastigodryas alternatus**	LC	5	3	4	12	M

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
*Mastigodryas dorsalis**	LC	5	5	4	14	H
Mastigodryas melanolomus	LC	3	4	4	11	M
Mastigodryas pleei	NE	3	7	4	14	H
Oxybelis aeneus	NE	1	1	3	5	L
Oxybelis brevirostris	NE	1	7	4	12	M
Oxybelis fulgidus	NE	1	2	4	7	L
*Oxybelis wilsoni**	EN	5	8	4	17	H
Phrynonax poecilonotus	LC	1	3	3	7	L
Pituophis lineaticollis	LC	4	2	4	10	M
Pseudelaphe flavirufa	LC	4	4	4	12	M
Rhinobothryum bovallii	LC	3	8	5	16	H
*Scolecophis atrocinctus**	LC	5	3	5	13	M
Senticolis triaspis	LC	3	1	3	7	L
Spilotes pullatus	NE	1	1	4	6	L
Stenorrhina degenhardtii	NE	3	3	3	9	L
Stenorrhina freminvillii	LC	1	2	4	7	L
Symphimus mayae	LC	4	7	3	14	H
*Tantilla albiceps**	DD	6	8	2	16	H
Tantilla alticola	NE	4	5	2	11	M
*Tantilla armillata**	LC	5	4	2	11	M
*Tantilla bairdi**	DD	6	8	2	16	H
*Tantilla brevicauda**	LC	5	6	2	13	M
Tantilla cuniculator	LC	4	7	2	13	M
*Tantilla hendersoni**	DD	6	8	2	16	H
Tantilla impensa	LC	2	5	2	9	L
*Tantilla jani**	VU	4	8	2	14	H
*Tantilla lempira**	EN	5	7	2	14	H
Tantilla melanocephala	NE	3	7	2	12	M
Tantilla moesta	LC	4	7	2	13	M
*Tantilla olympia**	NE	6	8	2	16	H
*Tantilla psittaca**	VU	5	8	2	15	H
Tantilla reticulata	NE	4	7	2	13	M
Tantilla rubra	LC	3	1	2	6	L
*Tantilla ruficeps**	LC	5	5	2	12	M
Tantilla schistosa	LC	2	3	2	7	L
Tantilla supracincta	NE	4	7	5	16	H
*Tantilla taeniata**	LC	5	5	2	12	M
*Tantilla tecta**	DD	6	8	2	16	H
*Tantilla tritaeniata**	CR	6	8	2	16	H
*Tantilla vermiformis**	LC	5	7	2	14	H
*Tantilla vulcani**	LC	5	6	2	13	M

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
Tantillita brevissima	LC	4	3	2	9	L
Tantillita canula	LC	4	6	2	12	M
Tantillita lintoni	LC	4	6	2	12	M
Trimorphodon biscutatus	NE	3	1	4	8	L
*Trimorphodon quadruplex**	LC	5	5	4	14	H
Family Dipsadidae (144 species)						
*Adelphicos daryi**	EN	6	8	2	16	H
*Adelphicos ibarrorum**	EN	5	8	2	15	H
Adelphicos quadrivirgatum	LC	4	4	2	10	M
Adelphicos sargii	LC	4	6	2	12	M
*Adelphicos veraepacis**	VU	5	7	2	14	H
Amastridium sapperi	LC	4	4	2	10	M
Amastridium veliferum	LC	4	7	2	13	M
Atractus clarki	NE	4	8	2	14	H
*Atractus darienensis**	DD	6	8	2	16	H
*Atractus depressiocellus**	DD	6	7	2	15	H
*Atractus hostilitractus**	DD	6	8	2	16	H
*Atractus imperfectus**	DD	6	8	2	16	H
*Chapinophis xanthocheilus**	EN	5	8	3	16	H
Clelia clelia	NE	1	5	4	10	M
Clelia equatoriana	NE	4	6	4	14	H
Clelia scytalina	LC	3	5	4	12	M
Coniophanes bipunctatus	LC	2	5	3	10	M
Coniophanes fissidens	NE	1	3	3	7	L
Coniophanes imperialis	LC	3	3	3	9	L
*Coniophanes joanae**	DD	5	7	3	15	H
Coniophanes piceivittis	LC	1	3	3	7	L
Coniophanes quinquevittatus	LC	4	6	3	13	M
Coniophanes schmidti	LC	4	6	3	13	M
Conophis lineatus	LC	4	3	4	11	M
Conophis vittatus	LC	3	5	4	12	M
*Crisantophis nevermanni**	LC	5	7	4	16	H
Cubophis brooksi	NE	3	8	3	14	H
Diaphorolepis wagneri	NE	3	8	3	14	H
*Dipsas articulata**	LC	5	8	2	15	H
*Dipsas bicolor**	LC	5	7	5	17	H
Dipsas brevifacies	LC	4	7	4	15	H
*Dipsas nicholsi**	LC	5	8	2	15	H
Dipsas temporalis	NE	3	8	2	13	M
*Dipsas tenuissima**	NT	5	7	2	14	H
*Dipsas viguieri**	LC	4	7	2	13	M

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
Enuliophis sclateri	NE	4	7	2	13	M
*Enulius bifoveatus**	CR	6	8	2	16	H
Enulius flavitorques	NE	1	1	2	4	L
*Enulius roatanensis**	EN	6	8	2	16	H
Erythrolamprus bizona	LC	3	4	5	12	M
Erythrolamprus mimus	LC	4	6	5	15	H
*Geophis bellus**	DD	6	8	2	16	H
*Geophis brachycephalus**	LC	5	4	2	11	M
Geophis cancellatus	LC	4	6	2	12	M
Geophis carinosus	LC	3	4	2	9	L
*Geophis championi**	DD	6	8	2	16	H
*Geophis damiani**	CR	6	8	2	16	H
*Geophis downsi**	DD	6	8	2	16	H
*Geophis dunni**	DD	6	8	2	16	H
*Geophis fulvoguttatus**	EN	5	7	2	14	H
*Geophis godmani**	LC	5	7	2	14	H
*Geophis hoffmanni**	NE	5	5	2	12	M
Geophis immaculatus	LC	4	8	2	14	H
Geophis nasalis	LC	4	3	2	9	L
*Geophis nephodrymus**	VU	6	8	2	16	H
Geophis rhodogaster	LC	2	7	2	11	M
*Geophis ruthveni**	LC	5	7	2	14	H
*Geophis talamancae**	EN	5	8	2	15	H
*Geophis tectus**	LC	5	6	2	13	M
*Geophis zeledoni**	LC	5	8	2	15	H
*Hydromorphus concolor**	LC	5	5	2	12	M
*Hydromorphus dunni**	DD	6	8	2	16	H
Imantodes cenchoa	NE	1	3	2	6	L
Imantodes gemmistratus	NE	1	3	2	6	L
Imantodes inornatus	LC	4	6	2	12	M
*Imantodes phantasma**	DD	6	8	2	16	H
Imantodes tenuissimus	LC	4	7	2	13	M
Leptodeira frenata	LC	4	4	4	12	M
Leptodeira maculata	LC	3	1	4	8	L
Leptodeira nigrofasciata	LC	1	3	4	8	L
*Leptodeira rhombifera**	LC	5	3	4	12	M
*Leptodeira rubricata**	LC	5	8	4	17	H
Leptodeira septentrionalis	NE	1	2	4	7	L
Liophis epinephelus	NE	1	4	5	10	M
Liophis lineatus	NE	3	8	4	15	H
Ninia atrata	NE	3	8	2	13	M
*Ninia celata**	NT	5	8	2	15	H

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
Ninia diademata	LC	1	3	2	6	L
*Ninia espinali**	NT	5	7	2	14	H
*Ninia maculata**	LC	5	5	2	12	M
*Ninia pavimentata**	LC	5	8	2	15	H
*Ninia psephota**	LC	5	6	2	13	M
Ninia sebae	LC	1	1	2	4	L
Nothopsis rugosus	LC	1	7	2	10	L
*Omoadiphas aurula**	VU	6	8	2	16	H
Omoadiphas cannula	CR	6	8	2	16	H
*Omoadiphas texiguatensis**	CR	6	8	2	16	H
Oxyrhopus petolarius	NE	1	6	5	12	M
Phimophis guianensis	NE	3	8	2	13	M
Pliocercus elapoides	LC	4	1	5	10	M
Pliocercus euryzonus	LC	1	6	5	12	M
Pseudoboa neuwiedii	NE	3	6	5	14	H
*Rhadinaea calligaster**	LC	5	7	2	14	H
Rhadinaea decorata	NE	1	6	2	9	L
*Rhadinaea pulveriventris**	NE	5	7	2	14	H
*Rhadinaea sargenti**	LC	5	7	2	14	H
*Rhadinaea stadelmani**	EN	5	6	2	13	M
*Rhadinaea vermiculaticeps**	NT	5	8	2	15	H
*Rhadinella anachoreta**	LC	5	7	2	14	H
Rhadinella godmani	LC	2	5	2	9	L
Rhadinella hannsteini	DD	4	5	2	11	M
*Rhadinella hempsteadae**	EN	5	6	2	13	M
*Rhadinella kinkelini**	LC	5	6	2	13	M
Rhadinella lachrymans	LC	4	2	2	8	L
*Rhadinella montecristi**	VU	5	7	2	14	H
*Rhadinella pegosalyta**	VU	6	8	2	16	H
*Rhadinella pilonaorum**	NE	5	8	2	15	H
Rhadinella posadasi	EN	4	8	2	14	H
*Rhadinella rogerromani**	NT	6	8	2	16	H
*Rhadinella serperaster**	LC	5	6	2	13	M
*Rhadinella tolpanorum**	CR	6	8	2	16	H
*Sibon annulatus**	LC	5	7	2	14	H
*Sibon anthracops**	LC	5	5	5	15	H
*Sibon argus**	LC	5	7	4	16	H
*Sibon carri**	NE	5	7	2	14	H
Sibon dimidiatus	LC	1	5	4	10	M
*Sibon lamari**	EN	6	8	2	16	H
*Sibon longifrenis**	LC	5	7	2	14	H

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
*Sibon manzanaresi**	NT	5	8	2	15	H
*Sibon merendonensis**	CR	6	8	2	16	H
*Sibon miskitus**	NT	5	8	2	15	H
Sibon nebulatus	NE	1	2	2	5	L
*Sibon noalamina**	NE	5	8	2	15	H
*Sibon perissostichon**	DD	6	8	2	16	H
Sibon sanniolus	LC	4	6	2	12	M
Siphlophis cervinus	NE	3	8	5	16	H
Siphlophis compressus	LC	3	8	5	16	H
*Tretanorhinus mocquardi**	NE	5	8	2	15	H
Tretanorhinus nigroluteus	NE	2	5	2	9	L
*Trimetopon barbouri**	DD	5	8	2	15	H
*Trimetopon gracile**	LC	5	7	2	14	H
*Trimetopon pliolepis**	LC	5	5	2	12	M
*Trimetopon simile**	EN	5	6	2	13	M
*Trimetopon slevini**	NT	5	7	2	14	H
*Trimetopon viquezi**	CR	5	8	2	15	H
Tropidodipsas fasciata	NE	4	4	4	12	M
Tropidodipsas fischeri	LC	4	3	2	9	L
Tropidodipsas sartorii	LC	3	2	5	10	M
Urotheca decipiens	NE	2	6	2	10	M
Urotheca fulviceps	NE	3	8	2	13	M
*Urotheca guentheri**	LC	5	5	2	12	M
*Urotheca myersi**	DD	5	8	2	15	H
*Urotheca pachyura**	LC	5	7	2	14	H
Xenodon rabdocephalus	NE	1	5	5	11	M
Family Elapidae (18 species)						
Hydrophis platurus	LC	—	—	—	—	—
*Micrurus alleni**	LC	5	6	5	16	H
Micrurus ancoralis	NE	3	7	5	15	H
Micrurus browni	LC	3	1	5	9	L
*Micrurus clarki**	NE	5	7	5	17	H
Micrurus diastema	LC	3	1	5	9	L
Micrurus dissoleucus	LC	3	7	5	15	H
Micrurus dumerilii	NE	3	8	5	16	H
Micrurus elegans	LC	4	4	5	13	M
*Micrurus hippocrepis**	LC	5	8	5	18	H
Micrurus latifasciatus	LC	4	4	5	13	M
Micrurus mipartitus	NE	3	7	5	15	H
*Micrurus mosquitensis**	LC	5	7	5	17	H
*Micrurus multifasciatus**	LC	5	5	5	15	H

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
Micrurus nigrocinctus	NE	2	3	5	10	M
*Micrurus ruatanus**	CR	5	8	5	18	H
*Micrurus stewarti**	LC	5	7	5	17	H
*Micrurus stuarti**	LC	5	7	5	17	H
Family Leptotyphlopidae (5 species)						
*Epictia ater**	LC	5	4	1	10	M
Epictia goudotii	NE	3	1	1	5	L
Epictia magnamaculata	NE	4	7	1	12	M
Epictia phenops	NE	3	1	1	5	L
Trilepida macrolepis	NE	3	8	1	12	M
Family Loxocemidae (1 species)						
Loxocemus bicolor	LC	1	5	4	10	M
Family Natricidae (5 species)						
Storeria dekayi	LC	3	4	2	9	L
Thamnophis cyrtopsis	LC	3	1	4	8	L
Thamnophis fulvus	LC	4	5	4	13	M
Thamnophis marcianus	LC	1	5	4	10	M
Thamnophis proximus	LC	3	2	4	9	L
Family Sibynophiidae (2 species)						
Scaphiodontophis annulatus	LC	1	5	5	11	M
Scaphiodontophis venustissimus	NE	1	7	5	13	M
Family Tropidophiidae (1 species)						
Trachyboa boulengeri	NE	3	5	3	11	M
Family Typhlopidae (5 species)						
*Amerotyphlops costaricensis**	LC	5	5	1	11	M
Amerotyphlops microstomus	LC	4	7	1	12	M
*Amerotyphlops stadelmani**	NE	5	6	1	12	M
Amerotyphlops tenuis	LC	4	6	1	11	M
*Amerotyphlops tycherus**	VU	5	8	1	14	H
Family Viperidae (32 species)						
Agkistrodon bilineatus	NT	3	5	5	13	M
*Agkistrodon howardgloydi**	NE	5	7	5	17	H
Agkistrodon russeolus	NE	4	6	5	15	H
*Atropoides indomitus**	EN	5	8	5	18	H
Atropoides mexicanus	LC	2	4	5	11	M
Atropoides occiduus	LC	4	6	5	15	H
Atropoides olmec	LC	4	6	5	15	H
*Atropoides picadoi**	LC	5	6	5	16	H
Bothriechis aurifer	VU	4	6	5	15	H
Bothriechis bicolor	LC	4	5	5	14	H
Bothriechis guifarroi	NE	6	8	5	19	H

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
*Bothriechis lateralis**	LC	5	6	5	16	H
*Bothriechis marchi**	EN	5	6	5	16	H
*Bothriechis nigroviridis**	NE	5	7	5	17	H
Bothriechis schlegelii	NE	2	4	5	11	M
*Bothriechis supraciliaris**	NE	5	7	5	17	H
*Bothriechis thalassinus**	NE	5	7	5	17	H
Bothrops asper	NE	1	4	5	10	M
Bothrops punctatus	NE	3	8	5	16	H
Cerrophidion godmani	LC	4	3	5	12	M
*Cerrophidion sasai**	NE	5	6	5	16	H
*Cerrophidion wilsoni**	NE	5	5	5	15	H
Crotalus simus	LC	2	2	5	9	L
Crotalus tzabcan	LC	4	7	5	16	H
Lachesis acrochorda	NE	3	6	5	14	H
*Lachesis melanocephala**	NE	5	7	5	17	H
*Lachesis stenophrys**	NE	5	7	5	17	H
Porthidium lansbergii	NE	3	7	5	15	H
Porthidium nasutum	LC	1	6	5	12	M
*Porthidium ophryomegas**	LC	5	4	5	14	H
*Porthidium porrasi**	LC	5	8	5	18	H
*Porthidium volcanicum**	DD	5	8	5	18	H
Order Testudines (24 species)						
Family Cheloniidae (5 species)						
Caretta caretta	EN	—	—	—	—	—
Chelonia mydas	EN	—	—	—	—	—
Eretmochelys imbricata	CR	—	—	—	—	—
Lepidochelys kempii	CR	—	—	—	—	—
Lepidochelys olivacea	VU	—	—	—	—	—
Family Chelydridae (2 species)						
Chelydra acutirostris	NE	1	4	6	11	M
Chelydra rossignonii	VU	4	7	6	17	H
Family Dermatemydidae (1 species)						
Dermatemys mawii	CR	4	7	6	17	H
Family Dermochelyidae (1 species)						
Dermochelys coriacea	CR	—	—	—	—	—
Family Emydidae (2 species)						
Trachemys grayi	NE	4	8	6	18	H
Trachemys ornata	NE	1	4	6	11	M
Family Geoemydidae (5 species)						
Rhinoclemmys annulata	NT	2	7	3	12	M
Rhinoclemmys areolata	NT	4	6	3	13	M

Appendix 2 (continued). Comparison of IUCN Ratings from the Red List website (updated to 16 July 2014) and Environmental Vulnerability Scores for 559 Central American crocodilians, squamates, and turtles. See text for explanation of IUCN and EVS rating systems. EVS category abbreviations: L = low; M = medium; H = high. * = species endemic to Central America.

Species	IUCN Ratings	Environmental Vulnerability Scores				EVS Category
		Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score	
*Rhinoclemmys funerea**	NT	5	8	3	16	H
Rhinoclemmys melanosterna	NE	4	8	3	15	H
Rhinoclemmys pulcherrima	NE	1	4	3	8	L
Family Kinosternidae (4 species)						
Kinosternon acutum	NT	4	7	3	14	H
*Kinosternon angustipons**	VU	5	8	3	16	H
Kinosternon leucostomum	NE	1	4	3	8	L
Kinosternon scorpioides	NE	1	4	3	8	L
Family Staurotypidae (3 species)						
Claudius angustatus	NT	4	7	3	14	H
Staurotypus salvinii	NT	4	6	3	13	M
Staurotypus triporcatus	NT	4	7	3	14	H
Family Testudinidae (1 species)						
Chelonoidis carbonarius	NE	3	8	6	17	H

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SHORT COMMUNICATION

First report of the salamanders *Bolitoglossa leandrae* and *B. tamaense* (Urodela, Plethodontidae) for Venezuela

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Key words. Caudata, biogeography, Amazon, Orinoquia, Andes, Colombia

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Salamanders of the Family Plethodontidae constitute a major batrachological element in the Neotropic realm, though descending in species richness from North to South. Venezuela has an impoverished list of five species of salamanders so far: *Bolitoglossa altamazonica* (Cope 1874), *B. borburata* Trapido 1942; *B. guaramacalensis* Schargel, García-Pérez, and Smith 2002; *B. orestes* Brame and Wake 1962, and the recently described *B. mucuyensis* García-Gutiérrez, Escalona, Mora, Díaz de Pascual, and Fermín 2013. The best studied species, both taxonomically and genetically, is *B. orestes*. An apparently isolated population was described as *B. spongai* by Barrio-Amorós and Fuentes (1999), and later some ecological traits were published (Barrio-Amorós et al. 2010). Inconsistencies of the formal description and molecular data led Fermín et al. (2012) to conclude that *B. spongai* is a junior synonym of *B. orestes*, a position that we follow here. We use the order name Urodela Duméril 1805 instead of Caudata Fischer von Waldheim 1813, following the Dubois and Raffaelli (2012) rationale.

Schargel and Rivas (2003) assigned tentatively the juvenile specimen ULABG (Universidad de Los Andes, Laboratorio de Biogeografía, Mérida, Venezuela) 3392 to *Bolitoglossa altamazonica*, but the evidence they offered (a series of measurements) are hard to corroborate as clearly diagnostic for this species, especially because the only comprehensive description of the species (Brame and Wake 1963) is old and needs verification and comparison with topotypic specimens (D.B. Wake, pers. com.; Brcko et al. 2013).

Recently, Acevedo et al. (2012) described two salamanders of the genus *Bolitoglossa* from the Colombian side of the Tamá Massif in the Cordillera Oriental de Colombia. The southwestern half of this massif is Colombian and the northeastern half is Venezuelan, but geologically and ecologically it represents a continuum. *Bolitoglossa leandrae* Acevedo, Wake, Márquez, Silva, Franco, and Amézquita 2013 was diagnosed as the smallest *Bolitoglossa* known from Colombia, with 30.3 mm mean snout-vent length (SVL) for males and the only female known of 39.2 mm SVL, 23–24 maxillary teeth (MT), and 18–19 vomerine teeth (VT). It inhabits lowland piedmont rainforest at around 600 m asl. On the other hand, *B. tamaense* Acevedo, Wake, Márquez, Silva, Franco, and Amézquita 2013 is a somewhat larger species with males up to 40.3 mm and females up to 52.7 mm, 38–42 maxillary teeth, and 17–23 vomerine teeth (including both males and females). Genetic data also confirm the proper specific status of both species.

Here we report for the first time the presence on Venezuelan territory of two species of salamanders (*Bolitoglossa leandrae* and *B. tamaense*). The citation of *B. altamazonica* by Schargel and Rivas (2003) is probably a misidentified *B. leandrae*, but we cannot be certain as we

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were unable to access the specimen ULABG 3392—the specimen is a juvenile that makes its proper identification more difficult.

Specimens CVUNET (Colección de Vertebrados, Universidad Experimental del Táchira, San Cristóbal, Venezuela) 644 (female; Fig. 1B), CVUNET 645 (male; Fig. 1A), CVUNET 669 (male), and CVUNET 670 (male) from Quebrada La Espuma, Río Frío, Táchira state 7.3540 N, 72.1012 W, 650 m asl (Fig. 2), are herein assigned to *B. leandrae* by having all the set of characters diagnostic for the species in Acevedo et al. (2013), such as a very small size; actually the smallest species of *Bolitoglossa* of Colombia and Venezuela (females up to 39.2 mm; in our sample, females up to 34.4 mm and our sample of males expands the maximum size to 35 mm), extensive webbed digits on hands and feet (see Fig 1A and 1B; Table 1 for measurements).

CVUNET 615 (female; Fig. 1C), CVUNET 626 (female; Fig. 1D), CVUNET 703 (sex unknown) CVUNET 726 (sex unknown), from Matamula, between Bramón and Delicias, Táchira state, 7.2833 N, 72.4333 W, 2,020 m asl (Fig. 2), and MHNLS 1268 (male) from Río Chiquito, Junín, Táchira state, 7.32 N, 72.20 W, ca. 2,000 m asl (Fig. 2), are assigned herein to *B. tamaense* following the diagnostic characters given by Acevedo et al. (2013), such as small size between the range given by the original description, the webbed hands with broadly triangular and pointed finger tips (Fig 1C), coloration similar to that in Fig 3E and G in Acevedo et al. (2012) (see our Fig 1 C, D); measurements presented in Table 1.

With the data at hand, the range of MT is slightly wider in both species, ranging now from 21–24 for males and 28–29 for females of *B. leandrae*; and from 31–39 for males of *B. tamaense*. The same is valid for VT, with males now ranging from 17–19 and females from 18–20 in *B. leandrae*; and males ranging from 16–19, and females 17–23 in *B. tamaense*.

As explained, the area where both species occur in Colombia and Venezuela, conform a continuum, only separated by an artificial frontier line on maps. *Bolitoglossa leandrae* inhabits primary (in Venezuela) and secondary (in Colombia) lowland rainforests up to 650 m asl (600 m in Colombia). It is active at night on vegetation up to 1.5 m (own observations). *Bolitoglossa tamaense* occurs at cloud forests between 2,000 and 2,700 m asl (2,000 to 2,020 m in Venezuela), also on low vegetation and mossy rocks.

The Valle del Río Doradas is an important area for Orinoquian and Upper Amazonian herpetofauna (contrasting with the surrounding typical Llanos and Andes elements), as demonstrated by Barrio-Amorós and colleagues for other amphibian species like *Hypsiboas lanciformis* Cope 1871, *H. boans* (Linnaeus 1758), *Scinax wandae* (Pyburn and Fouquette 1971), *Lithodytes linea-*

Fig. 1. *Bolitoglossa leandrae*: subadult male CVUNET 645 **(A)** and adult female CVUNET 644 **(B)**, both from Quebrada La Espuma, Río Frío, Táchira state, Venezuela. *Bolitoglossa tamaense*: adult females CVUNET 615 **(C)** and CVUNET 626 **(D)**, both from Matamula, between Bramón and Delicias, Táchira state, Venezuela. *All photos by CBA except D by ACO.*

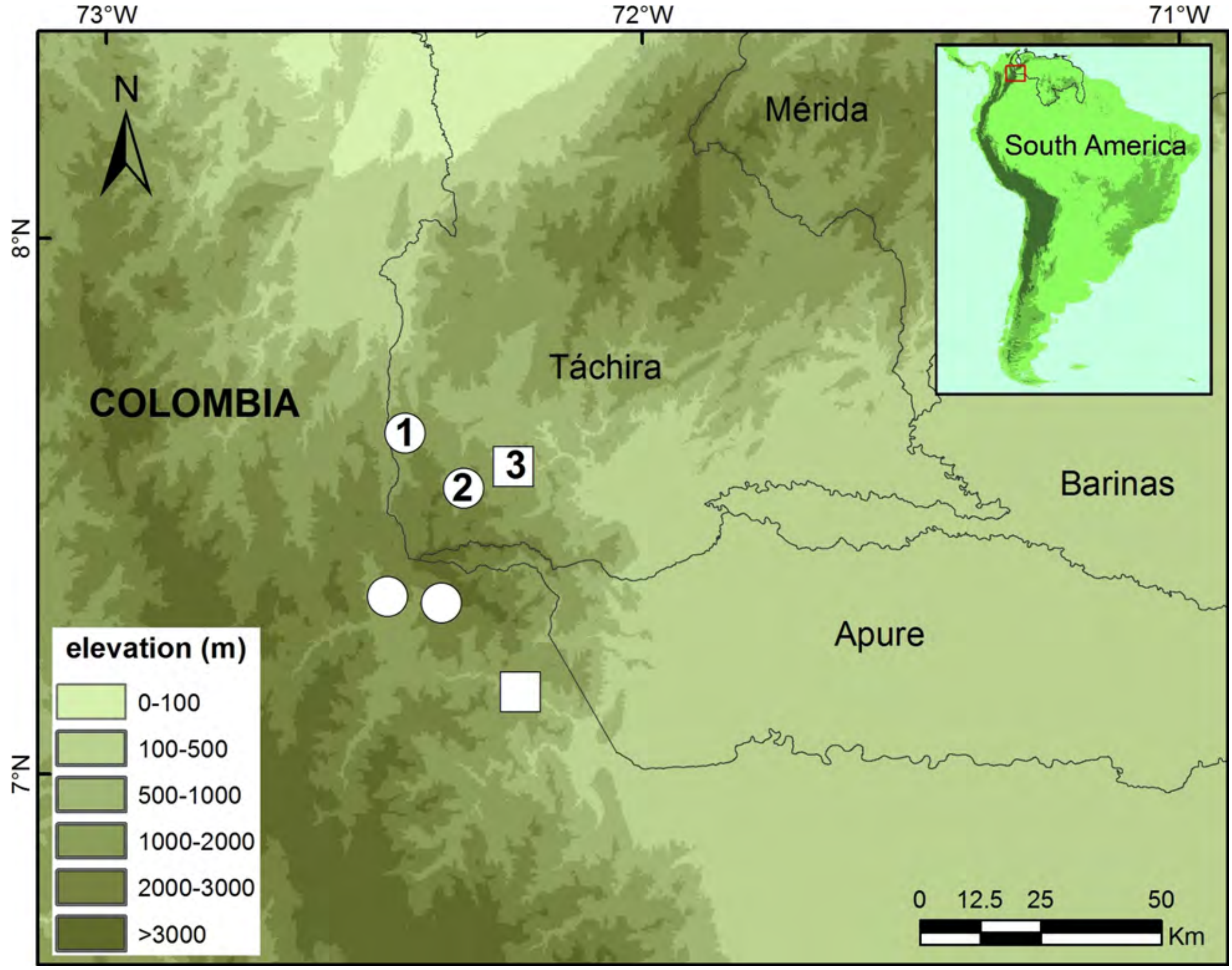

Fig. 2. Known distribution of *Bolitoglossa leandrae* (open squares) and *B. tamaense* (open circles) in Colombia and Venezuela. Colombian records are from Acevedo et al. (2013). 1: Matamula, between Bramón and Delicias. 2: Río Chiquito. 3: Quebrada la Espuma, Río Frío.

tus (Schneider 1799), and *Rhaebo glaberrimus* (Günther 1869), among others (respectively Barrio et al. 1999; Barrio, 1999; 2001; Barrio-Amorós and Chacón, 2004; Chacón et al., 2002) and therefore, we cannot rule out that ULABG 3392 is indeed *Bolitoglossa altamazonica*, though we retain it as *B.* aff. *altamazonica*. Thus, we do not exclude this late species from the list of Venezuelan amphibians, but caution about the proper identification of further specimens from the same general area. Both, morphological and genetic data would be desirable to identify this species complex in the Upper Amazon of Peru, Ecuador, and Colombia, continuing the study of Brazilian material by Brcko et al. (2013).

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Table 1. Measurements of *Bolitoglossa leandrae* and *B. tamaense* as presented by Acevedo et al. (2013) and compared with the Venezuelan specimens at CVUNET and MHNLS. Data of *B. altamazonica* from Brame and Wake (1963) considering only Upper Amazon Peruvian specimens as *B. altamazonica sensu stricto*. We do not include the data for *B. altamazonica* from Table 1 in Acevedo et al. (2013) as they mix specimens from different origins. SVL (snout-vent length, snout to posterior end of vent), CG (costal grooves between fore and hindlimb), HL (head length), HW (head width), TaL (tail length), AG (axilla-groin length), and HFW (hind-foot width). MT: maxillary teeth. VT: vomerine teeth. M= male; F= female. Sex was determined by external morphology (swollen cloaca in males vs not swollen in females; presence of a hedonic mental gland in males and development of the nasolabial groove elongated in males, by only one or a combination of characters).

	Bolitoglossa altamazonica	***Bolitoglossa leandrae*** **(Acevedo et al. 2012)**	**CVUNET 644 (F)**	**CVUNET 645 (M)**	**CVUNET 670 (M)**	**CVUNET 669 (M)**	***Bolitoglossa tamaense*** **(Acevedo et al. 2012)**	**CVUNET 615 (F)**	**CVUNET 626 (F)**	**CVUNET 703 (unknown sex)**	**CVUNET 726 (unknown sex)**	**MHNLS 1268 (M)**
SVL	F = *n*4: 37.9–42.5 M = 30.6	F = 39.2 M = 30.3	34.4	33.4	33.6	35.0	F = 39.2–52.7 M = 36.2–40.3	49.8	41.0	25.2	29.9	37.1
CG	13	13	8	8	8	8	13	10	10	11	10	13
HW	F = *n*4: 5.6–5.8 M = 4.9	F = 6.3 M = 5.8	5.3	5.1	5.4	5.8	F = 7.6 M = 7.1	8.8	6.3	3.8	7.8	6.4
TaL	F = *n*4: 31.0–44.5	22.1–28.8	34.2	32.2	34.9	34.9	?	52.3	41.1	14.6	29.7	28.2
AG	F= *n*4: 20.9–24.8 M = 15.5	F = 23.4 M = 19.5	22.3	21.2	22.9	23.2	F = 29.4 M = 23.1	31.2	24.9	14.1	19.5	21.0
HFW	—	—	4.1	4.0	3.9	4.2	—	4.9	5.1	1.8	3.4	3.8
MT	F = *n*4: 14-20	F = 29 M = 23–24	28	22	21	22	F = 39–42 M = 38–39	41	42	39	40	31
VT	F = *n*4: 9–17 15	F = 20 M = 18–19	18	17	18	17	F = 19–23 M = 17–19	21	17	16	18	16

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Appendix 1. Specimens examined

Bolitoglossa adspersa. MBUCV (Museo de Biología Universidad Central de Venezuela, Caracas) 418, from Páramo de Cruz Verde, Cordillera Oriental, Cundinamarca, Colombia.

Bolitoglossa borburata. EBRG (Museo de la Estación Biológica Rancho Grande, Maracay) 3173, from Fila la Guerrillera, Sierra de Aroa, Yaracuy state, Venezuela. MBUCV 6563, Altos de Choroní, Aragua state, Venezuela. MBUCV 6664, Rancho Grande, Aragua state, Venezuela.

Bolitoglossa leandrae. CVUNET 644, CVUNET 645, both from Quebrada La Espuma, Río Frío, Táchira state, Venezuela. 7.3540 N, 72.1012 W, 650 m asl, collected on 20 May 2012 by W. Tovar, A. Chacón, and C.L. Barrio-Amorós. CVUNET 669, CVUNET 670 both from Quebrada La Espuma, Río Frío, Táchira state, Venezuela. 7.3540 N, 72.1012 W, 650 m asl, collected on May 2013, by William Tovar, Lionel Fernandez, and Andres Chacón Ortiz.

Bolitoglossa orestes. MBUCV 6570 (holotype of *B. spongai*), from Hato La Carbonera, Fila la Cuchilla, Mérida state, Venezuela. MBUCV 6571-72, MCNC (Museo de Ciencias Nacional de Caracas, Caracas) 8116-17, EBRG 3583-84, all from the same last locality and referred as paratypes of *B. spongai*. MCNC 6432, 6484, from San Eusebio, Andres Bello District, Mérida state, Venezuela.

Bolitoglossa tamaense. MHNLS 1268. Río Chiquito, Junín municipality, Táchira state, Venezuela (7.32 N, 72.20 W, ca. 2,000 m asl), collected on February 1956, by Ramón Urbano. CVUNET 615, CVUNET 626, both from Matamula, between Bramón and Delicias, Táchira state, 7.2833 N, 72.4333 W, 2,020 m asl, collected on February 2012 by W. Tovar, A. Chacón and C.L. Barrio-Amorós, CVUNET 703, CVUNET 726 both from Matamula, between Bramón and Delicias, Táchira state, 7.2833 N, 72.4333 W, 2,020 m asl, collected on June and August 2013 respectively, by Marian Chacón Jaimes, Andres Chacón Ortiz, and Carla Ochoa.

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Breeding and rearing the Critically Endangered Lake Oku Clawed Frog (*Xenopus longipes* Loumont and Kobel 1991)

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***Abstract.*—The Lake Oku Clawed Frog *Xenopus longipes* is a Critically Endangered, dodecaploid anuran endemic to Lake Oku in Cameroon. An *ex situ* population of this species was established at Zoological Society of London (ZSL), London Zoo in 2008, as well as at several other institutions, with the intention of providing data on the biology and husbandry of this species. We report the first captive breeding of the species. Adult frogs maintained under environmental conditions designed to mimic field data produced clutches of 7–300 eggs; eggs measured 1.23 mm in diameter, and were laid singly after a period of 6.5 hours in axial amplexus. Spawning took place only during the day. Tadpoles hatched in 2–3 days and development was very long compared to congeners, lasting 193–240+ days until metamorphosis. Tadpoles grew very large (maximum 79 mm total length), particularly compared with the relatively small adult size (maximum 36 mm Snout to Vent Length [SVL]). Tadpoles proved to be highly sensitive to total dissolved solids (TDS) in the water and only thrived when low levels (20 mg/L) were used. Metamorphosis concluded with an SVL of 19–25 mm and F1 animals began first sexual activity at 5–6 months post metamorphosis. These data will inform future husbandry in captivity as well as illuminating facets of biology previously unknown and difficult to determine in the field.**

Key words. Amphibian; *ex situ*; captive husbandry; water quality; Cameroon; West Africa; field data

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The creation of *ex situ* populations for research and conservation breeding has become an important part of the international conservation response to global amphibian declines (Browne et al. 2011; Gascon 2007; Koute et al. 2012; Wilkinson et al. 2013), which represent one of the greatest conservation challenges in history (Zippel et al. 2011). The requirements of amphibians in captivity are poorly understood and many species are presently difficult to maintain and breed (Antwis et al. 2014; Antwis and Browne 2009; Browne et al. 2006; Dugas et al. 2013; King 2011; Ogilvy et al. 2012; Verschooren et al. 2011). *Ex situ* programs have experienced difficulty in providing conditions under which animals survive (Norris 2007; Gagliardo et al. 2008) or successfully breed (Birkett et al. 1999; Gratwick 2012). Moreover, information on how to rear tadpoles is particularly lacking in peer reviewed literature (Pryor 2014).

The Lake Oku Clawed Frog *Xenopus longipes* Loumont and Kobel 1991 (Fig. 1) is an entirely aquatic, dodecaploid frog found only in Lake Oku, a high elevation crater lake in the north west region of Cameroon. *Xenopus longipes* is classified as Critically Endangered by the IUCN (Stuart et al. 2008) due to its restricted range and therefore vulnerability to stochastic factors. Between 2006 and 2010 recurring, enigmatic *X. longipes* morbidities and mortalities were observed, but the overall impact of these events is unknown (Doherty-Bone et al. 2013). A captive-breeding program was considered vital in case of a catastrophic collapse of the population due to the potential introduction of fish to the lake as well as habi-

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tat degradation and disease threats (Tinsley and Measey 2004a). *Xenopus longipes* is ranked as the 35th global priority for amphibian conservation on the basis of threat and evolutionary history by the Zoological Society of London's Evolutionarily Distinct and Globally Endangered (EDGE) program (Isaac et al. 2012).

Captive colonies of the Critically Endangered *X. longipes* were established in 2008 at Antwerp Zoo (later moved to Cologne Zoo and one private breeder), Zoological Society of London (ZSL), London Zoo, and more recently in 2013, at the Steinhart Aquarium in the USA, for conservation research purposes (Browne et al. 2009; T. Ziegler pers. comm.; P. Janzen pers. comm.; D. Blackburn pers. comm.). The zoo colonies were intended to be assurance populations for conservation breeding. However, due to concerns over biosecurity and suitability of animals for release to the wild, the ZSL population was assimilated into the main collection with the focus now on conservation research aiming to document the reproductive biology of the species, as little is currently known. Such information is of importance for developing *in situ* conservation management strategies. Despite repeated attempts in all these institutions, however, efforts to breed and rear this species in captivity have failed, even with the use of artificial reproductive techniques (P. Janzen, pers. comm.; D. Blackburn pers. comm.).

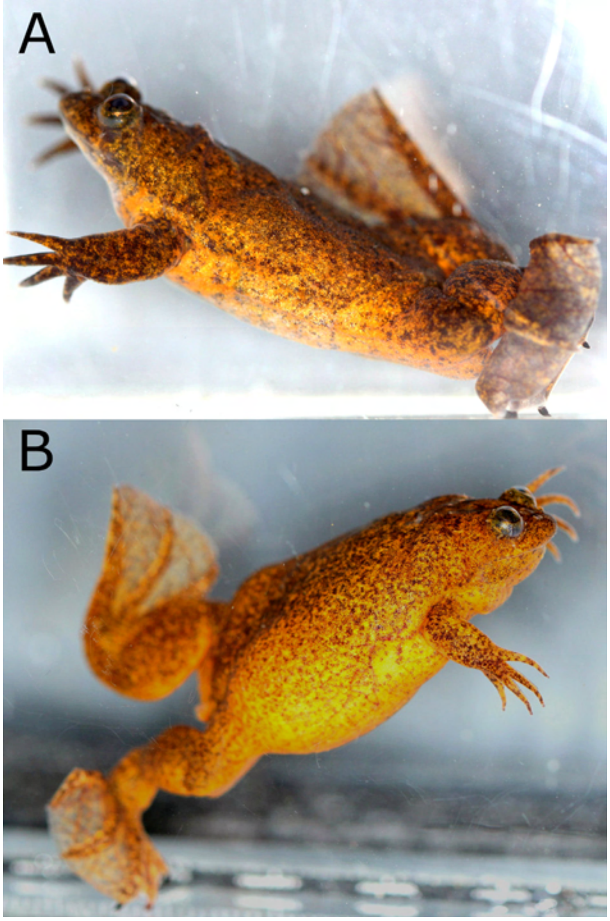

Fig. 1. Male (top) and female (bottom) adults of *Xenopus longipes* in the collection at ZSL London Zoo (ZIMS ID 7441).

Here we report the first captive breeding success of *X. longipes* and the rearing of the tadpoles until metamorphosis.

Methods

In 2008, frogs were collected from Cameroon after consultation with local communities (Permit No. 0742/CO/MINFOF/SG/DFAP/SDVEF/SC and No. 0928/PRBS/MINFOF/SG/DFAP/SDVEF/SC). Lake Oku is considered sacred by the Oku villages and permission had to be granted before any contact with the lake could be made. Thirty-nine founders were housed at Zoological Society of London (ZSL), London Zoo.

Table 1 summarizes the initial and subsequent husbandry used for these frogs between 2008 and 2014. In 2012 the husbandry of *X. longipes* was reviewed (Table 1) as breeding had not occurred and the temperature regime and water parameters did not reflect conditions in the field (Table 2). Captive management should be informed by field data (Tapley and Acosta 2010; Michaels and Preziosi 2013; Michaels et al. 2014) and replicating field conditions has improved captive breeding success of *X. laevis* (Godfrey and Sanders 2004). In 2012, all 32 (30.2) remaining founders were sexed; males being smaller, slimmer, and having keratinized nuptial pads (Fig. 2A and C) and females possessing a trio of cloacal papillae (Fig. 2B). These features became more prominent around breeding events, but were noticeable year round. All 30 female frogs were continuously heavily gravid and amplexus was occasionally observed, but without spawning. Additional founders including four more males were imported from Cameroon in July 2012 and after completing their quarantine period were assimilated into the existing *X. longipes* colony.

In June 2013 mixed sex groups varying from 1.6 to 3.3 were transferred to a custom-made system (Fig. 3; Table 1). A new environmental regime based on longitudinal field data collected monthly from Lake Oku by Doherty Bone et al. (2013) was adopted (Tables 1 and 2; Fig. 4). Lake Oku water temperature and pH were simulated initially, and Total Dissolved Solids (TDS) was subsequently added to the parameters being replicated in 2014 (Table 1). Total Dissolved Solids was measured using Micro 800 Optical DO meter (Palintest) and pH using a Micro 600 pH meter (Palintest). The feeding regime was also modified (Table 1) and a more diverse array of food items were offered to compensate for potential dietary deficiencies as knowledge regarding the nutritional requirements of amphibians is lacking (Densmore and Green 2007).

Results

On 20.3.14, two pairs of *X. longipes* spawned naturally and without hormonal induction, followed by a number

Table 1. Changes in enclosures, life support systems, environmental parameters and diets used for *X. longipes* between 2008 and 2014. Reproduction occurred in 2014.

Dates	Enclosure type and size	Life support systems and furnishings	Photo-period	Water parameters	Diet
2008–2012	Acrylic aquaria (Exo Terra, Rolf C. Hagen) 20 L enclosures	Air-stream sponge filter; Plastic plants	10:14	pH c. 8.5 TDS: c. 350 mg/L Temperature: 19–22 °C	Blood worm (*Chironomus*), Nutrafin Max cichlid sinking capsules, Tetra prima granules and King British blood worm (freeze dried)
2012	Acrylic aquaria 20 L enclosures	Air-stream sponge filter; Plastic plants	10:14	pH c. 8.5 TDS: c. 350 mg/L Temperature: 18–19 °C	Mixed invertebrates: blood worm (*Chironomus* sp); glass worm (*Chaoborus crystallinus*); water fleas (*Daphnia* sp); hatchling crickets (*Gryllus bimaculatus* and *G. assimilis*) and worms (*Eisenia* sp.)
2013	48 L enclosures linked to 100 L sump	TR10 Teco chiller/heater and UV filter; External canister filter (FX6 Fluval). Plastic tubes, plastic and live plants (*Vallisneria* spp., *Echinodorus* spp.)	12:12	pH c. 7.5 TDS: c. 150 mg/L Temperature: 17–19 °C, with seasonal variation	Mixed invertebrates (as above)
2014	48 L enclosures linked to 100 L sump	TR10 Teco chiller/heater and UV filter; External canister filter (FX6 Fluval). Plastic tubes, plastic and live plants (*Vallisneria* spp., *Echinodorus* spp.)	12:12	pH c. 7.5 TDS: 20 mg/L Temperature: 17–19 °C with seasonal variation	Mixed invertebrates (as above)

of other spawning events (Table 3). In the initial spawning event a single pair in each of two tanks containing 1.2 animals spawned. Audible vocalizations, consisting of metallic clicks typical for *Xenopus* (Tinsley and Kobel 1996) were only heard very infrequently from spawning and non-spawning males and were not closely associated with spawning activity; being heard sporadically during both spawning and non-spawning periods. Amplexus and spawning behavior were only observed throughout the day, with no evidence of spawning occurring over-night. Amplexus was axial and the process of oviposition lasted 6.5 hours from initiation to termination of amplexus. Eggs, numbering seven to 300 per clutch (Table 3), were deposited singly over all available surfaces in aquaria. Egg diameter was 1.23 mm one hour after laying. Occasionally, multiple males attempted to amplex single females, but were dislodged by vigorous kicking on the part of the original male. Laying and non-laying females were observed feeding on the eggs, even during amplexus, so non-amplectant animals were removed immediately. Mating pairs were removed as soon as spawning was complete. Animals could not be individually identified, so it is unclear how many clutches were produced by individual animals. The initial spawning event occurred after increasing the temperature from 17.5 to 19.1 °C. This was done by adding warm tap water to the system, resulting in a pH shift from 7.5 to 8.09 to replicate the seasonal temperature and pH regime in Lake Oku, although being done two months earlier than this shift occurs in the field (Fig. 4). This shift occurred over a period of less than one hour after warm water was added in a single dose. However, as the breeding season is not documented in the field, there is no evidence that this seasonal change accompanies the initiation of breeding in nature, other than this relationship observed in congeneric species (Kobel et al. 1996). Later spawning events in the following months (see Table 3) were not associated with manipulation of water parameters, but did follow heavy feeds with earthworms (*Eisenia* sp.). Fertility was highly variable; some clutches were almost entirely infertile, but in most cases fertility rates were close to 100%. Eggs developed and hatched in 2–4 days, with tadpoles initially clinging to hatch sites via the cement gland. Eventually eyes and pigmentation developed before becoming free swimming after 2–4 days. Free-swimming tadpoles initially congregated in areas of slow current, swimming against the water flow. Hatch rate varied between clutches, with later clutches being more consistently successful than earlier clutches.

A variety of combinations of conditions were used in attempts to rear tadpoles (see Table 4). However, we only had success by maintaining tadpoles in water with a very low TDS of 20 mg/L (measured at roughly weekly intervals) and without any live plants or accumulation of humic detritus, and only in aquaria isolated from the adult system possibly as a result of secretions from adults or toxins from PVC pipework used in the aquatic system. Mortality of tadpoles remained high until the TDS of the systems fell below 80 mg/L, with tadpoles becoming weak, opaque, and finally sinking to the floor of the aquaria before dying. Following gradual replacement of high TDS water with low TDS reverse-osmosis water, surviving tadpoles began to feed, swim normally, and to develop. Doherty-Bone et al. (2013) report a TDS of <10 mg/L (See Table 2), but our value of 20 mg/L was the lowest possible output from the RO system in use (Pen-

Fig. 2. Keratinized nuptial pads on the inside surfaces of the front limbs of male (A and C) and cloaca of a female *X. longipes* (B); note the cloacal papillae, which are absent in male frogs.

tair PRF; Fileder) and appears to be adequate for larval rearing.

Tadpole enclosures were glass aquaria measuring 50 × 36 × 30 cm (L × W × H) held in a temperature controlled room with water temperature at 18–20 °C. Between three and 15 tadpoles were housed per aquarium (maximum density of one tadpole per 3.6 litres). Aquaria were filtered with air-stream sponge filters set to the minimum effective flow to reduce turbulence, which would have disturbed the swimming and foraging behavior of tadpoles. Tadpoles were fed 2–4 times throughout the day on a suspension consisting initially of blanched and blended spinach or nettle, commercial *Xenopus* tadpole food, SERA Micron powdered food, and *Spirulina* alga, which was strained prior to use to remove larger plant fragments. After several weeks, the diet was changed to only include commercial *Xenopus* tadpole food, SERA Micron (SERA), and *Spirulina* (3:1:1 by mass, suspended in water before adding to aquaria) to avoid the high oxalate content of spinach (Noonan and Savage 1999), which may interfere with calcium metabolism (Rosol et al. 1995). Food was added throughout the day dependent on the rate at which food was consumed in a given aquarium, with food density of 5.3 mg/L aquarium water provided immediately after feeding; density reduced gradually as food was consumed by tadpoles. Uneaten suspended food accumulated on the bottom of aquaria, where tadpoles were unable to consume it. Additionally, the low carbonate content of the water reduced the capacity for biological filtration. Consequently, nitrogenous

Table 2. Water temperature, pH, and TDS measured at the Lake Oku shoreline (modified from Doherty-Bone et al. 2013).

Parameter	Mean Value	±	Units
Water temperature	17.27	4.17	Celsius
pH	7.58	0.24	-
Total Dissolved Solids	8.72	2.27	Ppm

Fig. 3. Aquarium for *X. longipes*, set within a custom built, centrally filtered system (inset photograph) at ZSL London Zoo. Life support system and sump not shown – see text for details.

waste (measured using Photometer 7100 [Palintest]) was difficult to manage and tadpoles were briefly exposed to high levels of ammonia (>1 mg/L) and, later, nitrite (up to 2.4 mg/L) without mortality. A regime of 10% water changes in the morning and 50% water changes in the afternoon, both accompanied by removal of uneaten food on the bottom of tanks by siphon and thorough cleaning of sponge filters in aquarium water, helped to suppress nitrogenous waste to more acceptable, but still detectable levels (Ammonia: <0.1 mg/L; Nitrite: <0.5 mg/L) for most of the tadpole rearing period.

The tadpoles of *X. longipes* are described separately (Tapley et al. 2015). Development in the most rapidly developing tadpole (Fig. 5) lasted 193 days between hatching and metamorphosis. We report development using Gosner (1960) stages, as it was impossible to accurately apply the more detailed Nieuwkoop and Faber (1994) stages for *Xenopus laevis* development to live tadpoles without restraining them. This would likely have proven fatal for these delicate and Critically Endangered tadpoles, though could be employed in future offspring once captive population growth has been assured. However, developmental rates were highly variable and the more slowly developing tadpoles had not yet metamorphosed at the time of writing. A maximum total length of 68 mm was reached in the first tadpole to metamorphose (Fig. 5), and the largest tadpole reached a maximum total length of 79 mm. Metamorphs measured 19–25 mm SVL and captive-bred males began to exhibit amplexus six months post metamorphosis, by which time they had nearly reached adult size. Further details of tadpole development are provided by Tapley et al. (2015). Once front limbs emerged from the operculum, tadpoles were separated by placing them in identical systems with

Table 3. Spawning dates and clutch sizes for *X. longipes*.

Date	Clutch number	Clutch size
20.03.14	1	93
	2	115
21.03.14	1	190
22.03.14	1	40–50
	2	40–50
05.04.14	1	40
25.08.14	1	50
04.09.14	1	Not counted
16.09.14	1	20
17.09.14	1	120
18.09.14	1	80
20.09.14	1	Not counted
29.09.14	1	50
04.10.14	1	120
05.10.14	1	300

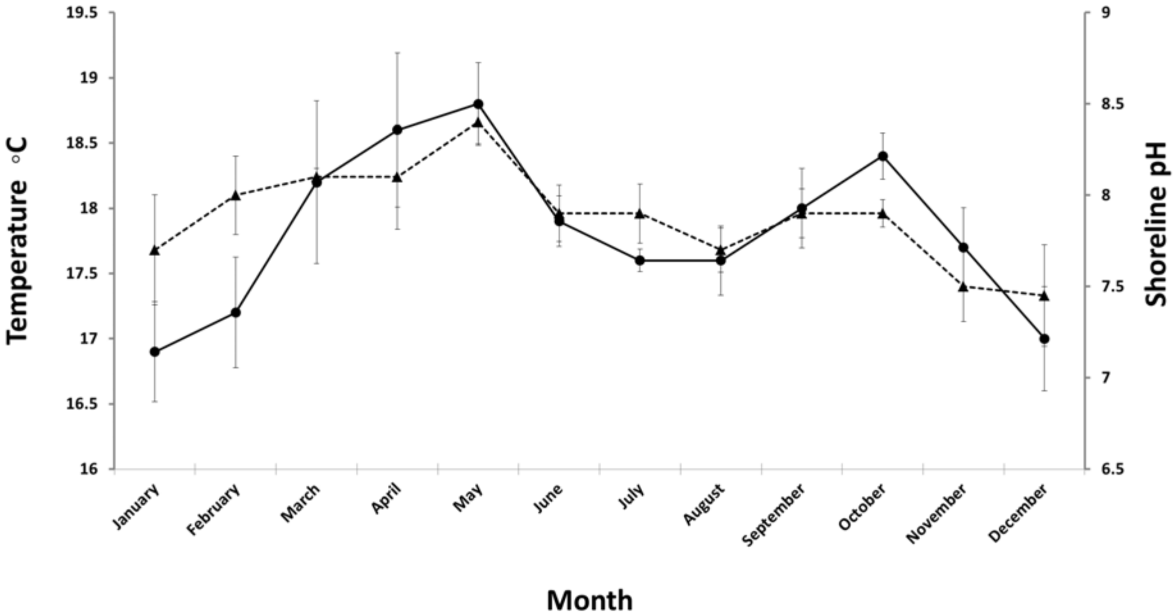

Fig. 4. Monthly water temperatures (circles) and pH (triangles) recorded from the shoreline of Lake Oku between 2008/2009 and 2013. Error bars represent SEM.

Table 4. Combinations of conditions used to rear *X. longipes* tadpoles, and the outcome in terms of tadpole survival.

Water TDS (mg/L)	Refugia (live plants)	Detritus	Lighting	Tannins	Isolated from adult system?	Tadpoles survived?
20	-	-	-	-	+	+
	-	-	+	-	+	
	-	-	-	-	-	-
	-	-	+	-	-	
	+	-	+	-	-	
	+	+	+	-	-	
	-	-	-	+	-	
	-	-	+	+	-	
	+	-	+	+	-	
	+	+	+	+	-	
	+	+	+	-	+	
	+	+	+	+	+	
150	-	-	-	-	-	
	-	-	+	-	-	
	+	-	+	-	-	
	+	+	+	-	-	
	+	+	+	+	-	
	-	-	-	+	-	
	-	-	-	-	+	
	-	-	+	-	+	
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	-	-	-	+	+	

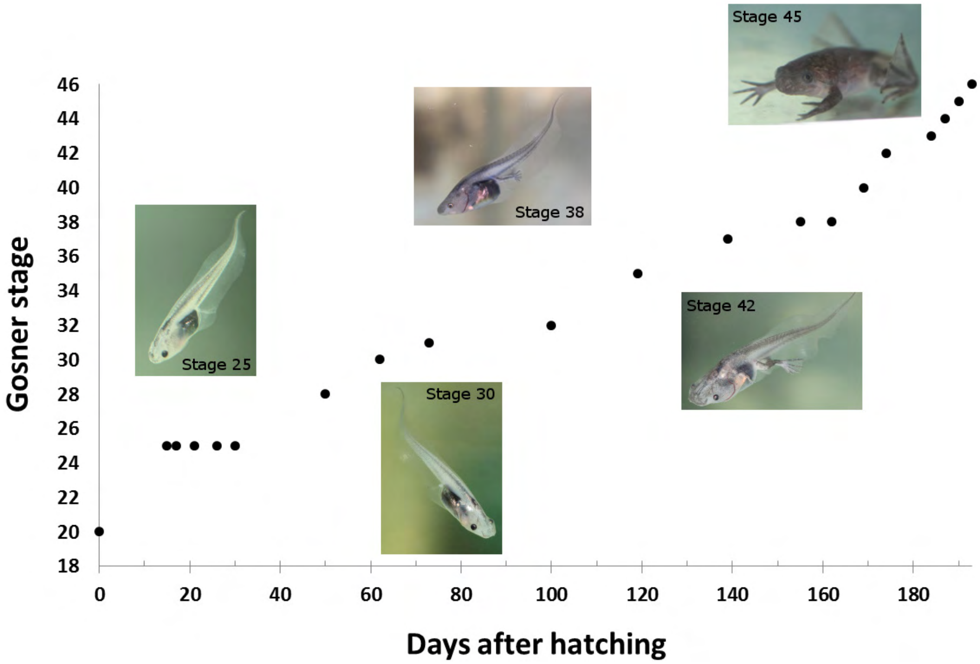

Fig. 5. Gosner stage progression of the most rapidly developing *X. longipes* tadpole. Hatching to metamorphosis took 193 days, but smaller tadpoles had only reached stage 35 by this point.

sponge filters that had been matured in the system housing the adult frogs, but with a shallower water depth of 15 cm to facilitate access to the surface for breathing. Metamorphosis from this point took around seven days to complete. Froglets fed on a similar range of prey items to adults.

Discussion

Although the husbandry of adult *X. longipes* is largely similar to that established for other *Xenopus* species (Green 2012), and adult frogs are able to survive a range of water parameters, the tadpoles are more sensitive. The dietary requirements of tadpoles are similar if not identical to those of *X. laevis* and *X. tropicalis*, but tadpoles appear to be more sensitive to the mineral/solute content of water. Tadpoles maintained in water with a TDS higher than around 80 ppm died rapidly and tadpoles developed well with a TDS of around 20 ppm. Total Dissolved Solids represent the total amount of dissolved mobile charged ions, including minerals, salts or metals and is closely related to hardness, but includes a broader range of dissolved substances. Typically, very low solute content of aquarium water can lead to osmotic imbalances in amphibians, but species may adapt evolutionarily to relatively pure water (Odum and Zippel 2008). Sensitivity to hardness or TDS values in *Xenopus* is not without precedent. The tadpoles of the softwater specialist *X. gilli* from the Cape also appears to be intolerant of hard, alkaline conditions (Rau 1978), while the reproductive success of captive *X. laevis* is improved by matching the hardness of their wild environment (Godfrey and Sanders 2004). Other amphibians including the Hellbender *Cryptobranchus alleganiensis* have been shown to be reproductively sensitive to TDS levels (Ettling et al. 2013). The closely related *X. amieti* has been reproduced with hormonal induction in captivity (Xenopus Express pers. comm.), and the tadpoles of this species were maintained in hard water with success. However, there are no field data for water quality in its wild range and the larger distribution of *X. amieti*, which is not restricted to a single lake (Tinsley and Measey 2004b), may have led to the evolution of less specific environmental requirements. Our combinations of environmental conditions, summarized in Table 3, were not fully exhaustive and so the effects of some parameters (particularly tannins) cannot be fully elucidated based on these data. Tannins are thought to be important in reducing the frequency of fungal infections in the tadpoles of some anuran species (e.g., *Theloderma corticale*; Rauhaus et al. 2012), but there are no data concerning the tannin levels in Lake Oku. The forested shores of Lake Oku do produce inputs of leaf litter (so far unquantified) suggesting some levels of tannins, but this needs to be confirmed. Underwater photographs of the lake suggest relatively clear water (T. Doherty-Bone pers. obs.), which may mean that tannins are unimportant or potentially harmful in this species.

Amplexus and egg-laying behavior is similar to other *Xenopus*, although we did not observe calling in close association to spawning. Indeed, calls were very rare in general and we were unable to record them despite repeated efforts. Amplexus and oviposition were exclusively diurnal, in comparison to the often nocturnal habit of *X. laevis* (Green 2012) and the apparent strictly nocturnal amplexus, calling, and spawning reported from hormone induced *X. amieti* (Xenopus Express pers. comm.). Specific triggers involved in stimulating spawning activity remain unclear. In a species from a habitat that is relatively stable year round (Fig. 4), and with no periods of drought and pond drying, it is possible that reproduction can take place year round and strong environmental stimuli are not required. Although initial spawning was associated with a change in temperature and pH, the breeding season is not documented in the wild and there is no evidence that this seasonal change accompanies the initiation of breeding in nature. Our observations suggest that heavy feeding may contribute to spawning activity, and so breeding may be more linked to a threshold in body condition than to external triggers. Kobel et al (1996) have suggested that some *Xenopus* species breed following first rains, when nutrients in the water have increased and secondary productivity of invertebrates is thus stimulated. Our observations indicated the initial stimuli of changing temperature, but correlated more strongly with increased availability of food. These speculations merit further investigation.

Clutch size (7–300; Table 3) was smaller than that produced by *X. laevis* (500–30,000 eggs Green, 2012) or *X. tropicalis* (1,000–3,000 eggs; Green, 2012). This may partly reflect the smaller body size of *X. longipes*, but may also be a function of breeding in a more stable lake system habitat, where there may be advantage in producing a smaller number of larger eggs. The fact that egg size is similar for *X. laevis* and *X. longipes* (1.3 mm [Brown 2004] and 1.23 mm, respectively), as well as for a number of other *Xenopus* species much larger than *X. longipes* (Kobel et al. 1996) supports this hypothesis. The pattern of small clutch size and relatively large eggs is continued in the very large tadpoles of this species (maximum total length 79 mm), particularly compared with adult size (32–36 mm snout-to-vent length [SVL]; Loumont and Kobel 1991); see Tapley et al. (2015). The closely related *X. amieti*, which has larger adults than *X. longipes*, has a tadpole of only 40 mm total length (Channing and Rodel 2012), while the very large *X. laevis* has tadpoles of 80 mm compared with adults of over 140 mm SVL (Green 2012).The metamorphs of *X. longipes* are correspondingly large relative to adult size, being similar in size to the metamorphs of *X. laevis* despite a fivefold difference in adult size between the two species (see Tapley et al. (2015), for further discussion of larval size).

Larval development was slower in *X. longipes* than congeners. Larval duration was 193 days at 17–19 °C for the fastest developing larva, in comparison to the faster development of *X. laevis* (42–56 days (Green 2012); 53 days at 18 °C; Gomez-Mestre et al. 2010) or *X. tropicalis* (21–42 days; Green 2012). Several healthy tadpoles of *X. longipes* remained untransformed at 240 days post hatching. This may, again, be linked to a relatively stable breeding habitat at higher altitude, where very low seasonal variation in environmental parameters (Fig. 4), lower temperatures, and no risk of the water body drying out may select for a longer larval phase (Werner 1986). In *X. gilli*, which is found in more temperate lowland habitat in the extreme south of the African Cape, lower temperatures comparable with those measured in Lake Oku are also associated with the long developmental duration of this species (120 days; Rau 1978), albeit still shorter than for *X. longipes*.

The observations presented herein provide the first insight into the behavior, development, and captive requirements in *X. longipes*. This is of particular note as to the best of our knowledge the tadpoles of this species have never been observed alive in the field and so nothing is known of their habits in nature. In particular, the high sensitivity to mineral content and smaller clutch size of this species than in commonly maintained *Xenopus* may make *X. longipes* more susceptible to aquatic pollution and less able to recover quickly from declines. Moreover, this characteristic highlights the limitations of the "analogue species" concept (Preece 1998; Michaels et al. 2014), whereby common relatives of a threatened species are used as models to develop husbandry strategies before working with target, usually Critically Endangered, species. The relative ease of breeding and rearing *X. laevis* in captivity does not entirely transfer to *X. longipes*, particularly where water TDS for tadpoles is concerned.

Our findings will hopefully improve success with this species in other institutions, and contribute to the long-term viability of captive colonies. This includes attaining reproduction from the first generation of captive bred *X. longipes*. Once reproduction is achieved regularly, a studbook should be developed to ensure that a viable population of this species is maintained in captivity long-term, both for conservation breeding and for research purposes. A studbook would require individual marking techniques as *X. longipes* do not have distinctive skin markings. Such marking techniques has not yet been trialled in this species. *Xenopus longipes* is one of only two vertebrates known to be dodecaploid (the other being *X. ruwenzoriensis*) and so there is considerable interest in this species as a model laboratory organism. Inclusion of *X. longipes* in research captive colonies may help to secure the future of this species in captivity.

Although the current captive populations of *X. longipes* are not managed under strict enough biosecurity controls to be suitable for reintroduction efforts (IUCN/SSC 2014), laboratory techniques for other *Xenopus* exist to generate "clean" animals (e.g., Kay and Peng 1991). There is therefore potential to use these techniques to create biosecure cohorts that could safely be used for reintroduction should it be required. Moreover, husbandry protocols can also be distributed to Cameroonian specialists so that conservation breeding facilities can be developed in country if necessary; this option is often preferable due to reduced risk of disease transmission and reduced cost. More work is required to fully understand and control the reproduction of this species in the laboratory as well as the field.

Conclusions

Although superficially similar to other *Xenopus* species better established in captivity, the husbandry and captive breeding of *X. longipes* differs in several important aspects. The breeding triggers are poorly defined and less obvious than for many other species, which often breed in response to large water changes with cool water. Clutches are small and eggs are relatively large for the adult body size compared with other *Xenopus* species. The tadpoles are also very large and take a very long time to develop in comparison with other species. Moreover, they are highly sensitive to dissolved solids. These characters may reflect adaptation to a single volcanic lake with a stable environment.

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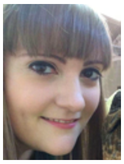

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Notes on the natural history and morphology of the Ningshan Lined Snake (*Stichophanes ningshaanensis* Yuen, 1983; Ophidia: Colubridae) and its distribution in the Shennongjia National Nature Reserve, China

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***Abstract.*—The present study reports on the natural history of the Ningshan Lined Snake (*Stichophanes ningshaanensis*) in the Shennongjia National Nature Reserve (NNR) in western Hubei Province, China. Prior to this work, little was known about the natural history of this species due to a paucity of specimens since the original description in 1983. Since its discovery, only the original three specimens were known to science, all of which are now lost or destroyed. Over the course of five summers, we observed 24 specimens within the Shennongjia NNR. We report on its natural history, including seasonal activity, habitat and environmental preferences, breeding behavior, sexual dimorphism, and incubation data for the eggs. We reiterate the morphological differences between *Stichophanes*, its former genus *Oligodon*, and members of Pareatidae. In China, *Stichophanes* is not protected under law due to the species being classified as "Data Deficient." The species exhibits sexual dimorphism and dichromatism, i.e., males are smaller than females and the sexes differ in color. The species has unique breeding habits in mid-summer, and copulation occurs immediately after oviposition of the females. The number of eggs per clutch ranges from eight to nine, and takes 64 days to hatch.**

Key words. *Oligodon*, *Pareas*, Asia, slug eaters, reproduction

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Little is known about the Ningshan Lined Snake, *Stichophanes ningshaanensis* Yuen, 1983. The species was discovered in Ningshan County, Shaanxi Province, China, in the southern part of the Qinling Mountains (Yuen 1983) and was described based on three specimens, which presently are all lost or destroyed (Wang et al. 2014). No additional specimens were found until in 2006 a survey revealed 17 new specimens in Shennongjia NNR, western Hubei Province (Yang et al. 2009). In the original description, the species was assigned to family Colubridae and placed in the genus *Oligodon*. But few of its morphological characters match up to the genus, additionally, none of the characters fit easily into any other Asia genera. It was for this reason the species was recently assigned to the new genus *Stichophanes* (Wang, Messenger, Zhao, and Zhu 2014). The specific epithet *ningshaanensis* is named for Ningshan County in Shaanxi Province (note the double "aa" in the specific epithet, which is not a typo and distinguishes Shaanxi Province from Shanxi Province. In this circumstance, it is used to correctly pronounce the extended vowel sound of Shaanxi compared to Shanxi in the Mandarin language), where the type specimen was found. The generic epithet *Stichophanes* breaks down into *stichos-* (Greek), meaning "line or row," and *–phanes* (Greek), meaning "appearing, conspicuous," in reference to the dorsal and lateral lines of the body.

Due to its elusive behavior, and the paucity of specimens, little was known about the natural history of the species. Aside from the initial description, the only other

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work of the species was an examination of the microstructure of the skin by Li and Liang (2007), which revealed a canaliculated type structure. Additionally, prior to the 2006 field work, this snake was among the rarest of China's species, with only three specimens known to science at the time. Even though the species is locally common at select locations within Shennongjia NNR, this species could very well be a species of conservation interest if no additional populations are found in its range. For these reasons, it is important to understand the natural history of the species.

This study reports on the natural history, breeding ecology, and distribution of the species as observed in the Shennongjia NNR, and additional commentary on aspects of its unique morphology, with special regard toward the genus *Oligodon* and members of the family Pareatidae.

Materials and Methods

Fourteen field sites were surveyed within the Shennongjia NNR in western Hubei Province, China (Fig. 1). Approximately one week was spent at each field station. At field stations, the primary surveying technique was walking habitat day and night, flipping natural cover objects such as rocks and logs, and actively searching using visual and auditory stimuli. The first survey was conducted in 2006 from May to September. A second survey was completed in July 2008. A final intense survey was carried out during the summer of 2011. Beginning in 2012, only one month every summer was surveyed opportunistically.

If the reserve museum did not have a specimen, then an animal was preserved as a voucher. Subsequent individuals were photographed and released unless they differed from the previous specimens in such attributes as pattern, gender, or age. Specimens were deposited with the museum officials in Shennongjia, headquartered in the town of Muyu. Specimens were later relocated to the research lab at Guanmenshan within the reserve. Locations of finds were marked with GPS coordinates (accuracy < 3 m). Environmental data such as ambient temperature, substrate temperature, habitat, and elevation were recorded as well as precipitation and time of day or night.

Upon capture, each animal was sexed via probing and measured snout-to-vent (SVL) and total length (TL) to the closest 0.25 cm using a tape measure. Measurements of eggs were taken with digital slide calipers to the closest 0.01 mm. Dorsal scale rows were counted one head length posterior to the head, at mid-body, and one head-length distance anterior to the vent.

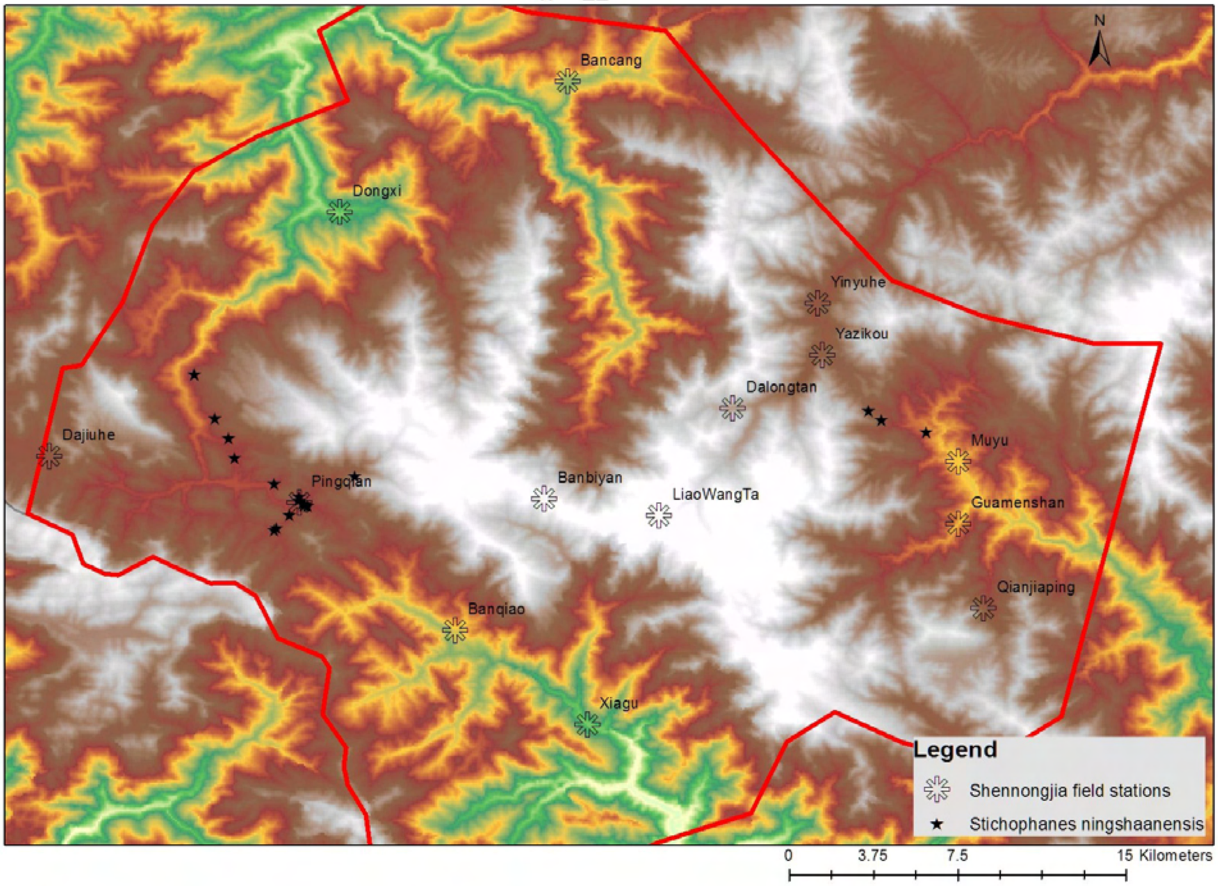

Fig. 1. Locations of field stations and of *Stichophanes ningshaanensis* ($n = 22$) within the Shennongjia NNR.

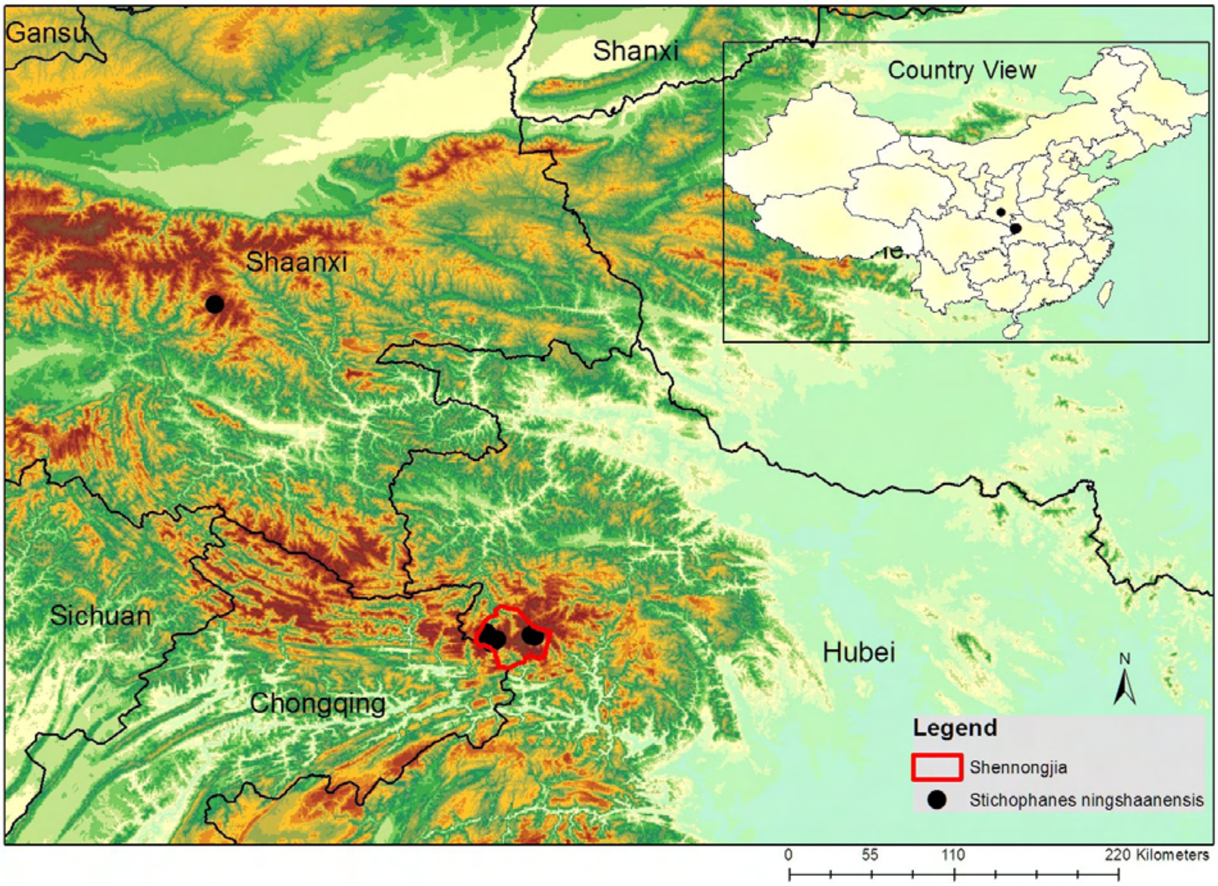

Fig. 2. Current known range of *S. ningshaanensis*; type locality located in Shaanxi province.

Results

From 24–26 June 2006, we found six females and three males near Pingqian. Three of the females were dead (one beat to death by villagers, two were road kill); all males were alive. In July 2008, we found eight live specimens, and one dead specimen, all adults except one sub-adult. Three new locations within the reserve were recorded: a high mountain road near the town of Xiangshui, another record between the towns of Banqiao and Pingqian, and several individuals (*n* = 3) on the outskirts of Muyu. In July 2011, we found an additional three specimens in Pingqian and another on the mountain road near Xiangshui (N31.531231° E110.113914°). In the years 2012–2014, no additional new locations were discovered. In 2012, we had a single observation, representing the earliest known observation of the species since its discovery in 1983. In 2012, surveys were conducted in late May, early June, and early August. In 2013, major construction and development at the core site, Pingqian, began, and only a single specimen was found in July, ironically crossing habitat just bulldozed. The year 2014 represented the first year that surveys failed to find an individual, despite surveying during the active time of year for the species. The development started in 2013 was much more extensive in 2014 and much of the habitat in Pingqian, where individuals had been found previously, was completely destroyed or urbanized.

The finds in Shennongjia NNR represented a range extension of 280 km to the southeast of the type locality, and the first major population found since the species' discovery in 1983 (Yang et al. 2009; Fig. 2).

Description Based on Specimens from Shennongjia NNR

Dorsal scales are smooth, with counts of 13, 13, and 12 anteriorly, mid-body, and posteriorly, respectively. The anal scale is divided. Head scales consist of two postoculars, one pre-ocular, no loreal scale, six supralabials (3rd and 4th in contact with eye), five infralabials, one anterior temporal, and two (sometimes one) posterior temporals. The rostral scale is smooth and not upturned or protruding as is characteristic of the genus *Oligodon*. The subcaudal scales are paired.

Males are olive-brown or olive-green, and females are yellow-brown in color. In both sexes, the venter is a cream-colored version of the dorsal background color. Both sexes have a single row of dots on the lateral edges of each ventral scale. These spots tend to fade posteriorly. Anteriorly, there are five distinct black lines immediately posterior to the head. One line is along the spine

Fig. 3. Close up of the head, showing detail of the scales, and illustrating the indistinct neck of the species. *Photo by Kevin R. Messenger.*

Fig. 5. Typical habitat of *Stichophanes ningshaanensis* in the Pingqian area pre-2013. *Photo by Kevin R. Messenger.*

but quickly fades from black to brown to indistinct and blending with the background coloration toward the tail. Two pairs of lines are situated dorso-laterally and run the length of the body with consistent boldness, often the inferior edge of the line is brown and the superior edge remains black. The final two pairs of lines are located ventro-laterally, between or along the 1st and 2nd scale rows. The iris is golden-brown in females and golden-yellow in males. The head is indistinct from the neck (Fig. 3).

The largest individual found was a female measuring 730 mm total length (TL) and 578 mm Snout-to-vent length (SVL). The largest male measured 654 mm TL and 495 mm SVL. Hatchlings (*n* = 17) averaged 150 mm TL (SD + 4 mm) and 119 mm SVL (SD + 2 mm).

Natural History Notes

Specimens were found during the day and in the evening, as late as 80 minutes after sunset. Twenty four specimens were found: locals beat one specimen to death, two were found dead on the road, two specimens were under rocks, and the rest were actively moving about. Species observations were primarily terrestrial, but lacking specimens outside the breeding season, species are suspected to be primary fossorial and only move above ground during the breeding season. No specimens were found in an arboreal setting. During the breeding season, several specimens (*n* = 8) were also found dead on the road. The average elevation of provenances of specimens was 1628 (SD + 126 m) (range 1,550–2,200 m). May surveys failed to find specimens. The earliest observation date was a female found on 07 June 2012, but in general, late June and early July were best times finding species as this is the breeding season and snakes were actively moving above surface (Fig. 4). The latest documented date occurrence was on 20 July 2008. Surveys in August and September failed to detect any specimens. The species was usually in proximity to water, i.e., within ~300 m of a water source, and was often encountered actively moving after rainstorms. The species was active on overcast and cool days with temperatures ranging 20–24 °C.

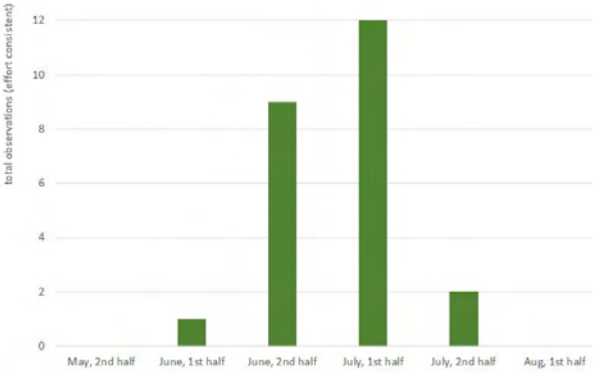

Fig. 4. Seasonal activity of *Stichophanes ningshaanensis* observations (*n* = 24).

With respect to habitat, between 1,500–2,600 m elevation, the habitat is classified as temperate deciduous broadleaf coniferous forest including Farges' Fir and Fortune's Rhododendron (Zhao et al. 2005). Average annual temperature of locations where individuals were found were 16.2 °C (range: 15.6–16.7). Average annual precipitation of locations where individuals were found was 222.85 mm (range: 209–235). Individuals were found in ephemeral stream beds, in short grasses, commonly found on the outskirts of agriculture land, and in habitat adjacent to permanent streams (Fig. 5). Individuals were never far from a source of water.

Stichophanes ningshaanensis shares its habitat with the following species: Snakes: *Achalinus spinalis*, *Azemiops feae*, *Dinodon* [=*Lycodon*] *rufozonatum*, *Elaphe carinata*, *Lycodon* cf. *fasciatus*, *Orthriophis taeniurus*, *Protobothrops jerdonii*, *Pseudoxenodon macrops*, *Rhabdophis nuchalis*, *Sibynophis chinensis*; Lizards: *Plestiodon capito*, *P. elegans*, *Scincella modesta*, *Sphenomorphus indicus*, *Takydromus septentrionalis*; Anurans: *Amolops chunganensis*, *A. granulosus*, *Bufo* cf. *andrewsi*, *Megophrys wushanensis*, *Odorrana margaratae*, Paa *quadranus*, *Rana chensinensis*; Salamanders: *Liua shihi* and *Ranodon tsinpaensis* (pers. obs.).

When confronted, the species was reluctant to bite. No amount of provocation elicited a defensive bite.

Fig. 6. Tail-curling defensive behavior characteristic of *Oligodon*: *O. formosanus* (left), *O. ornatus* (right), and enlarged rostral scale. *Photos by Kevin R. Messenger.*

Fig. 7. Courtship behavior by the male, rubbing his chin along the female, observed on 28 June 2006. *Photo by Kevin R. Messenger.*

Fig. 8. Courtship behavior by the male observed on 28 June 2006, and illustration of dichromatic differences. *Photo by Kevin R. Messenger.*

Many members of *Oligodon* effectively use their unique teeth when restrained and harassed and will bite readily. *Stichophanes* thrashes about and readily produces musk but does not display the characteristic tail-coiling known to some other species within the genus *Oligodon* (Seshadri 2014; Fig. 6).

Notes on Reproduction

The species exhibits strong sexual dimorphism, not only in size, but also in color (sexual dichromatism), an uncommon trait among snakes (Boulenger 1913; Jacob and Altenbach 1977; Shine and Madsen 1992). There are only a handful of other species that have been reported to exhibit sexual dichromatism, such as *Crotalus lepidus klauberi*, in which males have a greenish hue and females have a purple hue (Jacob and Altenbach 1977). Shine and Madsen (1992) noted dichromatism in the genus *Vipera*. In *S. ningshaanensis*, males are smaller than females. Females are yellowish-brown, while males are olive-brown or olive-green. Males also have a longer tail than females. In males, the tail is 24–27% of the total body length, whereas the value for females is 21% (Wang et al. 2014).

Despite the fact snakes were found in mid-summer (late June), males attempted to mate with gravid females. Courtship behavior was observed on multiple occasions. It consisted of a male rubbing his chin along the length of a female and positioning his cloaca next to hers (Figs. 7, 8). No copulation was observed with these gravid females before oviposition. There is no documentation of other colubrids trying to copulate with gravid females nearly full term, although this is commonly observed in crotalids (Duvall et al. 1992) in which mating and birthing occur in the same season, typically fall. *Stichophanes ningshaanensis* is similar. Immediately after females laid eggs in late summer, males commence with copulation.

A clutch of eight and nine eggs was recorded from two females on 29 and 30 June 2006 (Fig. 9). The time span between successive eggs was 15 minutes, and each egg took two minutes to exit the cloaca. In the first female, after oviposition, a male immediately courted her and successfully copulated (Fig. 10).

The eggs measured 26.98 mm long and 9.52 mm wide. All 17 eggs were placed in a plastic container and covered with a damp paper towel. They were kept at room temperature (generally 24 ºC but reaching a maximum of 29 ºC). After 62 days, the first eggs started to pip. By 64 days all 17 eggs had pipped, and the young began to emerge from the eggs (Fig. 11).

Fig. 9. Nine eggs from a female measuring 533 mm SVL and 673 mm TL on 30 June 2006. *Photo by Kevin R. Messenger.*

Fig. 11. Hatching and emergence after 64 days of incubation. *Photo by Kevin R. Messenger.*

Fig. 13. Comparison of typical head scales and head shapes of *Oligodon* (top); 8 supralabials, 4 and 5 in contact with eye, 2 pre-oculars, 2 post-oculars, 1+2 temporals, 1 loreal, enlarged, upturned rostral scale, to the head scales of *Stichophanes* (bottom); 6 supralabials, 3 and 4 in contact with eye, 1 pre-ocular, 2 post-oculars, 1+2 temporals, no loreal, blunt rostral scale. *Photos by Kevin R. Messenger.*

Fig. 10. Copulation on 30 June 2006, post oviposition by the female. *Photo by Kevin R. Messenger.*

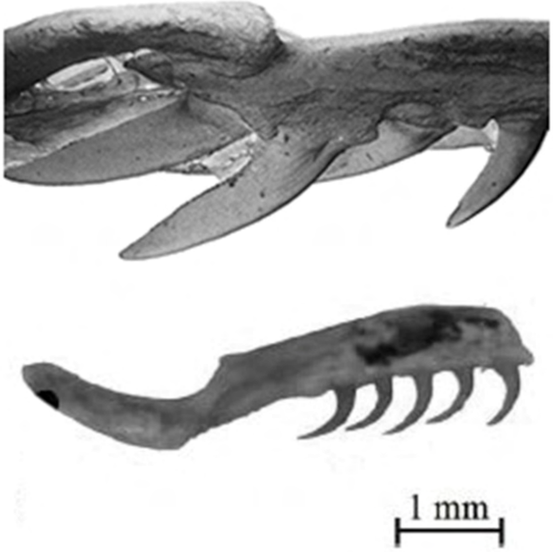

Fig. 12. Comparison of right maxillae; *Oligodon* on the top, with the characteristic kukri-shaped rear teeth which it uses to saw into eggs, distinguished from the anterior teeth (from Coleman et al. 1993), *Stichophanes* on the bottom, anterior teeth all the same, and a lack of rear-specialized teeth (from Wang et al. 2014).

Fig. 14. Photograph of *Pareas formosensis* (van Denburgh 1909) from Taiwan, illustrating the concave tongue notch opening that is typical of *Pareas* members. *Photo by Daniel Rosenberg.*

Comparison with Species of *Oligodon*

The genus *Oligodon* Fitzinger 1826 is a very broadly characterized genus. There are approximately 74 species within the genus as of 2013 and as such bring a wide variety of characteristics and diversity (Green 2010; Vassilieva et al. 2013). Five robust characters tend to apply to most species (Green 2010). These are:

1) Presence of unique posterior maxillary teeth, appearing in shape to Ghurka kukri knives, for which the genus gets its common name, “Kukri Snake.”
2) Large, slightly upturned rostral shield, protruding when viewed from above.
3) Many species possess a distinct dark chevron mark on the nape and a stripe across the anterior part of the head and down over/through the eye.
4) Majority of species have blotched and/or reticulate pattern, usually not prominently striped.
5) Most species possess a loreal scale.

Stichophanes ningshaanensis differs on several levels and conflicts with each of these five robust characters: in addition to the defensive behavioral differences mentioned previously (i.e., lack of tail curling, refusing to bite defensively), *S. ningshaanensis* does not possess the distinctive rear teeth for which *Oligodon* was named (Fig. 12). Most *Oligodon* use these specialized teeth to slice or “saw” into reptile eggs (Coleman et al. 1993). They use their upturned snout to dig up eggs, similar to species in the North American genera *Cemophora* and *Phyllorhynchus*. Once an egg is opened, they insert their head inside the egg to consume the contents. *Stichophanes ningshaanensis* lacks this upturned rostral shield, instead, having a very blunt and squared-off head (Fig. 13). Additionally, the species does not prey on eggs or any of the known prey ingested by other *Oligodon* species but rather eats snails and slugs exclusively (Wang et al. 2014). The species lacks chevron markings on the nape and lacks a stripe across the anterior part of the head or through the eye. The species is distinctly striped and not blotched, and lastly, all specimens lack a loreal scale. From an internal perspective, the hemipene morphology does not conform to that of *Oligodon*. From a morphological and behavioral standpoint, these key differences give credence to the species not belonging to the genus *Oligodon*.

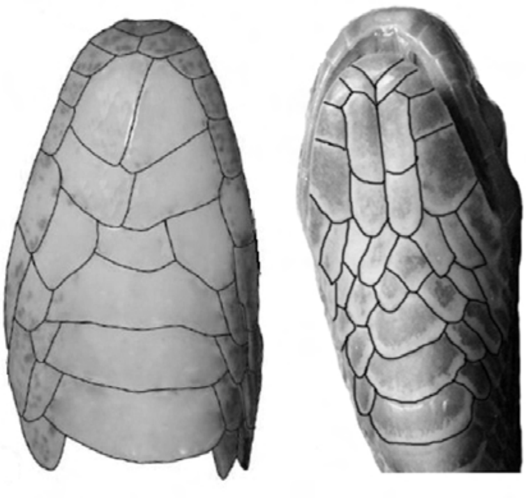

Fig. 15. Left: underside view of *Pareas vindumi* (from Vogel 2015), showing the lack of a mental groove due to asymmetrical chin shields. Right: underside view of *Stichophanes* (from Wang et al. 2014), showing symmetrical chin shields and the presence of a mental groove.

The next most likely genus for the species to be placed in, from a morphological and dietary standpoint, is *Pareas*, the Asian snail eaters.

Comparison with Asian Snail and Slug Eating Species

Due to its shortened, square head, as well as its exclusive diet of gastropods, it seems likely that *Stichophanes* could be closely related to members of the Asian snail and slug eaters: Pareatidae. Currently only three genera are known in Pareatidae. These are:

Aplopeltura: a genus containing a single species, *A. boa*, the Blunt-headed Slug Eating Snake. This genus is arboreal. The head is very distinct from the neck. This genus is located outside of China.

Asthenodipsas: a genus containing five species (Loredo et al. 2013). Members are characterized by a large head, distinct neck, lacking a mental groove, very large eyes, and an arboreal lifestyle. The mouth possesses a slotted opening that facilitates ingestion of snails and slugs. All members of the genus are located outside of China.

Pareas: a genus containing 13 species (You et al. 2015; Vogel 2015). Members are characterized by a blunt snout, lacking a mental groove, distinct neck, and no teeth on the anterior part of the maxilla (Guo and Deng 2009). The tongue notch possesses a concave opening to facilitate the ingestion of snails and slugs (Fig. 14). The majority of the species are found in China.

Stichophanes ningshaanensis does not fit into any of these genera. The species is strictly terrestrial and fossorial, there is little to no distinction between the head and neck, it possesses teeth on the anterior part of the maxilla (Fig. 12), it possesses a mental groove (Fig. 15), and does not have a slotted notch on the mouth. From a morphological, dietary, and behavioral standpoint, the species does not fit into any known Asian genus and is quite unique, not only in appearance but also in its ecology. Genetic work by Wang et al. (2014) further supported what the morphological data suggested and could not

Fig. 16. Downtown Pingqian. *Stichophanes ningshaanensis* was commonly found crossing this road and in the habitat adjacent to the road. Picture taken June 2011. *Photo by Kevin R. Messenger.*

Fig. 17. View of Downtown Pingqian in June 2014, covering same view (different angle) as Figure 16. *Photo by Kevin R. Messenger.*

place the species in any known genus, at which point, a new genus was erected, *Stichophanes*.

Discussion

The purpose of this paper was to provide insight into this rarely observed and studied species. The population in the Shennongjia NNR has provided opportunities to observe several aspects of the species' natural history, from activity periods, to seasonal differences, to courtship, breeding, and incubation of eggs. The species has a unique reproductive strategy, which is not documented among other species of colubrids, or is, at the very least, quite uncommon.

Prior to 2013, the species was locally abundant in Shennongjia NNR, and specifically in Pingqian, and was among the more common and predictable species when in its habitat. The changing habitat due to development of the Pingquin village may be a turning point for the species in the area, for the worse (Figs. 16, 17). Future investigations in this area will hopefully yield knowledge on the urban tolerance (or intolerance) of the species. Investigations in 2014, despite being done during the height of the breeding season, failed to turn up a single specimen. Currently, the species is not under any special protection, currently classified as "Data Deficient." It is hoped this paper will bring us closer to understanding the species and its potential distribution, and this information will reduce the deficiency of data for this species.

Aside from the natural history aspects, another goal was to further illustrate the morphological distinction of the species from closely aligned genera, such as its original placement in *Oligodon* and its next most likely genus, *Pareas*—these differences were briefly touched on in Wang et al. (2014), and deserved greater scrutiny.

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Short Communication

On the distribution, taxonomy, and natural history of the Indian Smooth Snake, *Coronella brachyura* (Günther, 1866)

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***Abstract.*—The Indian Smooth Snake *Coronella brachyura* is one of the least studied endemic species of snake from India with regard to distribution, taxonomy, and natural history. In the present study, we verified literature, museum specimens and distributional records which enabled us to correct erroneous reports and map the distribution of this species. Additionally, we provide information on taxonomy, morphology, microhabitat, and behavior of the species based on three live specimens and voucher specimens in the collection of the Bombay Natural History Society, Mumbai.**

Key words. Colubridae, endemic, India, rare, morphology, scalation

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Members of colubrid snake genus *Coronella* Laurenti, 1768 are among the least studied snakes across the world. The genus is represented by three species namely *C. austriaca* Laurenti, 1768, *C. girondica* (Daudin, 1803), and *C. brachyura* (Günther, 1866) (Wallach et al. 2014; Uetz and Hošek 2015). The former two species are distributed in western Palaearctic (from southern Norway in the north to northern Algeria in the south; Portugal in the west to northern Iran in the east) and the latter, endemic to India (Wallach et al. 2014; Uetz and Hošek 2015). Günther (1866) described this species from Poona (Pune) in the Indian state of Maharashtra. Subsequently, the species was reported from several localities based on which the distribution range of the species was considered to be restricted to three states in the western part of India namely; Maharashtra, Gujarat, and Madhya Pradesh. Reported localities from Maharashtra state are: "Wun, S. E. Berar" (now Wani, Yavatmal district) referred by Blanford (1870), Anderson (1871), Theobald (1876), Boulenger (1890), Sclater (1891), and Wall (1923); Chink Hill and Kurduwadi in Solapur district (Lindberg 1932); Visapur, Ahmednagar district (Gharpurey 1935); Marole (Andheri)—Salsette Islands, Mumbai (Abdulali 1935); Nashik (Mistry 2005); Melghat, Amravati district (Nande and Deshmukh 2007); Latur, Latur district (Kamble 2010); Khed, Pune district (Ghadage et al. 2013), and Jalna (Z. Mirza, pers. comm.). Furthermore, the species was reported from Gujarat state (Vyas and Patel 2007) and Ujjain, Madhya Pradesh state (Ingle and Sarsavan 2011). Sarasin (1910) referred to this species but did not provide any specific localities. Whitaker and Captain (2004) gave the range of this species as "few localities in Maharashtra." According to Smith (1943) the range of this species is "Northern India. Poona district and Visapur, near Bombay; S. E. Berar," however, it is unclear why he included "Northern India" in its range. In the recent past, we came across three live individuals of *C. brachyura* from Surat, Gujarat. Based on museum specimens, published literature, and additional data from live individuals we provide additional morphological and distributional data, as well as natural history observations for this poorly known species.

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Material and Methods

Three live specimens (two females and one male: field number assigned as: NCS 01-03) rescued by snake rescuers and brought to us (they were photographed, examined, and released at the same locality within a few days), and seven specimens catalogued in the museum of Bombay Natural History Society (BNHS), Mumbai as *Coronella brachyura* from six localities were also examined. The pholidosis and morphometric data of museum specimens and live specimens are given in Table 1.

Ventral scales were counted following the method proposed by Dowling (1951). Head measurements of voucher specimens were measured with a digital calliper to the nearest 0.01 mm and other body measurements were recorded with string and a ruler to the nearest mm. Descriptions and mensural characters were compared with available literature (Smith 1942; Mistry 2005; Vyas and Patel 2007). The number of dorsal scale rows were counted at approximately one head length behind the head, midbody, and one head length before the vent, respectively. Subcaudal counts reported here do not include the terminal scute. The supralabials touching the eye are given in brackets after the number of supralabials. Values for symmetric head characters are given in right/left order. Abbreviations used to describe scalation and other comparable characters are: V, ventrals; SC, subcaudals; D, dorsal rows; SL, supralabials; L, loreal; PrO, preocular; PO, postocular; T, temporal; IL, infralabial; SVL, snout-ventral length; TaL, tail length; TL, total length; HL, head length; and HW, head width.

Results

Morphology and coloration: Head short, comprising 2.3% of total length; longer than wide (HL/HW ratio: 1.55); slightly distinct from neck; eyes circular with round pupil; nostrils large; body circular. Dorsal color of live individuals was olive brown, with indistinct light variegation on head and forebody (Fig. 1); labials pale olive; lateral scale rows dark brown, forming indistinct lateral stripe on each side from nostril to tail, which is prominent between nostril to eye; underside cream white.

Lepidosis: Dorsal scale rows (DSR) smooth, in most specimens 23:23:19 (23:23:21 in BNHS 3407; 23:23:17 in NCS 2); with single apical pit on the posterior margin. Ventrals 209–237 (maximum 224 *fide*. Smith 1943); anal undivided; subcaudals 43–54 (46–53 *fide*. Smith 1943); rostral wider than high, scarcely visible from above; 2 internasals, wider than long; 2 prefrontals, as long as wide, longer than the internasals; frontal bell shaped, slightly longer than wide; parietals longer than wide, slightly longer than frontal; 1 loreal, as long as high, rarely longer than high; 1 preocular reaching top of head; 2 postoculars; 2 anterior temporal scales; 2, rarely 1 posterior temporal scale(s); 8, sometimes 9 (8 *fide*. Smith 1943) supra-

Fig. 1. Dorsal aspect of *Coronella brachyura* in life, from Surat, Gujarat, India.

Fig. 2. Lateral aspect of *Coronella brachyura* (NCS 2); a, left side showing 8 supralabials and 5th supralabial partly divided; b, right side showing 9 supralabials, 4–6th touching eye.

labials, the 4th and 5th, sometimes 5th and 6th and rarely 4th to 6th (4th and 5th *fide*. Smith 1943) touch the eye (Fig. 2); 9–11 infralabials.

Fig. 3. BNHS 794, collected by Abdulali (1935) from Mumbai, India.

Distribution: The present study and published records (Günther 1866; Blanford 1870; Anderson 1871; Theobald 1876; Boulenger 1890; Scarlet 1891; Wall 1923; Lindberg 1932; Gharpurey 1935; Smith 1943; Whitaker and Captain 2004; Mistry 2005; Vyas and Patel 2007; Nande and Deshmukh 2007; Ingle and Sarsavan 2011; Ghadage et al. 2013) shows that the species is narrowly distributed in western India (Table 2).

Four museum specimens BNHS 793, 796, 798, and 3407 were examined. Two specimens BNHS 795 and 797 were damaged; therefore unable to examine for pholidosis and morphometric data. The specimen BNHS 794 (Fig. 3) from Marol, Mumbai collected and reported as *C. brachyura* by Abdulali (1935); was re-examined by the senior author. It had 23 scale rows at mid body; 217 ventrals; anal scale damaged; 96+ subcaudals, divided; 8 supralabials; 1 presubocular; 2+3 temporals; and measured 285 mm total length. All these characters clearly matched with *Argyrogena fasciolata* (Shaw, 1802). The coloration of this specimen has faded likely due to long

Table 1. Scale counts, measurements (mm), and collection details for specimens of *Coronella brachyura*.

Specimen No	**BNHS 793**	**BNHS 796**	**BNHS 798**	**BNHS 3407**	**NCS 1**	**NCS 2**	**NCS 3**
Locality	Visapur, Ahmednagar, Maharashtra	Talegaon, Pune, Maharashtra	Bhopal, Madhya Pradesh	Piplod, Surat, Gujarat	Surat, Gujarat	Piplod, Surat, Gujarat	Piplod, Surat, Gujarat
Date	—	October 27, 1956	July 1945	March 2006	December 5, 2012	February 12, 2014	Feburary 17, 2014
TL	375	523	507	495	410	620	560
SVL	322	447	443	445	360	552	480
TaL	53	66	64	50	50	68	80
D	23:23:19	23:23:19	23:23:19	23:23:21	23:23:19	23:23:17	23:23:19
V	221	216	209	237	223	223	220
A	Undivided	Undivided	Undivided	Undivided	Undivided	Undivided	Undivided
SC	45	49	47	45	47	43	54
SL	9(5,6)/8(4,5)	8(4,5)/8(4,5)	8(4,5)/8(4,5)	8(4,5)/8(4,5)	9(5,6)/8(4,5)	9(4 to 6)/8(4,5)	8(4,5)/8(4,5)
L	1/1	1/1	1/1	1/1	1/1	1/1	1/1
IL	10/10	9/10	10/10	9/9	10/10	11/11	9/9
PreO	1/1	1/1	1/1	1/1	1/1	1/1	1/1
PO	2/2	2/2	2/2	2/2	2/2	2/2	2/2
T	2+2/2+2	2+2/2+2	2+2/2+2	2+1/2+1	2+2/2+2	2+2/2+2	2+2/2+2
Sex	ND=Not Determined	ND	ND	ND	Female	Female	Male

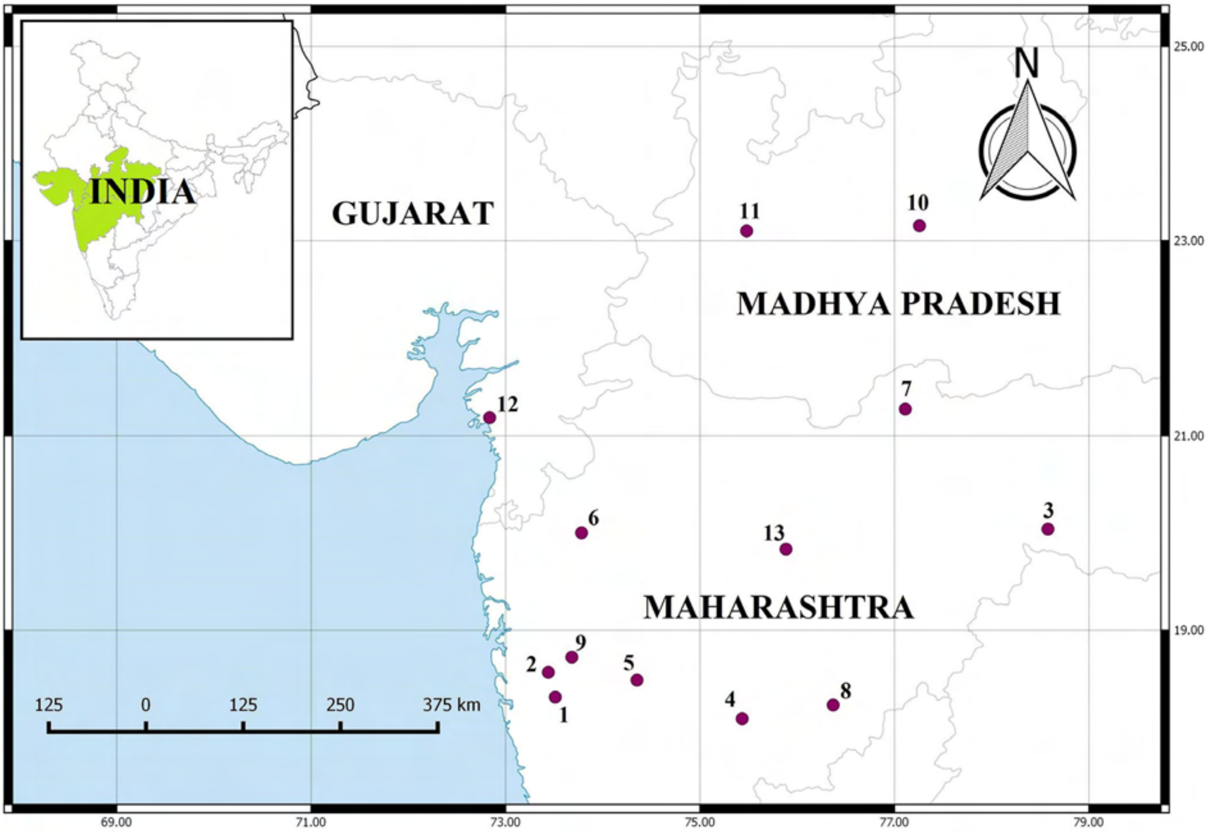

Fig. 4. Map showing distribution range of *Coronella brachyura* (For all the localities: 1–13, reference Table 2).

term preservation. However, it shows remains of 27+ vestigial whitish bands in the forebody which became paler in posterior half and became indistinguishable—which is found in juveniles of *A. fasciolata*. Based on our observations we here conclude that the specimen cited by Abdulali (1935) is conspecific with *A. fasciolata* and is an erroneous report from Mumbai, and should be removed from the known distribution range of *C. brachyura*.

Vyas and Patel (2007) collected *C. brachyura* from Surat, Gujarat and in the same publication they also presented two more localities (Ahmedabad and Bhavnagar) from Gujarat based on photographs of a striped snake which they attributed to *C. brachyura*. However, specimens were not available to the authors and hence the exact identity of specimens from these two localities remains in question. Fresh specimens are needed to confirm the presence of *C. brachyura* from these localities.

Habit, habitat, and natural history: *Coronella brachyura* are found in plains and hillocks; majority of known localities are situated around 500 m a.s.l. The species appears to occur in a wide range of habitats from arid scrub lands to dry deciduous forests; they are also found in human habitations. Two live individuals (NCS 02 and 03) were found in a water body near a newly developing urban area; NCS 01 was found near a water body. The specimens were active during day time and did not show any aggression when handled. Live individuals were kept for a few days; juveniles of *Hemidactylus* sp. were offered food but none accepted. However, some authors reported that the species feeds on juvenile geckos in captivity (Whitaker and Captain 2004; Ingle and Sarsavan 2011).

Discussion

Distribution: Our observations coupled with published information of the species shows this endemic species is widely distributed encompassing a geographical area of 2,80,000 sq. km across three Indian states, namely Maharashtra, Madhya Pradesh (west), and Gujarat (south), only (Fig. 4). This has a very similar distribution range recorded in another endemic colubrid snake, *Psammophis longifrons* (Vyas and Patel 2013).

Conservation status: *Coronella brachyura* is legally protected as a Schedule IV species under the Indian Wildlife Protection Act of 1972 and categorized as Least Concern by the IUCN Red List of Threatened Species (Srinivasulu et al. 2013). During the study no specific threats to the species were observed, except the general threats to the reptilian fauna as reported by Vyas (2007), including expansion of urbanization, agricultural lands, habitat loss, and habitat alteration, and large numbers of snakes killed by laymen due to fear.

Taxonomy: The genus *Coronella* has shown to be paraphyletic based on molecular data from western Palaeart-

Table 2. List of localities for *Coronella brachyura* based on new collections or observations[1], examined specimens[2], literature or database records,[3] and photographic records.[4]

No	Locality	Coordinates	Elevation, m a.s.l.	District	State
1	Pune[2,3]	18.31°N 73.51°E	561	Pune	Maharashtra
2	Talegaon[2,3]	18.72°N 73.68°E	670	Pune	Maharashtra
3	Wani[3]	20.03°N 78.57°E	228	Yavatmal	Maharashtra
4	Kurduwadi[2,3]	18.08°N 75.43°E	502	Solapur	Maharashtra
5	Visapur[2,3]	18.48°N 74.35°E	620	Ahmednagar	Maharashtra
6	Nashik[3]	20.00°N 73.78°E	600	Nashik	Maharashtra
7	Melghat[3]	21.26°N 77.11°E	575	Amravati	Maharashtra
8	Latur[3]	18.23°N 76.36°E	620	Latur	Maharashtra
9	Khed[3]	18.56°N 73.43°E	715	Pune	Maharashtra
10	Bhopal[2]	23.15°N 77.25°E	527	Bhopal	Madhya Pradesh
11	Ujjain[3]	23.10°N 75.47°E	511	Ujjain	Madhya Pradesh
12	Surat[1,2,3]	21.18°N 72.83°E	13	Surat	Gujarat
13	Jalna[4]	19.83°N 75.88°E	489	Jalna	Maharashtra

ic species by recent workers (Pyron et al. 2010, 2013; Utiger et al. 2002). Recently, Hoser (2012) removed *C. brachyura* from the genus *Coronella* and allocated it to the genus *Wallophis*; it was earlier suggested by Werner (1929). In doing so, Hoser (2012) did not provide any valid taxonomic characters to support partitioning the genus *Coronella*. *Coronella brachyura* differs from its congeners by the higher number of scale rows at mid body (23 vs. 21 in *C. girondica* and 19 in *C. austriaca*); by the higher number of supralabials (8–9 vs. 7 in *C. austriaca* and 8 in *C. girondica*). However, the status of Indian taxa remains unresolved as there is no comparative study on the morphology or molecular data of *Coronella* with other colubrid genera. We believe for now, the Indian species should be considered as a member of the genus *Coronella*. Future studies involving detailed comparison of the genus *Coronella*, with the aid of molecular techniques, will be essential for the correct allocation of Indian species.

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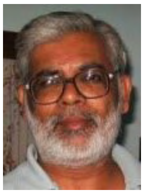

Raju Vyas is an enthusiastic herpetologist, presently working at the Sayaji Baug Zoo, Vadodara-Gujarat, India as a Zoo Biologist. After his post graduate education in Zoology, he pursued a doctorate in philosophy, his research dissertation titled "Snakes of Gujarat State," from Bhavnagar University, Gujarat-India (1995). For almost two decades, he has extensively explored the natural heritage of Gujarat state and its territorial extensions contributing significantly toward the enrichment of base line data on amphibian and reptiles of the state. Apart from his exposure to *ex-situ* conservation, he's active in breeding many native reptilian species. Presently, his activities include conservation of urban wildlife, especially Mugger Crocodiles, and has an affiliation with the Vishwamitri River Project, Vadodara Municipal Corporation, Vadodara. Raju has been monitoring the urban crocodile population in Gujarat and has published several reports about the same. Lastly, Raju is optimistically promoting mitigation measures for man-animal conflicts locally and nationally.

Shantilal K. Tank is a Professor at the Department of Biosciences, Veer Narmad South Gujarat University, Surat. For the past two decades Dr. Tank has worked in the fields of environmental toxicology, bioremediation, and ichthyology. Recently, he works in biodiversity documentation and conservation.

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Cover: A juvenile Lined House Snake (*Bothrophthalmus lineatus*) caught in a funnel trap in closed canopy lowland evergreen forest during a herpetological survey of the West Nimba Nature Reserve, Nimba County, Libera (07° 29'33.0"N, 008° 41'59.5"W, 432 m a.s.l., 19 November 2011). *Photograph: Bill Branch.*

Instructions for Authors: Located at the *Amphibian & Reptile Conservation* website: http://amphibian-reptile-conservation.org/submissions.html

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