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DOI

[10.1643/CH-06-233](https://doi.org/10.1643/CH-06-233)

Publication date

2008

Published in

Copeia

[Link to publication](#)

Citation for published version (APA):

Blackburn, D. C., Kosuch, J., Schmitz, A., Burger, M., Wagner, P., Gonwouo, N. L., Hillers, A., & Rödel, M.-O. (2008). A new species of *Cardioglossa* (Anura: Arthroleptidae) from the Upper Guinean forests of West Africa. *Copeia*, 2008(3), 603-612. <https://doi.org/10.1643/CH-06-233>

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A New Species of *Cardioglossa* (Anura: Arthroleptidae) from the Upper Guinean Forests of West Africa

David C. Blackburn¹, Joachim Kosuch², Andreas Schmitz³, Marius Burger⁴, Philipp Wagner⁵, L. Nono Gonwouo⁶, Annika Hillers⁷, and Mark-Oliver Rödel⁸

We describe a new frog species of the genus *Cardioglossa* from the Upper Guinean forests of West Africa. *Cardioglossa occidentalis*, new species, is found in primary rainforests in Ghana, Ivory Coast, Guinea, Liberia, and Sierra Leone. We demonstrate that this species is morphologically and genetically distinct from *C. leucomystax*, the species to which these populations were previously assigned. *Cardioglossa occidentalis* differs from similar congeners by the following combination of markings: fusion or near fusion of all three dorsal lobes (cephalic, scapular, and lumbar); prominent white line extending anteriorly from arm terminates ventral to eye; dark mask extending posteriorly from eye continues unbroken beyond posterior border of scapular lobe; lateral body covered in very few, large dark spots rimmed with thin white. *Cardioglossa occidentalis* appears related to *C. leucomystax*, *C. melanogaster*, and *C. schioetzi*. This description brings the number of *Cardioglossa* species to 16.

Nous décrivons une nouvelle espèce de grenouille du genre *Cardioglossa* de forêt tropicale du bloc de la Haute Guinée de l'Afrique de l'Ouest. *Cardioglossa occidentalis*, espèce nouvelle, est trouvée dans les forêts primaires de Ghana, Côte d'Ivoire, Guinée, Libéria, et Sierra Leone. Nous démontrons que cette espèce est morphologiquement et génétiquement distincte de *C. leucomystax*, l'espèce auxquelles ces populations ont été classées précédemment. *Cardioglossa occidentalis* diffère des autres espèces de *Cardioglossa* par la combinaison des caractéristiques suivantes: la fusion (ou presque fusion) de chacune des trois macules dorsales (céphalique, scapulaire, et lombaire); la ligne blanche proéminente étendant antérieurement du bras se termine ventral de l'œil; le masque foncé étendant postérieurement de l'œil continue ininterrompu au delà du cadre postérieur de la macule scapulaire; le corps latéral est couvert de très peu, grandes taches qui sont bordées d'un linéament blanc. Parmi *Cardioglossa*, *C. occidentalis* semble être très proche à *C. leucomystax*, *C. melanogaster*, et *C. schioetzi*. Cette description apporte le nombre d'espèces de *Cardioglossa* à 16.

THE Upper Guinean forest zone of West Africa contains many endemic anuran species and is recognized as one of the world's most important biodiversity hotspots (Myers et al., 2000; Brooks et al., 2002; Stuart et al., 2004). In many cases, anuran species endemic to the Upper Guinean rain forests have close relatives in the forests of Central Africa (Rödel and Ernst, 2000; Rödel et al., 2002). Some are members of genera that are more diverse in the latter region (Gartshore, 1984), in particular the highlands of Cameroon and adjacent Nigeria, e.g., *Petropedetes* (Amiet, 1973a), *Astylosternus* (Amiet, 1977), and *Cardioglossa* (Amiet, 1972a). While most *Cardioglossa* species are found in Cameroon, only a few species are endemic to other regions. In this paper we contribute to the understanding of the anuran fauna of the Upper Guinean forests through the description of a previously unrecognized species of *Cardioglossa*. Ironically, more is published on the

natural history of this new species than on any other *Cardioglossa* species (Lamotte, 1961; Rödel et al., 2001).

The genus *Cardioglossa* comprises 15 currently recognized species (Amiet, 1972a, 1981; Ohler, 1999; Herrmann et al., 2004; Blackburn, 2005; Frost, 2007). Of these 15 species, only three are found beyond the lowland and montane forests of Cameroon and immediately adjacent countries. *Cardioglossa aureoli* is known only from the Freetown Peninsula in Sierra Leone (Schioetz, 1964a; A. Barrie and T. Papenfuss, pers. comm.; A. Hillers and M.-O. Rödel, unpubl. data), whereas *C. cyaneospila* is found in the mountains of Burundi, Rwanda, and easternmost Democratic Republic of Congo (Laurent, 1950). Of all *Cardioglossa* species, *C. leucomystax* has been believed to occupy the largest geographic range, encompassing the forests of Central Africa, including Cameroon, Central African Republic, Congo, Democratic Republic of Congo, Equatorial Guinea,

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Submitted: 29 September 2006. Accepted: 4 December 2007. Associate Editor: T. W. Reeder.

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Gabon, and Nigeria (Schjötz, 1963; Largen and Dowsett-Lemaire, 1991; Frétey and Blanc, 2000; Burger et al., 2006; M.-O. Rödel, unpubl. data), and the Upper Guinean forest zone of West Africa (Rödel et al., 2001). In this paper, we demonstrate that populations from forests west of Benin, previously recognized as *C. leucomystax*, represent a morphologically, genetically, and possibly ecologically distinct species. The geographic range of *C. leucomystax* remains larger than that of any other *Cardioglossa* species.

MATERIALS AND METHODS

Specimen preparation followed standard procedures, as provided in Rödel and Ernst (2002). Measurements were taken with a dial caliper (± 0.1 mm) or with an ocular micrometer in a dissecting microscope (± 0.1 mm, Zeiss Stemi SV 6). All measurements are given in mm (snout-vent length: SVL). Geographic position was taken from The Global Gazetteer (<http://www.fallingrain.com/world>) or collected with a GPS receiver. Osteological study was conducted through a digital radiographic analysis using a Thermo Kevex digital x-ray (Model PXS10) in combination with a PaxScan amorphous silicon sensor array (Model 4030R) and ViVa version 2.0 (Varian Medical Systems, Inc.). Institutional abbreviations are as listed in Leviton et al. (1985).

We analyzed 496 base pairs (bp) of mitochondrial 16S ribosomal DNA (GB = GenBank number) from all available *Cardioglossa* species: two *Cardioglossa aureoli*, four *C. leucomystax*, four *C. gracilis*, six *C. pulchra*, one *C. gratiosa*, one *C. elegans*, and seven individuals of the new West African species.

DNA was extracted using either QIAamp or DNeasy tissue extraction kits (Qiagen). We used the primers 16SA and 16SB of Palumbi (1991) or 16SC and 16SD (Pauly et al., 2004) to amplify approximately 560 bp of the 16S rRNA gene. Standard PCR protocols were used and PCR products were purified using QIAquick purification kits (Qiagen). Purified templates were directly sequenced using an automated sequencer (ABI 377). Sequences were validated using the computer program Sequence Navigator (Applied Biosystems), aligned using the Clustal option in QuickAlign 1.6, and refined by eye. Uncorrected pairwise sequence divergence was calculated using PAUP* (vers. 4.0b10, D. L. Swofford, PAUP*: phylogenetic analysis using parsimony [*and other methods], Sinauer, Sunderland, MA, 2002).

Cardioglossa occidentalis, new species

Figures 1B, 1C, 2, 3A

Cardioglossa leucomystax Guibé and Lamotte, 1958; Lamotte, 1961; Hughes, 1988; Rödel and Branch, 2002; Rödel and Bangoura, 2004; Rödel and Ernst, 2004; Rödel et al., 2004, 2005.

Cardioglossa leucomystax (part) Rödel et al., 2001.

Holotype.—SMNS 9632.2, adult male, Ivory Coast, Taï National Park, transect 1, at the bank of a small creek in swampy, primary rainforest, 05°50'03.5"N, 007°20'57.0"W, 30 March 2000, G. Schorr.

Paratypes.—Ghana: SMNS 12328, male, Draw River, 5°09'41.95"N, 2°23'31.16"W, 23 October 2003, A. C. Agyei and R. Ernst; MVZ 244911 (GB: EF621777), Western Region,

Ankasa Conservation Area, 5°16'1"N, 2°36'5"W, 28 June 2004, A. D. Leache, R. Diaz, and M. K. Fujita; ZMB 70371 (GB: EF641006), female, Kakum National Park, 05°26.819'N, 001°24.873'W, forest with swampy area and stream, 11 August 2005, A. C. Agyei and A. Hillers. Guinea: MHNG 1039.87–88, males, MHNG 1039.91–92, females, Monts Nimba, Ya Forest, Zouguépo Forest, forests near Dolomou, 1956/1957, M. Lamotte and J.-L. Perret; SMNS 123231, juvenile, Mont Béro Classified Forest, 08°08'20.7"N, 08°34'23.7"W, river and gallery forest, 4–5 December 2003, M. A. Bangoura and M.-O. Rödel; ZMB 70372 (GB: EF641002), female, other data as SMNS 123231; SMNS 12329–30, Simandou, approximately 6 km from Banko village, approximately 1.5 km within forest reserve, 08°31.499'N, 08°56.204'W, primary forest along river, 650 m a.s.l., 4 December 2002, M. A. Bangoura and M.-O. Rödel. Ivory Coast: PEM A7398 (GB: EF641003), male, Haute Dodo Classified Forests, 4°43'–5°22'N, 6°56'–7°25'W, W. R. Branch and M.-O. Rödel; SMNS 9632.1, 9632.3, 2 males, 30 March 2000, other data as holotype; SMNS 9633.1–5, 1 male, 4 females, Taï National Park, near Guiroutou, 5°25'N, 7°10'W, primary rainforest, April 1996, M.-O. Rödel; SMNS 9634.1–3, 1 male, 2 females, Taï National Park, primary rainforest near SRET station, 05°49'59.8"N, 007°20'32.6"W, April/May 1999, R. Ernst and M.-O. Rödel; SMNS 9635, male, April/May 1999 (call recording), R. Ernst and M.-O. Rödel, other data as holotype. Liberia: ZMB 70374 (GB: EF641007), male, Gola National Forest, 7°27.352'N, 10°41.483'W, small stream in a somewhat swampy area within forest, 30 November 2005, A. Hillers; ZMB 70375 (GB: EF641005), female, Grebo National Forest, 5°24.108'N, 7°44.011'W, sandy stream with temporary puddles in mature secondary forest with thick undergrowth, 7 December 2005, A. Hillers; ZMB 70376, male, North Lorma National Forest, 8°02.043'N, 9°43.970'W, swampy forest on sandy soil, stream with rocky bed, 22 November 2005, A. Hillers. Sierra Leone: FMNH 83121–22, North Kambry, 15 January 1957, J. I. Menzies.

Non-type material.—Ivory Coast: ZMB 70373, tadpole, transect 1, river bed in leaf litter, 12 June 2002, M.-O. Rödel, other data as for holotype; T01.22 (GB: EF641004), tissue sample without corresponding voucher, other data as for holotype. Liberia: MNHN 1998–2629, juvenile, 12 mm, Monts Nimba, Grassfield, 7°29'20"N, 8°34'1"W, forest.

Diagnosis.—The new species differs from other *Cardioglossa* by the following unique combination of markings: fusion or near fusion of all three dorsal lobes (cephalic, scapular, and lumbar); infratympanal white line extending anteriorly from arm and terminating ventral to eye (Fig. 3); dark mask, rimmed with thin white line, extending posteriorly from eye and continuing unbroken posteriorly until reaching posterior border of dorsal scapular lobe; lateral body covered in very few, large dark spots rimmed with thin white line; belly covered in loose array of lightly colored spots, sometimes surrounded by ill-defined white line. Unlike *C. melanogaster* and *C. schioetzi*, the first and second vertebrae are unfused in *C. occidentalis* (as in *C. leucomystax*).

Description.—Body shape elongate; elongate, rounded snout and long extremities (Figs. 1–3); canthus rostralis almost rounded; tympanum large and prominent; distance between eyes approximately equal, or slightly less, than maximum

Fig. 1. (A) Type locality and typical breeding habitat of *Cardioglossa occidentalis* in the primary rainforest of Taï National Park, Ivory Coast. (B) Male *Cardioglossa occidentalis* (SMNS 12330, paratype) from Pic de Fon in southeastern Guinea; photo: Piotr Naskrecki. (C) Male *Cardioglossa occidentalis* from Guinea (not collected, photo: Piotr Naskrecki). (D) Female *Cardioglossa leucomystax* (ZMB 70393) from Dzanga-Sangha forest reserve, Central African Republic.

diameter of eye; nostril widely separated from eye, located very near to tip of rostrum; skin of snout, loreal region, dorsal and ventral surfaces appears smooth; dorsal skin slightly granular; neither finger nor toe tips significantly enlarged; feet lack webbing; palmar surface of hands exhibits prominent, almost conical palmar tubercle; femur approximately equal in length, or slightly shorter than tibia; third digit of manus in males elongate, more than twice length of second finger; third finger of males with prominent spines along proximodistal axis of medial surface (holotype—right hand, 29 spines; left hand, 26 spines); spines begin near metacarpal-phalangeal joint and reach finger tips; most distal part of finger typically exhibits double row of spines; base of second digit of manus exhibits two much smaller spines on lateral surface; in males most caudal region of dorsum, inguinal area, and dorsal part of proximal thigh densely covered with small, grayish white conical spines.

Coloration.—Holotype is grayish brown (Fig. 2); dorsum exhibits dark hourglass-like pattern, comprising three lobes: cephalic, scapular, and lumbar (following Amiet, 1972b); cephalic lobe diamond-shaped, stretching caudally from the rostrocaudal midline of the eyelids to the level of the arm; cephalic lobe separated by a small gap from the immediately

caudal, larger scapular lobe; scapular lobe also diamond-shaped, situated on the rostral half of the dorsum, and fused with the lumbar lobe; lumbar lobe has the appearance of a fat, compressed “V” with the apex pointing rostrally; small dark spots scattered irregularly over the dorsum; two dark brown transverse bars, each bordered by a thin white line on the forearm, thigh, leg, and ankle; posterior surface of thigh exhibits thick, black, irregularly shaped line running proximodistally; loreal region with dark black mask that extends caudally along lateral surface of the rostrum behind the arm to approximately behind scapular lobe of dorsum; mask completely covers tympanum and broken into a few large black spots along the posterior lateral surface; mask and large black spots all rimmed by a thin white line; this line is most conspicuous along the ventral border of the mask terminating immediately ventral to eye; a black inguinal spot extends dorsally onto the most posterolateral surface of dorsum; ventral surface bears large irregularly shaped brownish blotches on a brownish-gray background; these blotches also present, but slightly obscured, on the brownish-violet colored throat of males; color pattern in alcohol is only slightly faded.

The basic color of both males and females varies from gray to a deep brown. The size and shape of the dorsal lobes

Fig. 2. Holotype of *Cardioglossa occidentalis* (adult male, SMNS 9632.2) in dorsal, ventral, and lateral view; photos: J. Penner.

varies but are usually fused in an hourglass pattern. In several specimens, there is a narrow gap between the first and the second lobe, as in the holotype. The rostral lobe often exhibits three tips pointing rostrally, thus resembling a crown. Both the scapular and lumbar lobes can be notched caudally such that they appear as a “V” with the apex pointed rostrally. The number, size, and arrangement of additional, smaller dark spots vary on the dorsum. The number and size of black spots on the lateral surfaces also vary but generally are large in size and few in number (compare Figs. 1–3, and fig. 2 in Rödel et al., 2001 for variation). In comparison to males, females exhibit a gular region that is typically lighter in color but do not show any obvious differences in the coloration of the belly. In several females, the ventral surface is predominantly white and the black spots are comparatively small.

Measurements of holotype (in mm).—Snout–vent length 26.9; head width 7.2; femur length 11.4; tibia length 11.8; eye diameter 2.5; tympanum 1.6; interorbital distance 3.0; distance from nostril to tip of rostrum 0.8; distance from nostril to eye 2.3; radioulna length 6.5; first finger length 3.6; second finger length 3.9; third finger length 8.4; fourth finger length 2.2; first toe length 1.8; second toe length 2.7; third toe length 4.8; fourth toe length 7.2; fifth toe length 3.4; anteroposterior length of inner metatarsal tubercle 1.1.

Variation.—Female *C. occidentalis* are larger than males (Mann–Whitney U-test, $Z = -3.784$, $P < 0.001$, $n = 25$,

Table 1). The finger tips of females are swollen, whereas the toe tips are slightly expanded.

Vocalization.—The advertisement call is a loud, high whistle that is given either alone or in a series and can be heard from a distance of at least 50 m. Males also emit a ‘warble’ call which can only be heard from within 5 m. The dominant frequency of the advertisement call is 4.1 kHz with two weaker harmonics at 2 and 6.2 kHz (Rödel et al., 2001).

Distribution.—*Cardioglossa occidentalis* is known from the rainforest zone in Ghana, Ivory Coast, Liberia, Guinea, and Sierra Leone (Fig. 4) where it occurs from lowland forests ascending to approximately 650 m a.s.l. (Guibé and Lamotte, 1958; Rödel et al., 2001, 2004, 2005; Rödel and Bangoura, 2004; Hillers and Rödel, 2007). This species is very common in western Ivory Coast and south-eastern Guinea, but seems rarer or absent in other parts of the Upper Guinean Forest Zone as neither Schiøtz (1964a, 1964b, 1968) nor Lamotte (1971) recorded it. The type locality of *C. occidentalis* was chosen such that it is in the middle of the distribution of this species.

Natural history.—*Cardioglossa occidentalis* occurs predominantly in primary and some secondary rainforests, and is closely associated with flowing water (Rödel et al., 2001). This species is often found at sites with sandy soil and heavy accumulation of leaf litter (Fig. 1A). Males call predominantly in primary forest, usually within 2 m of brooks in which puddles tend to remain during the dry season; mean chorus size ranges from 11 to 19 calling males (Rödel et al., 2001). Most calling activity occurs at night, especially between 2100 and 0100 h. Males call from February to November (end of dry season throughout the whole rainy season), with most calling males observed between September and October (core rainy season; Rödel et al., 2001). A captive female laid a clutch of 33 white eggs that were 2.5–2.8 mm in diameter (3.0 mm including egg capsule; Rödel et al., 2001). The smallest juvenile in Taï National Park was 6 mm SVL and juveniles were recorded throughout the whole year. Lamotte (1961) reported that tadpoles of *C. occidentalis* are found in ponds in the forest which seems unusual as males call near streams. We found tadpoles of this species in the accumulated leaf litter of small streams. For more details of the natural history of *C. occidentalis* see Rödel et al. (2001).

Tadpoles.—Tadpoles are notable for their very small eyes that are positioned laterally, the absence of labial teeth, and a spiracle that projects posteriorly as a transparent funnel. Tadpoles are dorsoventrally depressed and have a tail that is more than twice the body length (Guibé and Lamotte, 1958; Lamotte, 1961). Our morphological findings are in accordance with the descriptions of these authors.

Etymology.—The name is chosen in reference to the geographic range of this species, which occurs throughout the Upper Guinean forests of West Africa.

DISCUSSION

Amiet (1981) proposed a close phylogenetic relationship between *Cardioglossa leucomystax*, *C. melanogaster*, and *C. schiøetzi*. *Cardioglossa occidentalis* is most similar to these species and especially to *C. leucomystax*, for which it was so

Fig. 3. Right lateral view of the head of various *Cardioglossa* species. (A) *Cardioglossa occidentalis*, new species (MVZ 244911; paratype). (B) *Cardioglossa leucomystax* (MCZ A46628). (C) *Cardioglossa melanogaster* (MHNG 1253.86; holotype). (D) *Cardioglossa schioetzi* (ZMUC R076631; paratype). (E) *Cardioglossa gratiosa* (MHNG 1253.85; holotype). (F) *Cardioglossa elegans* (UTA 44472). Scale bar equals 1 millimeter.

far mistaken. *Cardioglossa occidentalis* most obviously differs from *C. leucomystax* by the white infratympanal line which in *C. occidentalis* terminates immediately ventral to the eye (Fig. 3). In *C. leucomystax*, this line extends anterodorsally to the nostril. *Cardioglossa occidentalis* also differs from nearly all *C. leucomystax* specimens examined, in that the dark

loreal mask continues unbroken farther posteriorly and is broken into fewer and larger spots along the posterior lateral surface. *Cardioglossa leucomystax*, especially females (Fig. 1D), tends to have many more and comparatively smaller lateral spots than *C. occidentalis*. However, specimens of *C. leucomystax* collected in northeastern Democratic

Table 1. Measurements of *Cardioglossa leucomystax* and *C. occidentalis*, New Species. Given are mean (min–max) values in parentheses when only SVL and spine measures were taken; SVL = snout–vent length; HW = head width; F = femur length; T = tibiofibula length; E = eye diameter; TD = tympanum diameter; EE = interorbital distance; EN = distance from the anterior eye to the external naris; NS = distance from the external naris to the tip of the rostrum; LPD = length of pedal digit 1; MT = anteroposterior length of inner metatarsal tubercle; S = number of spines on third finger.

Species (sex)	n	SVL	HW	F	T	E	TD	EE	EN	NS	LPD	MT	S
<i>C. leucomystax</i> (females)	3 (17)	31.6 (27.0–38.8)	8.1 (7.3–9.4)	13.7 (12.1–14.8)	14.8 (13.5–17.2)	2.6 (2.5–2.8)	1.3 (1.2–1.5)	3.0 (2.8–3.2)	2.2 (2.0–2.7)	1.0 (0.9–1.2)	3.1 (2.5–3.8)	1.3 (1.0–1.8)	0
<i>C. leucomystax</i> (males)	2 (35)	26.8 (24.9–30.3)	6.5–7.3	13.3	13.8–14.2	2.2–2.5	1.3–1.4	2.5–3.0	1.6–2.0	0.8–0.9	2.4–2.5	1.0–1.1	14.4 (0–21)
<i>C. occidentalis</i> (females)	10 (12)	30.0 (26.2–31.9)	8.5 (7.2–9.7)	12.8 (10.2–15.1)	13.2 (11.6–15.1)	2.6 (2.2–3.0)	1.6 (1.4–2.0)	3.4 (2.8–3.7)	2.1 (1.8–2.4)	1.1 (0.9–1.3)	2.5 (1.9–3.0)	1.6 (1.1–1.9)	0
<i>C. occidentalis</i> (males)	10 (24)	26.1 (25.4–27.3)	7.8 (7.2–8.3)	11.4 (10.4–12.9)	12.0 (11.2–13.2)	2.6 (2.4–2.8)	1.5 (1.4–1.8)	3.0 (3.0–3.2)	2.1 (1.8–2.3)	0.9 (0.8–1.1)	1.8 (1.5–2.2)	1.0 (0.9–1.1)	22.1 (5–30)

Republic of Congo (MCZ A-21728–29, A-46629–31) exhibit few lateral spots and a mask that continues more or less unbroken to about the same anteroposterior level seen in *C. occidentalis*. In addition, two juvenile *C. leucomystax* (MCZ A-46625, A-46633) exhibit a mask that continues completely unbroken from the snout tip to the inguinal region, which indicates that there might be an ontogenetic change in this feature. Most *C. occidentalis* have much fewer and larger ventral spots than *C. leucomystax*. In general, *C. leucomystax* males show a tendency of being slightly larger than *C. occidentalis* males (Mann–Whitney U-test, $Z = -1.667$, $P = 0.095$, $n = 43$). *Cardioglossa leucomystax* females may reach larger sizes than *C. occidentalis* females; however, these differences are not significant (Mann–Whitney U-test, $Z = -1.685$, $P = 0.092$, $n = 29$; Table 1).

The dorsal markings of *C. leucomystax* and *C. occidentalis* differ from the probably closely related *C. melanogaster* and *C. schioetzi*. In the latter species, the dorsal cephalic lobe is not fused to the scapular lobe, whereas these are fused or almost fused in *C. leucomystax* and *C. occidentalis* (Amiet, 1972a, 1972b, 1981). In addition, in both *C. melanogaster* and *C. schioetzi* the white line extending rostrally from the level of the arm passes ventrally to the eye and then forms a slight sigmoid as it curves dorsally and terminates just posterior to the external naris (Fig. 3). This differs from the pattern in *C. leucomystax* in which the white line continues dorsally and joins with the white line continuing anteriorly from the anterior margin of the eyelid. Other *Cardioglossa* species with a dorsal hour-glass-like pattern are *C. gracilis*, *C. elegans* and *C. nigromaculata*. In these species the cephalic lobe is always separated from the scapular and lumbar lobes. In *C. gracilis*, the white line dorsal to the upper lip continues anteriorly to the external naris, forming a less pronounced sigmoid, and is often difficult to differentiate from the white upper lip of this species. Similar to *C. occidentalis*, a lateral white line extending anteriorly from the arm terminates ventral to the eye in *C. nigromaculata* and *C. gratiosa*. The overall dorsal pattern in *C. elegans* and *C. nigromaculata* is distinctly different from *C. occidentalis*. This white line is absent in *C. alsco*, *C. aureoli*, *C. cyaneospila*, *C. oreas*, *C. pulchra*, *C. trifasciata*, and *C. venusta*; it is variably present in *C. escalerae* in which it is absent in two specimens examined (TNHC 38697, 47889) but weakly visible and terminating ventral to the eye in the other two specimens examined (TNHC 38698, 47888). In *C. occidentalis*, the tympanum is large, easily visible, and pigmented as it is in all other *Cardioglossa* except *C. oreas* in which it is small and difficult to discern.

The holotypes of *C. melanogaster* and *C. schioetzi* are males with elongate manual third digits. Both specimens exhibit strongly developed spines that appear only along the medial surface of the third finger. Additional male specimens of *C. melanogaster* (MCZ A-137906, A-137907) and *C. schioetzi* (MCZ A-137914, A-147915, A-137926) also exhibit weakly developed spines on the medial surface of the second finger. In contrast, *C. leucomystax* and *C. occidentalis* males have spines lining the medial surface of the third finger and the lateral surface of the second finger. The spines on the third finger of *C. leucomystax* and *C. occidentalis* are arranged in a double row on the most distal fourth to third part of the fingers. *Cardioglossa occidentalis* males have more spines ($5-30$, $x: 22.1 \pm 6.8$ sd, $n = 24$) than *C. leucomystax* males ($0-21$, $x: 14.4 \pm 4.5$ sd, $n = 35$; Mann–Whitney U-test, $Z = -4.560$, $P < 0.001$, $n = 59$; Table 1). Spines on the elongate third finger also occur in most other arthroleptid frogs.

Fig. 4. Distribution of *Cardioglossa occidentalis*. Star = type locality, Tai National Park, SRET Station; 1 = North Kambry (unknown locality); 2 = Gola National Forest; 3 = North Lorma National Forest; 4 = Pic de Fon Classified Forest; 5 = Mount Bero Classified Forest; 6 = Monts Nimba, forêt du Ya; 7 = Monts Nimba, Zougouépo Forest; 8 = Monts Nimba, forests near Dolomou; 9 = Monts Nimba, Grassfield; 10 = Diécké Classified Forest (7°22'–7°39'N, 8°47'–9°06'W); 11 = Grebo National Forest; 12 = Cavally Classified Forest (5°50'–6°11'N, 7°32'–7°51'W); 13 = Tai National Park, near Guiroutou; 14 = Haute Dodo Classified Forest; 15 = Boi Tano Forest Reserve (5°30'40"N, 2°38'48"W); 16 = Ankasa Conservation Area; 17 = Draw River Forest Reserve; 18 = Kakum National Park; for exact locations of other sites see type series and non-types.

The advertisement call of *C. occidentalis* is similar to that of *C. leucomystax* but is distinguished by its slower pulse rate and different harmonics; the dominant frequency of the advertisement call of these two species is nearly identical (Amiet, 1973b; Rödel et al., 2001). *Cardioglossa schioetzi* also has a dominant frequency and harmonics similar to that of *C. occidentalis*, but differs by having a pulse rate that is faster than both this species and *C. leucomystax* (Amiet, 1981). The call structure of *C. melanogaster* is very similar to *C. schioetzi*, but it is more complex than all of these species by having at least three harmonics and combining a trill with a whistle (Amiet, 1973b).

Levels of DNA sequence divergence between *C. occidentalis* and *C. leucomystax* were inferred using data from the mitochondrial 16S ribosomal RNA gene. DNA sequence divergence between *C. occidentalis* and *C. leucomystax* is $8.2 \pm 0.4\%$ (7.6–9.3%, $n = 31$). This level of divergence is similar to that between *C. leucomystax* and all other available *Cardioglossa* included in our analysis (7–11%). Sequence divergence within *C. leucomystax* populations ranges from 0–4.1% ($2.3 \pm 1.7\%$, $n = 6$), whereas it is less than 2% ($0.6 \pm 0.6\%$, 0–1.6, $n = 27$) within the *C. occidentalis* examined.

Cardioglossa occidentalis is not only similar to *C. leucomystax* in appearance, but also in biology. Whereas many

Central African *Cardioglossa* seem to prefer higher elevation, both *C. leucomystax* and *C. occidentalis* are widespread in lower elevation forest. Males of *C. occidentalis* form choruses of approximately the same size as *C. leucomystax* (Amiet, 1972a) and seem to occupy similar ecological niches: small streams in forests on predominantly sandy soils (Lawson, 1993; Burger et al., 2004). *Cardioglossa leucomystax* and *C. occidentalis* may differ ecologically. *Cardioglossa occidentalis* mainly reproduces in the rainy season and prefers primary forest (Rödel et al., 2001). In contrast, *C. leucomystax* is assumed to reproduce in the dry season (Amiet and Perret, 1969; De la Riva, 1994) and occurs in both primary and secondary forests (Perret, 1966; Amiet, 1975; but see Lawson, 1993; De la Riva, 1994).

Currently, only two *Cardioglossa* species are known from the Upper Guinean Forest Zone: *C. aureoli* and the widespread *C. occidentalis*. *Cardioglossa aureoli* is believed to be endemic to the Freetown peninsula in Sierra Leone. Molecular, morphological, and life history data all point to *C. aureoli* as being very divergent from other *Cardioglossa* and possibly more closely related to other arthroleptid genera (18–21% DNA sequence divergence between *C. aureoli* and other *Cardioglossa* species included in our analysis; D. C. Blackburn, J. Kosuch, A. Hillers, and M.-O. Rödel, unpubl. data).

The specific distinctiveness of the formerly western populations of *C. leucomystax*, herein described as *C. occidentalis*, does not come as a surprise. The separation of Upper and Lower Guinean forests has resulted in the evolution of various species pairs in West and Central Africa, e.g., toads "*Bufo* (= *Amietophrynus sensu* Frost et al. [2006]) *tuberosus* group" (Rödel and Ernst, 2000; Tandy and Perret, 2000); hyperoliid treefrogs *Acanthixalus* (Rödel et al., 2003), and all sylvicolous *Hyperolius* and *Leptopelis* species (Schiotz, 1967); ranid frogs "*Amnirana* (= *Hydrophylax sensu* Frost et al. [2006]) *asperima*" and "*A. fonensis*" (Perret, 1977; Rödel and Bangoura, 2004); vipers of the *Atheris squamigera* group (Ernst and Rödel, 2002); Royal and Dwarf Antelopes (*Neotragus pygmaeus*, *N. batesi*; Hernández Fernández and Vrba, 2005); small carnivores like Johnston's Genet (*Genetta johnstoni*) and Aquatic Genet (*G. piscivora*; Gaubert et al., 2004); Otter Shrews (*Micropotamogale* spp.); and bats including *Rhinolophus* spp. (Fahr et al., 2002). The high genetic differences (2%) between populations of *C. occidentalis* from the Ghanaian and the Ivorian/Liberian/Guinean populations, respectively, are in accordance with the postulated existence of Pleistocene forest refugia near Monts Nimba and southwestern Ivory Coast as well as in western Ghana (Falk et al., 2003; Wieringa and Poorter, 2004; Rödel et al., 2005). Future study of other anuran species from the forests of West and Central Africa will continue to shed light on the evolution of faunae in these forests.

MATERIAL EXAMINED

Cardioglossa alsco. See type series in Herrmann et al. (2004) and Herrmann et al. (2005).

Cardioglossa aureoli. Sierra Leone: ZMUC R075881, male holotype, 22.4 mm, ZMUC R075885, male paratype, 20.5 mm, ZMUC R075586, female paratype, 23.6 mm, Freetown; CAS 230187, female, 24.1 mm, Freetown; ZMB 70389–90 (GB: EF640989 and EF640990), males, 16.6 and 16.7 mm, WAPFR near Wildlife Sanctuary.

Cardioglossa cyaneospila. Burundi: KU 154326, male, 31.0 mm, Bururi.

Cardioglossa elegans. Cameroon: UTA A44472, male, 23.5 mm, tissue in the Ambrose Monell Cryo Collections at the AMNH: AMCC 177611 (GB: EF621776), Southwest Province, Ntale Plateau. Gabon: IRSNB 251-P, 252-P, 253-P, 24.4, 18.6, and 13 mm, Estuary Province, Kinguéle, SEEG hydroelectric dam; IRSNB 510-P, 511-P, 28.8 and 23.3 mm, Woleu-Ntem Province, Haut-Komo Département, Song; IRSNB 762-P, 31.1 mm, Ogooué-Lolo Province, Offoué-Onoy Département, eastern flank of Mount Iboundji.

Cardioglossa escalerae. Cameroon: TNHC 38697–8, males, 24.6, 25.7 mm, Center Province, Ototomo Forest Reserve; TNHC 47888–9, males, 25.4, 26.5 mm, Center Province, Mt. Kala.

Cardioglossa gracilis. Cameroon: MCZ A-5605, female, 35.1 mm, Metet; MCZ A-35766, male, 32.2 mm, Foullassi; MCZ A-136796 (GB: EF621774), male, 31.5 mm, Southwest Province, Ntale Plateau; MVZ 234675 (GB: EF621773), male, 33.8 mm, Fopouanga; UTA A44454, female, 31.4 mm, tissue in the Ambrose Monell Cryo Collections at the AMNH: AMCC 117617 (GB: EF621775), Southwest Province, Ntale Plateau. Central African Republic: ZMB 70392 (GB: EF640994), female, 40.4 mm, Dzanga-Sangha Forest Reserve, Bayanga. Gabon: IRSNB 540-P, 32.4 mm, Ogoulou Département, Ngounié Province, Diyanga. Nigeria: ZMB 70391, female, 35.8 mm, Oban plateau.

Cardioglossa gratiosa. Cameroon: MHNG 1253.85, male holotype, 22.7 mm, Center Province, Mt. Kala, Ongot; MCZ A-3425, female, 33.7 mm, Metet; MCZ A-5595, male, 24.1 mm, Metet; ZMB 70421, male, 29.0 mm, Southwest Province, Mt. Manengouba. Central African Republic: ZMB 70388 (GB: EF641001), male, 24.2 mm, Dzanga-Sangha Forest Reserve, Bayanga. Democratic Republic of Congo: ZMB 70387, male, 26.7 mm, Lokutu area.

Cardioglossa leucomystax. Cameroon: MCZ A-2470, male, 26.7 mm, Dja River; MCZ A-20972, 27.4 mm, Southwest Province, Eschobi; MCZ A-20973, 29.4 mm, MCZ A-20974, male, 24.9 mm, Southwest Province, Makumunu; MVZ 234676 (GB: EF621772), female, 33.5 mm, MVZ 234677, male, 27.3 mm, West Province, Fopouanga; UTA A44585, female, 28.6 mm, Southwest Province, Ediensoa; UTA A52321, male, 30.5 mm, East Province, west of Nanga Eboko along the Tédé River; ZFMK 81628 (GB: EF640993), female, 32.0 mm, Littoral Province, Mt. Nlonako, Ekomtolo. Central African Republic: ZMB 70394 (GB: EF640991), male, 27.0 mm, ZMB 70395, male, 25.9 mm, ZMB 70393, female, 32.4 mm, Dzanga-Sangha Forest Reserve, Bayanga. Democratic Republic of Congo: MCZ A-21727, male, 28.8 mm, MCZ A-21728–9, juveniles, 23.0, 26.1 mm, MCZ A-21730, male, 28.4 mm, Buta, Bas Velé; MCZ A-21731, juvenile, 24.7 mm, Djamba; MCZ A-46622, male, 30.3 mm, MCZ A-46623, female, 35.1 mm, Kivu Province, Katuka; MCZ A-46624, male, 27.1 mm, MCZ A-46625, juvenile, 12.1 mm, Kivu Province, Abyalose Riviere; MCZ A-46626–28, females, 38.8, 31.8, 32.1 mm, Kivu Province, Semliki River; MCZ A-46629–30, A-46632, female, 32.0, 32.3, 38.1 mm, MCZ A-46631, male, 27.3 mm, MCZ A-46633, juvenile, 15.7 mm, Kivu Province, Samboko River. Gabon: IRSNB 827-P, 31.6 mm, Ngounié Province, Boumi-Louétsi Département, Itsiba; PEM A MB 20325 (field number M. Burger, GB: EF640992), Moukalaba-Doudou National Park. Nigeria: ZMB 70422, female, 29.2 mm, Oban plateau.

Cardioglossa melanogaster. Cameroon: MHNG 1253.86, male holotype, 24.6 mm, Southwest Province, Mwakoumele; MCZ A-137906, MCZ A-137907, males, 28.5, 26.6 mm, Southwest Province, Nsoug.

Cardioglossa nigromaculata. Cameroon: MHNG 1521.50, male, 24.2 mm, Nkunjock.

Cardioglossa oreas. Cameroon: MHNG 1253.87, female holotype, 26.7 mm, West Province, Mt. Bamboutos.

Cardioglossa pulchra. Cameroon: MHNG 1521.58, male, 26.6 mm, MHNG 1521.59, male, 28.5 mm, Southwest Province, Mt. Manengouba, Nsoug; ZMB 70423 (GB: EF640999), ZMB 70424 (GB: EF641000), ZMB 70425, female, 27.8 mm, ZMB 70426 (GB: EF640995), male, 27.9 mm, ZMB 70427 (GB: EF640996), ZMB 70428, female, 34.0 mm (GB: EF640997), ZMB 70429 (GB: EF640998), ZMB 70430, male, 27.0 mm, ZMB 70431, male, 24.8 mm, ZMB 70432, male, 30.2 mm, all Southwest Province, Mt. Manengouba. Nigeria: ZMUC R072173, male holotype, 29.5 mm, Ogoja Province, Obudu Plateau; ZMB 70385, female, 31.2 mm, ZMB 70386, male, 29.9 mm, Obudu Cattle Ranch.

Cardioglossa schioetzi. Cameroon: MCZ A-137914, MCZ A-147915, males, 24.2, 24.4 mm, West Province, Mt. Mbam; MCZ A-137926, male, 27.0 mm, Northwest Province, Elak-Oku. Nigeria: ZMUC R076631, male paratype, 27.3 mm, Obudu Plateau.

Cardioglossa sp. Cameroon: MCZ A-136933, male, 23.9 mm, Southwest Province, Mt. Manengouba.

Cardioglossa trifasciata. Cameroon: MHNG 1253.88, male holotype, 28.4 mm, Southwest Province, Mt. Manengouba, Nsoung.

Cardioglossa venusta. Cameroon: MHNG 1253.89, male holotype, 29.3 mm, Southwest Province, Fotabong.

ACKNOWLEDGMENTS

We thank A. Barrie, M. Gartshore, A. Leaché, A. Onadeko, T. Papenfuss, and O. Pauwels for access to their vouchers and field notes. J. Penner prepared Figure 2. J. Fahr provided many mammal examples for West and Central African species pairs. The ministries responsible for research and access to national parks in Cameroon, Central African Republic, Ivory Coast, Ghana, Guinea, Liberia, and Sierra Leone provided access and all necessary collection and exportation permits. Conservation International and WWF–Central Africa helped with infrastructural and financial support. We thank all the curators of the various herpetological collections from which we obtained specimens on loan. This study is part of the BIOLOG program of the German Ministry of Education and Science (MOR; BMB+F; Project W08 BIOTA-West, FZ 01 LC 00410) and ongoing research to understand arthroleptid diversity (DCB; Museum of Comparative Zoology, Harvard University, and AmphibiaTree, U.S. National Science Foundation). This support is gratefully acknowledged.

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