



<https://doi.org/10.11646/zootaxa.4429.3.3>

<http://zoobank.org/urn:lsid:zoobank.org:pub:75A5698E-758E-473A-AE16-5118880AA412>

A taxonomic review of the genus *Hemiphractus* (Anura: Hemiphractidae) in Panama: Description of Two New Species, Resurrection of *Hemiphractus panamensis* (Stejneger, 1917), and Discussion of *Hemiphractus fasciatus* Peters, 1862

ROBERT L. HILL¹, KATHRYN G. MARTIN², EDWARD STANLEY³ & JOSEPH R. MENDELSON III^{1,2}

¹Zoo Atlanta, 800 Cherokee Ave SE, Atlanta, GA 30315, USA. E-mail: rhill@zoatlanta.org; jmendelson@zoatlanta.org

²School of Biological Sciences, 950 Atlantic Dr., Georgia Institute of Technology, Atlanta, GA 30332, USA.

E-mail: kmartin4991@gmail.com

³Florida Museum of Natural History, 1659 Museum Rd., University of Florida, Gainesville, FL 32611, USA.

E-mail: mr.tedd@gmail.com

Abstract

We reviewed the taxonomic status of populations of frogs in the genus *Hemiphractus* in Panama, which have all been referred to *Hemiphractus fasciatus* Peters, 1862 for over 40 years. Although relatively few specimens have been collected, mostly juveniles, it is clear that these frogs inhabit three separate upland regions of the country: The Cordillera de Talamanca in western Panama, the Chagres Highlands and Cordillera de San Blas in central Panama, and the Serranía de Pirre in the far eastern portion of the country. In accordance with previously published molecular data, we identified distinctive features of the skulls of frogs representing these three allopatric populations and herein revalidate *H. panamensis* (Stejneger, 1917), describe the new species *Hemiphractus elioti* **sp. nov.** from the Cordillera de Talamanca, and the new species *Hemiphractus kaylockae* **sp. nov.** from the Serranía de Pirre. We also propose that the taxon *H. fasciatus* is a South American species not occurring in Panama.

Key words: Colombia, Ecuador, *Hemiphractus elioti*, *Hemiphractus kaylockae*, taxonomy

Resumen

Revisamos la situación taxonómica de las poblaciones de ranas del género *Hemiphractus* en Panamá, las cuales han sido referidas a *Hemiphractus fasciatus* Peters, 1862 durante más de 40 años. Aunque se conocen relativamente pocos ejemplares, la mayoría jóvenes, está claro que estas ranas habitan tres regiones separadas de elevaciones medias: La Cordillera de Talamanca al Oeste de Panamá, las Tierras Altas de Chagres y la Cordillera de San Blas en el centro de Panamá, y la Serranía de Pirre en el extremo oriental del país. En concordancia con datos moleculares previamente publicados, identificamos características distintivas de los cráneos de estas ranas que representan estas tres poblaciones alopatridas. De este modo, revalidamos *H. panamensis* (Stejneger, 1917) y describimos las especies nuevas *Hemiphractus elioti* **sp. nov.**, de La Cordillera de Talamanca, y *Hemiphractus kaylockae* **sp. nov.**, de la Serranía de Pirre. Proponemos que el taxón *H. fasciatus* es una especie sudamericana que no se encuentra en Panamá.

Palabras clave: Colombia, Ecuador, *Hemiphractus elioti*, *Hemiphractus kaylockae*, taxonomía

Introduction

The morphologically distinctive species of the genus *Hemiphractus* Wagler 1828, form a monophyletic group of Neotropical frogs (Mendelson *et al.* 2000; Sheil *et al.* 2001; Wiens *et al.* 2007; Castroviejo-Fisher *et al.* 2015). *Hemiphractus* historically have ranged from Panama to Peru (Trueb, 1974), however their numbers are currently in rapid decline in some areas (Coloma *et al.* 2008), with amphibian chytridiomycosis being an especial concern (Lips *et al.* 2006). *Hemiphractus* are egg-brooding frogs with females carrying eggs and the newly hatched young on

their backs (Duellman *et al.* 1988); they lack any variant of the dorsal brood pouches of other hemiphractids, e.g., *Gastrotheca*. *Hemiphractus* species have casqued skulls, with at least some co-ossification of the overlying skin, and with distinctive paraoccipital horns (Trueb, 1974).

Peters (1862) described *Hemiphractus fasciatus*, with the holotype listed as being from the Pastaza Valley, Ecuador (in error, according to Trueb, 1974). Jiménez de la Espada (1871, *fide* Trueb, 1974: 7) described a new genus, *Cerathyla*, to accommodate the more “hylid like” of these horned frogs (i.e., *bubalus*, *fasciatus*, and *proboscideus*), in contrast to the remaining “toad like” species he retained in *Hemiphractus*. Subsequently, Stejneger (1917) described *C. panamensis*, a species that was differentiated from *H. fasciatus* based on type material collected near Santa Isabel, Prov. Colon, Panama. *Cerathyla* was placed in the synonymy of *Hemiphractus* by Noble (1926). Trueb (1974) placed *H. panamensis* in the synonymy of *H. fasciatus*, based on comparisons of similarity of the type materials. Sheil *et al.* (2001) provided a phylogenetic tree for *Hemiphractus*, based on evidence from morphology in which *H. fasciatus* was recovered as the sister species to *H. scutatus*; their material examined for *H. fasciatus* all was collected in Panama, with one specimen from Prov. Napo, Ecuador, and one from Depto. Nariño, Colombia. Recent genetic analyses (Crawford *et al.* 2012) and combined molecular and morphological analyses (Castroviejo-Fisher *et al.* 2015) also recovered the sister relationship (*H. fasciatus*, *H. scutatus*) but suggested that *H. fasciatus* as currently delimited may represent three species. The prevailing concept of the distribution of *H. fasciatus* has remained unchanged from that proposed by Trueb (1974: fig.13). She considered it to range from the isolated western, central, and eastern cordilleras of Panama, onto the Pacific slopes of the Andes of Colombia and northwestern Ecuador. Considering the results from Castroviejo-Fisher *et al.* (2015), it is possible that one of the distinct lineages they reported within “*H. fasciatus*” could bear the name *H. panamensis* (Stejneger 1917). Stejneger’s (1917) holotype is an adult female (USNM 55320), and he also described its single apparent offspring (USNM 55321), both collected in Signal Loma, 3 mi (approx. 4.8 km) S Santa Isabel, N coast of Panama, Prov. Colon. This locality lies east of the Panama Canal (completed in 1914) in a region of low to moderate uplands referred to by Myers *et al.* (2012) as the Chagres Highlands. Nevertheless, prior to the construction of the canal, the Isthmus of Panama was naturally lowland area, thus also a likely natural barrier between the populations of *Hemiphractus* in the upland areas on either side of the isthmus. In this paper, we study morphological variation among mostly Panamanian populations and, in light of genetic data from Crawford *et al.* (2012) and Castroviejo-Fisher *et al.* (2015), provide a taxonomic review of *H. fasciatus*.

Materials and methods

Specimens from the following collections were examined: AMNH, KU, UMMZ, FMNH, CNHM, UTACV, ZSM, and USNM (see Appendix; acronyms following Sabaj-Perez 2014). Specimens from the geographically isolated uplands in eastern, central, and western Panama were allocated into three batches for statistical analyses. The few specimens available to us from South America were not included in statistical analyses. We had only one specimen from Colombia and, of the two from Ecuador, one (UMMZ 55523) is in very poor condition and sex cannot be determined. On the remaining specimens, standard morphometric measurements were made to the nearest 0.1 mm with digital calipers following Sheil & Mendelson (2001); all measurements herein are reported in mm. Similarly, measurements of the skulls were made mostly following Trueb (1974; Fig 1). Morphometric measurements were log-transformed because our morphological measurements varied in scale over several orders of magnitude. A stepwise discriminate-function analysis (DFA) was used to evaluate overall multivariate morphological distinctiveness of our three a-priori designated populations. Analysis of Covariance (ANCOVA) tests were used to determine the univariate morphological distinctiveness among our focal populations. Accurate counts of vomerine and neopalatine odontoids was not possible in most cases because these frogs appear to have exceptionally strong jaw muscles and inappropriate amounts of force and cutting would be required to make careful intrabuccal observations among the few extant specimens. Morphological analyses and observations were conducted separately for males and females; small juveniles were excluded from the analyses. Sex and sexual maturity were determined by direct observation of the gonads. Unfortunately, as was the case in Trueb’s (1974) revision, most specimens available are juveniles; this limited the power of our statistical analyses. Color descriptions are based on examinations of alcohol-preserved specimens.

High-resolution computed tomography (CT) scans were produced for six specimens from Panama that were identified in museum collections and the literature as *Hemiphractus fasciatus* using a Phoenix v|tome|x M (GE’s

Measurement & Control business, Boston, USA) scanner at the University of Florida. Scanning was carried out using a 180 kv x-ray tube and a diamond-tungsten target, with the following settings: 110 kV, 200 milliamps mA, 0.3 second detector time, averaging of three images per rotation and a voxel resolution ranging from 19.5–25.8 μm . From the Cordillera de Talamanca, we examined an adult male and female, and we did the same from the specimens available from the Serranía de Pirre; only a single adult female specimen was available to represent the Chagras Highlands and Cordillera de San Blas region. The holotype of *Hemiphractus fasciatus* (ZSM 36/0, an adult female) was scanned at its home institution, the Zoologische Staatssammlung München, under the following conditions: 60kV 120mA, 0.75s detector time, no image averaging, and a voxel size of 31.99372 μm . The resulting 2D x-ray data from both labs were processed using GE's proprietary datos|x software v 2.3 to produce a series of tomogram images. These CT image stacks were then viewed, sectioned, measured, and analyzed using VG StudioMax 3.0 (Volume Graphics, Heidelberg, Germany). Final figures were prepared with Photoshop and Illustrator (CS5, Adobe). Tomograms stacks (TIF format) and shape files (STL format) are freely available for viewing and downloading at https://www.morphosource.org/Detail/ProjectDetail/Show/project_id/240: *H. elioti* UMMZ-herps-152622 doi.org/10.17602/M2/M13541, *H. elioti* AMNH-A-124113 doi.org/10.17602/M2/M13469, *H. kaylockae* UMMZ-herps-152624, doi.org/10.17602/M2/M13538 *H.kaylockae* KU-H-93506 doi.org/10.17602/M2/M13536, *H. panamensis* KU-H-116353 doi.org/10.17602/M2/M13543, *H fasciatus* ZSM-36/0 (Holotype) doi.org/10.17602/M2/M18826. Annotated figures, showing key diagnostic characters, are freely available on Sketchfab: <https://skfb.ly/6vY6M>

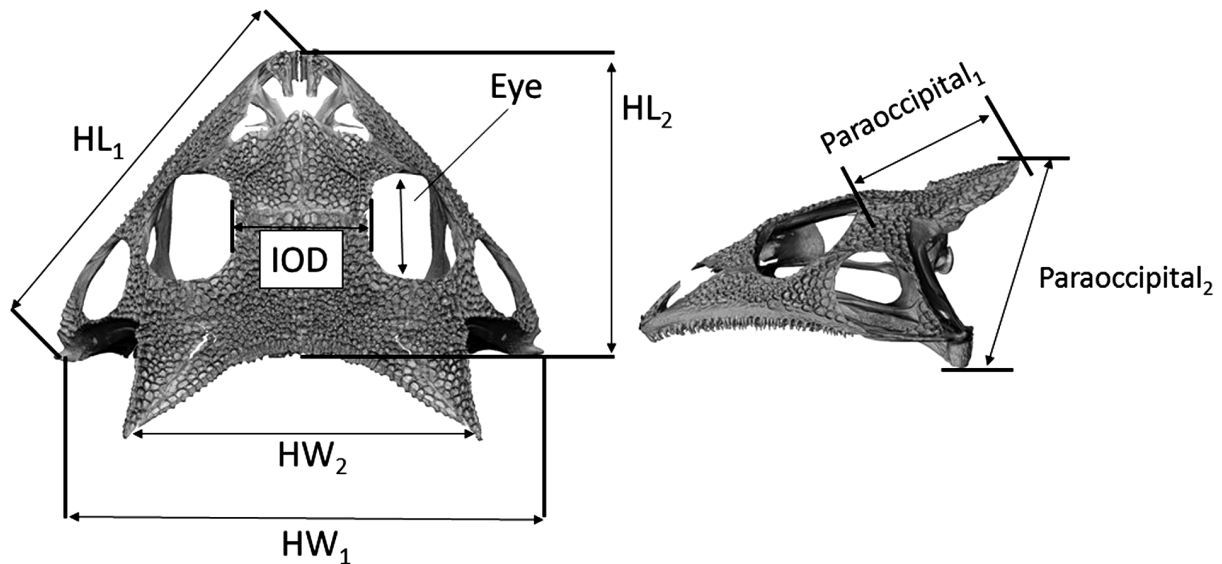


FIGURE 1. Dorsal and lateral views of the skull of *H. panamensis* (KU 116353) showing various cranial dimensions measured (modified from Trueb, 1974). Abbreviations: HL = head length; HW = head width; IOD = interorbital distance. In our study, “Eye” refers more explicitly to the longitudinal diameter of the bony orbit of the skull. Two measures of the paraoccipital process, not considered by Trueb (1974) also are illustrated.

Results

Morphometric measurements. Measurements are summarized in Table 1. The DFA for both males and females correctly classified all included specimens representing the a priori designated groups: western Panama (n = 11 males, n = 4 females), Chagras Highlands (n = 1 male, n = 3 females), and eastern Panama (n = 8 males, n = 9 females). The results of the ANCOVA tests did not identify any individual morphometric characters that differed among the three populations (results not shown). Nevertheless, we discovered discrete qualitative morphological differences (Table 2) that are consistent with the independent trajectories identified by the analyses of Crawford *et al.* (2012) and Castroviejo-Fisher *et al.* (2015). Below we present our revised taxonomy of the *Hemiphractus* species in Panama.

TABLE 1. Morphometric variation of adults of the three species of *Hemiphractus* recognized from Panama. Mean \pm 1 SD above range (in parentheses); all measurements in mm.

Variable	<i>Hemiphractus elioti</i>		<i>Hemiphractus kaylockae</i>		<i>Hemiphractus panamensis</i>	
	Males n = 11	Females n = 3	Males n = 8	Females n = 9	Males n = 1	Females n = 3
Snout–vent length	46.2 \pm 4.3 (39.5–51.3)	62.0 \pm 2.6 (59.6–64.7)	50.5 \pm 2.4 (47.6–55.6)	53.8 \pm 10.8 (33.2–65.8)	40.4	57.4 \pm 2.7 (54.4–59.3)
Tibia length	24.9 \pm 1.9 (22.3–27.2)	32.5 \pm 2.4 (30.4–35.1)	26.7 \pm 0.9 (25.6–27.9)	27.6 \pm 5.5 (18.0–34.0)	23.9	30.5 \pm 2.0 (28.2–32.0)
Foot length	22.1 \pm 1.8 (19.6–25.1)	29.1 \pm 1.0 (28.1–30.1)	24.1 \pm 1.8 (21.0–26.7)	24.5 \pm 4.6 (17.4–30.5)	19.3	25.5 \pm 2.2 (23.1–27.3)
Head length 1	21.5 \pm 2.0 (16.5–23.1)	28.5 \pm 3.3 (25.8–32.1)	22.9 \pm 1.3 (21.2–25.8)	24.7 \pm 4.8 (16.6–29.9)	20.0	26.2 \pm 0.8 (25.3–26.8)
Head length 2	18.2 \pm 1.3 (16.3–19.8)	23.1 \pm 1.6 (21.7–24.8)	19.3 \pm 0.9 (17.9–20.9)	20.1 \pm 3.6 (13.4–23.7)	16.6	21.7 \pm 1.0 (20.5–22.4)
Head width 1	24.0 \pm 1.8 (20.2–25.8)	32.1 \pm 2.6 (30.1–35.1)	25.6 \pm 1.3 (24.5–25.8)	26.9 \pm 5.6 (17.2–32.8)	21.1	31.0 \pm 2.5 (28.4–33.3)
Head width 2	21.1 \pm 2.5 (17.2–24.2)	29.1 \pm 2.5 (26.4–31.3)	22.2 \pm 2.5 (19.9–27.7)	23.3 \pm 5.1 (14.0–30.5)	16.7	26.3 \pm 0.6 (24.6–25.8)
Inter-orbital distance	8.0 \pm 0.8 (6.9–9.5)	10.8 \pm 0.9 (9.8–11.6)	8.7 \pm 0.6 (8.0–9.9)	9.3 \pm 2.1 (5.7–11.6)	7.3	10.2 \pm 1.6 (9.2–10.2)
Eyelid	4.4 \pm 0.4 (3.6–5.0)	5.6 \pm 0.1 (5.5–5.7)	4.8 \pm 0.4 (4.3–5.4)	5.1 \pm 0.8 (3.5–5.8)	9.2	4.8 \pm 0.3 (4.4–5.1)
Eye	6.0 \pm 0.6 (5.0–6.9)	7.4 \pm 0.4 (7.0–7.8)	6.2 \pm 0.3 (5.7–6.6)	6.2 \pm 1.1 (3.8–7.9)	5.5	6.8 \pm 0.5 (6.4–7.4)
Eye–nostril distance	5.8 \pm 1.2 (4.6–9.2)	6.2 \pm 0.6 (5.8–6.9)	5.5 \pm 0.4 (5.1–6.2)	5.7 \pm 1.4 (3.5–7.5)	8.1	7.1 \pm 1.5 (6.1–8.8)
Tympanum width	3.7 \pm 0.6 (2.8–4.8)	3.4 \pm 0.5 (3.0–4.0)	4.0 \pm 0.8 (2.4–5.0)	3.0 \pm 0.6 (1.9–3.6)	3.3	2.8 \pm 0.6 (2.3–3.5)
Tympanum height	5.9 \pm 0.3 (5.4–6.6)	6.4 \pm 0.7 (5.6–7.0)	6.4 \pm 0.6 (5.7–7.4)	5.9 \pm 1.2 (3.4–7.2)	5.3	5.4 \pm 0.3 (5.2–5.7)

TABLE 2. Summary of selected osteological characters among Panamanian *Hemiphractus* and *Hemiphractus fasciatus*, which we determine to be extralimital to Panama.

	<i>H. elioti</i>	<i>H. kaylockae</i>	<i>H. panamensis</i>	<i>H. fasciatus</i>
Neopalatine odontoids in contact at center of palatal region	Yes	Narrowly separated	No	No
Margin of paraoccipital horns	Straight	Indentation and angled	Straight	Straight
Supraorbital ridge	Absent or indistinct	Absent or indistinct	Present, weakly developed	Present, distinct
Canthal ridge	Absent or indistinct	Present	Present	Present
Subtemporal fenestra	Males very small, Females \sim 1/2 diameter of orbit	\sim 1/3 diameter of orbit in both sexes	1.5 times diameter of orbit in females; males unknown	\sim 1/2 diameter of orbit in females; males unknown
Lateral margin of quadratojugal in dorsal view	Not extending beyond profile of paraoccipital horns	Not extending beyond profile of paraoccipital horns	Extending beyond profile of paraoccipital horns	Not extending beyond profile of paraoccipital horns

Hemiphractus elioti new species

(Figs. 2–4, 6)

Hemiphractus panamensis Duellman 1970 [in part; for reference to specimens from western Panama.

Hemiphractus fasciatus Trueb 1974 [in part; for reference to specimens from western Panama]; Duellman 2001 [in part; for reference to specimens from western Panama]; Crawford *et al.* 2012 [in part, for samples from Río Blanco and El Copé, Prov. Coclé, and Altos de María, Prov. Panamá, Panamá]; Castroviejo-Fisher *et al.* 2015 [in part; for sample from El Copé Prov. Coclé, Panamá]; Köhler 2011 [fig. 467; in part, for map showing isolated populations in western Panama].

Holotype. UTACV A-64827, a small, adult male, obtained at Panamá: Prov. Panamá: Río María, Altos de María, N 08° 38.585', W 080° 04.357', 875 m, on 20 May 2005, by Edgardo Griffith and Heidi Ross.

Paratypes. Females: UMMZ 152622, 152623, Panama: Coclé: 6 mi [9.7 km] NNW El Copé, 600–800 m; AMNH A124114, Panama: Chiriqui: continental divide above Quebrada de Arena, 1200–1300 m. Males: AMNH A124113, A124115, Panama: Chiriqui: continental divide above Quebrada de Arena, 1200–1300 m; UMMZ 153118, Panama Coclé: 6 mi [9.7 km] NNW El Copé, on continental divide at sawmill, 600–800 m, USNM 572599, Panama: Coclé: N of El Copé.

Diagnosis. *Hemiphractus elioti* may be distinguished from all species of *Hemiphractus* except *H. fasciatus*, *H. kaylockae*, *H. panamensis*, and *H. scutatus* by not having a postorbital indentation. *Hemiphractus elioti* may be distinguished from *H. scutatus*, an Amazonian species not occurring in Panama, by its smaller size (maximum SVL in males 52.5 mm vs. 57.4 mm in *H. scutatus*; females 64.7 mm vs. 80.5 mm in *H. scutatus*; data for *H. scutatus* from Trueb 1974), and by having small expanded pads on the fingers and toes (absent in *H. scutatus*). *Hemiphractus elioti* differs from *H. fasciatus*, *H. kaylockae*, and *H. panamensis* by having neopalatine odontoids in contact with vomerine teeth at the center of the palatal region (narrowly separated in *H. kaylockae* vs. widely separated in both *H. panamensis* and *H. fasciatus*; condition unknown in *H. scutatus*; Fig. 6). *Hemiphractus elioti* further differs from *H. panamensis* and *H. fasciatus* by having approximately seven vomerine odontoids (vs. approximately two; condition unknown in *H. scutatus*; Fig. 6). *Hemiphractus elioti* may be distinguished from *H. kaylockae* by having straight margin of the lateral margins of the paraoccipital horns (with distinct indentation, forming an angular margin in *H. kaylockae*; Fig. 2); supraorbital ridges absent (evident, distinct in *H. fasciatus*, weakly developed in *H. panamensis*; Figs. 2, 9); canthal ridges usually absent or indistinct (evident, distinct in *H. fasciatus*, *H. kaylockae*, and slightly developed in *H. panamensis*; Figs. 2, 9). *Hemiphractus elioti* has a subtemporal fenestra very small in males, approximately one-half of orbit in females, whereas the fenestrae are approximately one-third diameter of the orbit in both males and females of *H. kaylockae* (Fig. 2), approximately ½ diameter of the orbit of females in *H. fasciatus* (Fig. 9; males unknown), very large, approximately 1.5 times size of orbit, in females of *H. panamensis* (Fig. 9; males unknown); lateral margins of the quadratojugals extend to level of the lateral tips of, or very slightly beyond, the paraoccipital horns in dorsal view (extending far beyond the lateral tips of the paraoccipital horns in *H. panamensis*; Figs. 2, 9).

Description of the holotype. Small, adult male, snout–vent length (SVL) 40.5 mm (not including proboscis); tibia length 22.3 mm (not including calcar); foot length 19.6 mm; head length 20.3 mm (not including proboscis); head width 20.2 mm; snout–paraoccipital process length 20.2 mm; tympanum ovoid, 5.4 mm high x 3.8 mm wide; eye diameter 5.5 mm; interorbital distance 6.9 mm; eye–tympanum distance 3.1 mm; body moderate; head large, wider than body, greatest width at level of pars articularis, bearing prominent paraoccipital processes; paraoccipital processes projecting posterolaterally in dorsal view, extending posterior to level of pars articularis; skin co-ossified over dorsal surface of skull; occipital and paraoccipital ridges present, weakly developed; supraorbital, zygomatic ridges absent; preorbital, canthal ridges barely evident, less prominent than occipital and paraoccipital ridges; canthus rostralis indistinct; loreal region flat; proboscis short, fleshy, pointed, triangular in cross section; snout angling posteriorly at less than 45° from horizontal; nostrils ovoid, slightly protuberant, projecting dorsally, slightly laterally; lips not flared. Top of head relatively flat; interorbital region 34 % head width; eye diameter 27 % head width; tympanum vertically ovoid, oriented posteriorly and slightly laterally, visible below paraoccipital processes in dorsal view, greatest diameter 1.5 times eye diameter; width of tympanum 1.2 times eye–tympanum distance; upper eyelid bearing single enlarged pointed projection and scattered smaller tubercles; interorbital, postorbital tubercles absent; skin over posterior surface of pars articularis bearing one small, fleshy tubercle. Tongue large, ovoid; vocal slits absent; mandible bearing serrations along entire length of lower jaw, with two prominent, tusk-like odontoids projecting from mentomeckelian bones. Axillary membrane absent; thoracic fold absent; dermal

folds on wrists absent; fingers long, slender, bearing enlarged distal pads; finger pads 2.6 times diameter outer metacarpal tubercle low, tripartite, diffuse; inner metacarpal tubercle ovoid, raised; relative lengths of fingers: III > IV > II > I; lateral flanges absent on fingers; forearm with scattered tubercles, low, round, bearing weakly developed lateral fringe; webbing on hands absent. Heels of adpressed hind limbs overlap; tibiotarsal articulation extending to snout when hindlimb extended; tarsal fold present, weakly developed; tibia length 55 % SVL; foot length 48 % SVL; outer metatarsal tubercle weakly developed, diffuse; inner metatarsal tubercle present, raised, ovoid; toes II–IV with prominent, lateral fringe; fringe of Toe V extending onto outer surface of base of tarsus; dorsal surface of hind limb relatively smooth, bearing irregular sets of tubercles concentrated on three transverse bands of dark-brown coloration on shank; calcar present, small; relative lengths of toes: IV > V > III > II > I; toe pads 2 x width of penultimate phalanges of digits; webbing basal. Cloacal opening directed posteroventrally at midlevel of thigh. Dorsum and flanks smooth; ventral surfaces and throat and chin irregularly granular; sacral diapophyses projecting laterally beyond transverse processes of all vertebrae; lateral termini of transverse processes of presacral vertebrae VI–VIII not co-ossified with skin (nearly to level of sacral diapophyses) and visible externally; six neural spines projecting dorsally, co-ossified with skin, visible externally. Pupil horizontal.

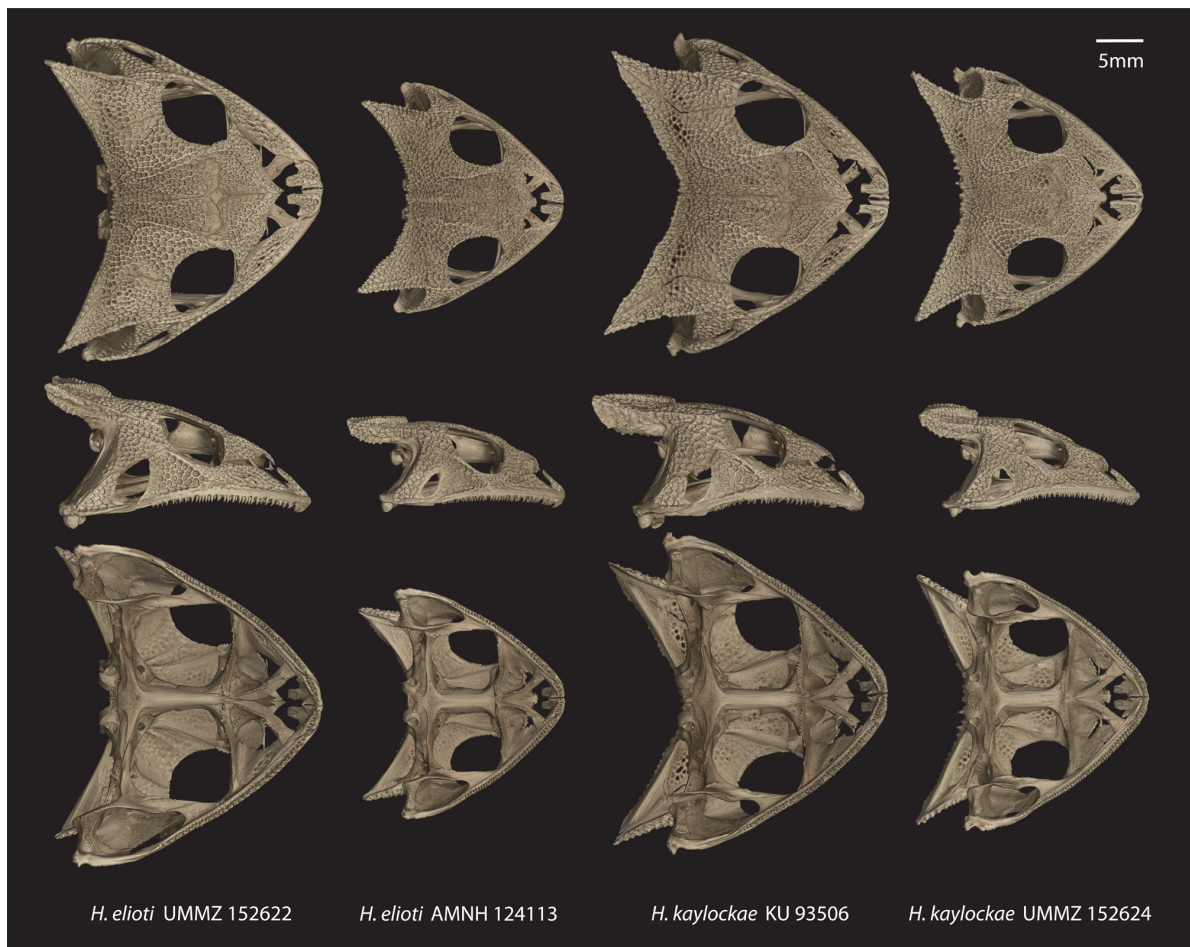


FIGURE 2. High-resolution Computed Tomography reconstructions of the skulls of *Hemiphractus elioti* new species (female: UMMZ 152622; male: AMNH 124113) and *H. kaylockae* new species (female: KU 93506; male: UMMZ 152624).

In alcohol, dorsum beige with minute black punctations (Fig. 4). Thigh and shank bearing three indistinct transverse bands of irregular, brown mottling on dorsal surfaces, corresponding with three bands of tubercles on shank only; ultimate and penultimate phalanges of toes IV–V dark brown; forearm bearing broad, brown, transverse band on dorsal surface; dorsal surface of manus more pale than forearm, ultimate and penultimate phalanges of fingers V–IV dark brown. Upper and lower lips with narrow, transverse, dark brown bands, not extending onto proximal surfaces. Flanks beige with diffuse brown punctations; venter beige with scattered diffuse, fine brown markings; throat beige with fine brown mottling. Ventral surface of forearm beige with fine, brown mottling; ventral surface of hand beige. Ventral surfaces of hind limb and foot beige with fine, pale brown mottling; toes I and II are uniformly beige, toes III–V uniformly brown.

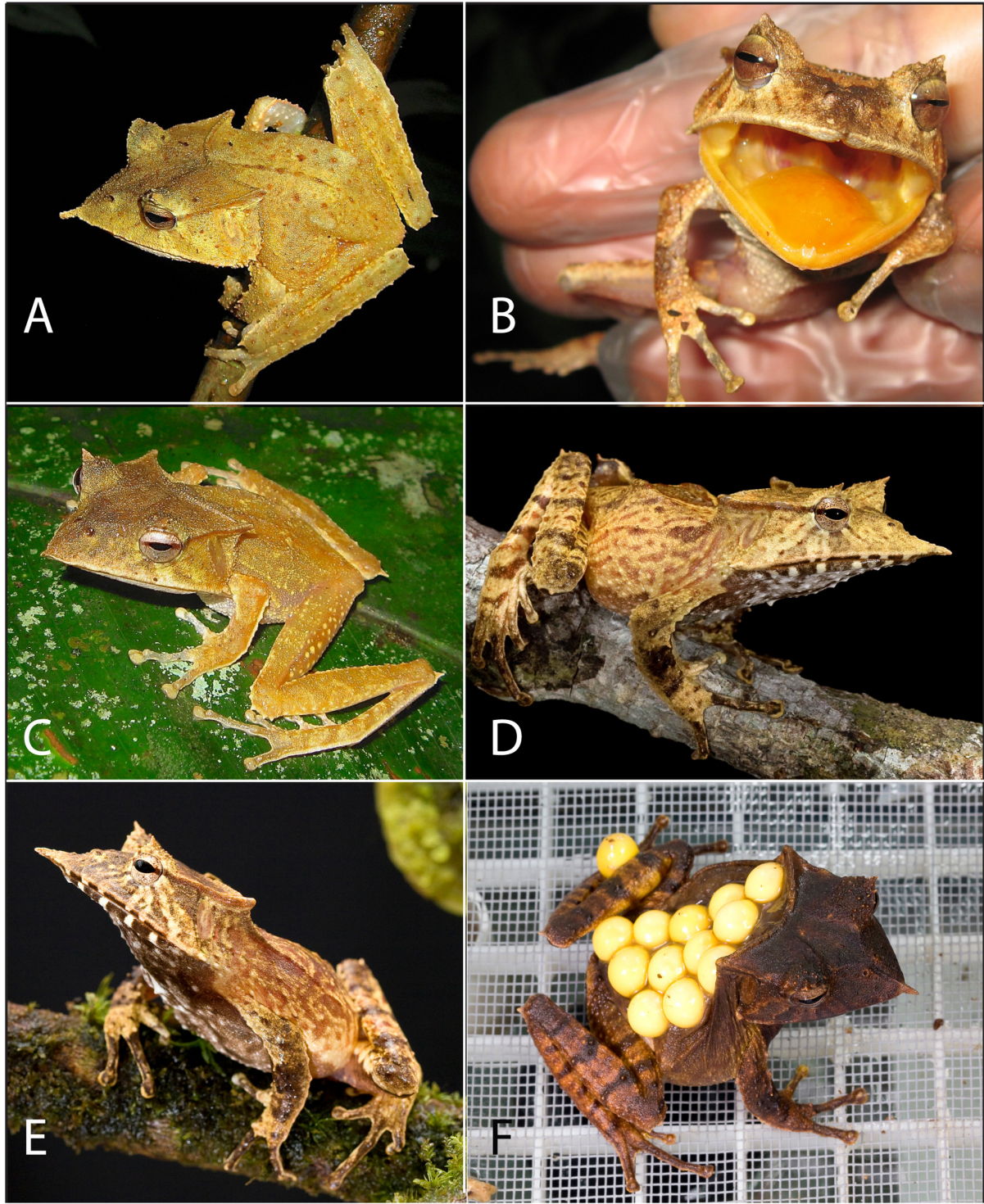


FIGURE 3. Photographs of live specimens of *Hemiphractus* from Panama. (A) Specimen of *H. panamensis* photographed *in situ* (T. Herman); sex and SVL unknown. (B) Specimen of *H. panamensis* displaying mouth gaping behavior while being handled (E. Baitchman); sex and SVL unknown. (C) Live specimen of *H. panamensis* photographed *in situ* (T. Herman); sex and SVL unknown. Specimens of *H. panamensis* all found at Cerro Brewster, Panama, Panama. (D, E) Adults of *H. elioti*, from Altos de María, near El Valle de Antón, Panama (B. Wilson, courtesy of El Valle Amphibian Conservation Center); probably males, SVL unknown. (F) Captive adult female of *H. elioti* with eggs (B. Wilson, courtesy of El Valle Amphibian Conservation Center); SVL unknown.

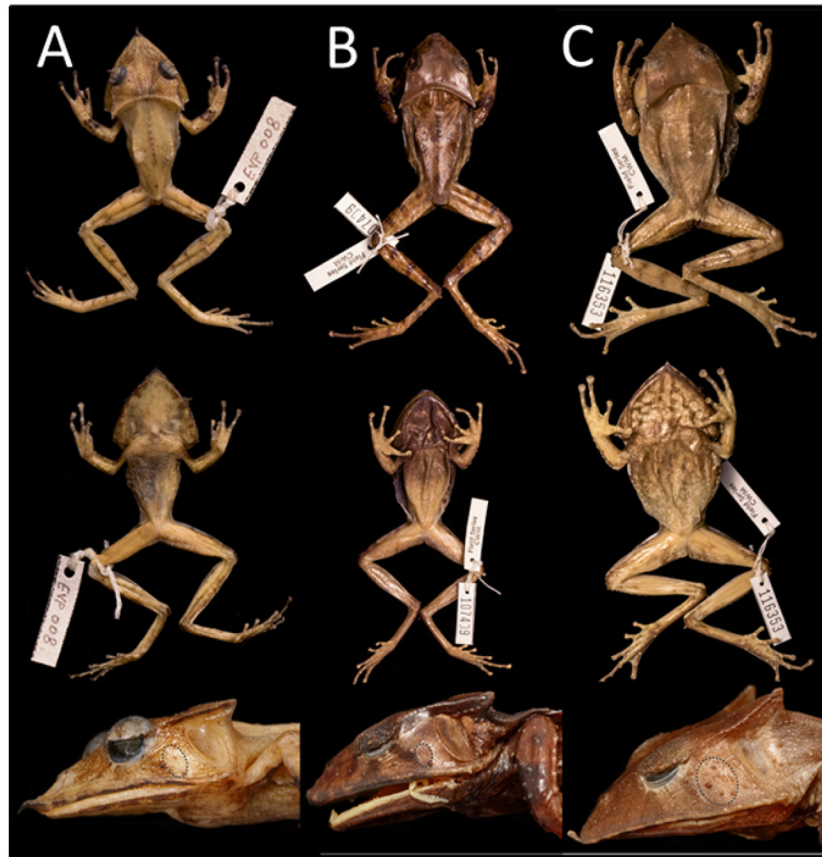


FIGURE 4. Dorsal, ventral, and lateral views of the heads and dorsal and ventral views of preserved specimens of *Hemiphractus* spp. from Panama. (A) *Hemiphractus elioti* (adult male holotype, SVL = 25.4 mm, head length = 12.0 mm). (B) *H. kaylockae* (adult female holotype, SVL = 54.2 mm, head length = 24.3 mm). (C) *H. panamensis* (adult female KU 116353, SVL = 40.4 mm, head length = 20.0 mm). The outline of the subtemporal fossae of the skulls typically are visible (and palpable) in preserved specimens; here they are delineated by dashed lines. Photographs by A. Thompson, courtesy of Zoo Atlanta.

Variation. Consistent sexual dimorphism in coloration or skin texture was not evident. Granulation of the throat in *Hemiphractus elioti* is variable among specimens examined, varying from smoothly granular with no tuberculation (e.g., USNM 153118, 297543, 572600, 572601) to smoothly granular with discrete tubercles present (e.g., AMNH 107955, 124113, 124115, UMMZ 167358, 297542, 572599). Texture of the venter ranges from smooth (e.g., UMMZ 152622, 152623) to uniformly granular (e.g., UMMZ 297543); some specimens (e.g., AMNH 107955, 124113, 124114, UMMZ 153118, USNM 297541, 297542, 572599) with granular venters also had variable numbers of discrete tubercles present. Throat coloration is highly variable, including specimens with uniform tan (e.g., AMNH 107955, USNM 297542, 297543) to uniform dark brown (e.g., AMNH 124113–15, UMMZ 152622, 152623, USNM 572599); either pattern may include a faint to prominent pale-colored stripe extending from the symphysis of the lower jaw onto the pectoral region, a speckled pattern of white and brown (e.g., USNM 572600), or a generally white ground coloration, with distinct marginal gray marbling (e.g., USNM 572601). Ventral coloration in most specimens typically is a continuation of the gular coloration of dark brown or tan extending to approximately mid-abdomen where it abruptly changes to a tan coloration (e.g., AMNH 107955, 124113–15, UMMZ 153118, 152622, 152623, USNM 572599). Ventral coloration of some specimens (e.g., USNM 297541–43) is uniformly pale tan, or white (e.g., UMMZ 167358, 572600, USNM 572601); one specimen (USNM 572600) is unique in having a speckled ventral pattern of brown and white. The dorsum is uniformly smoothly granular in all specimens and overall a uniform shade of brown. Most specimens show a single dark band on the forearm (absent or barely discernible in AMNH 107955, UMMZ 152623, USNM 297542, 297543, 572599, 572600); two or three dark transverse bands on the femoral and tibial regions (absent or barely discernible on

AMNH 10795, UMMZ 152623, 297541–43, 572599–601), and a dark band or chevron present on the sacral region (e.g., AMNH 124113–15, UMMZ 152623); in addition, specimen AMNH 124113 has a dark irregular vertebral stripe extending from the sacral band to the occiput. The posterior surface of the thigh of USNM 572599 bears a pattern of tan spots over a brown background coloration, and UMMZ 152623 has a distinct white stripe along this surface.

Etymology. Edgardo Griffith and Heidi Ross have greatly contributed to the knowledge base of the natural history, reproductive biology, and conservation of Panamanian amphibians, including *Hemiphractus*. We are proud to acknowledge the efforts of our friends and colleagues by naming this new species of *Hemiphractus* in honor of their son, Eliot. The specific epithet is the singular genitive case of the name Eliot.

Distribution and ecology. Specimens of *Hemiphractus elioti* have been collected from various localities in the Cordillera de Talamanca, including sites in the provinces of Bocas del Toro, Chiriquí, Coclé, and Panamá in western Panama (Fig. 5). Habitat is pre-montane moist primary forest ranging in elevation from 600–1600 m. Living specimens have been observed from ground level to < 1 m in vegetation at night. Coloration and morphological features provide excellent camouflage amongst leaf litter on the forest floor. Captive specimens at the El Valle Amphibian Conservation Center fed readily on other anurans, geckos (*Hemidactylus* spp.), newborn mice (*Mus musculus*), and earthworms (H. Ross and E. Griffith pers. comm., RLH pers. obs.). While dissecting specimens to determine sex, unidentified anurans were evident in the stomachs of specimens. Numerous unidentified nematode worms were also observed in the coelom and imbedded in the peritoneum and tissues of other abdominal organs. Myers (1966) described a distinctive mouth gaping behavior, yellow oral coloration, and defensive biting in specimens referable to *H. panamensis* (Fig. 3B) and *H. kaylockae* (Fig. 8C). Similar behaviors have been observed in *H. elioti*. Repeated observations of captive reproduction of this species at the El Valle Amphibian Conservation Center have shown that females carry eggs and young on their backs, as is known to occur in all described species of *Hemiphractus*.

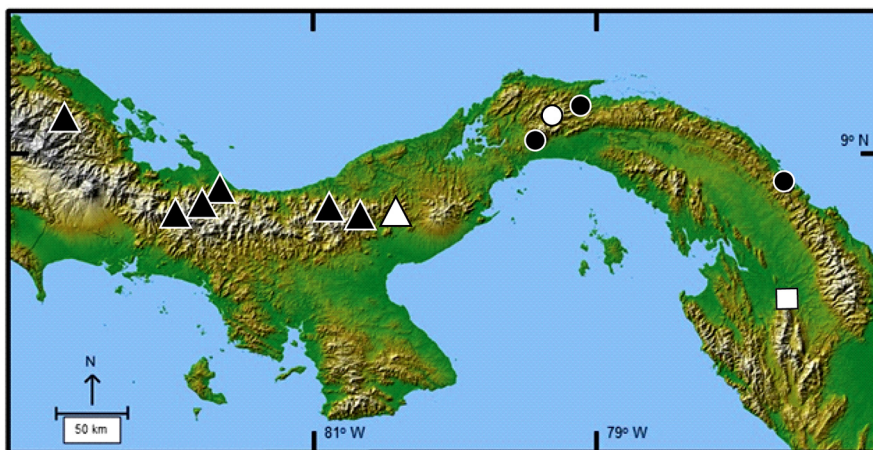


FIGURE 5. A map of the known distributions of the three species of *Hemiphractus* recognized herein, from Panama. Type localities are white symbols, black symbols represent localities for museum vouchers and photographic records (see Fig. 3). Symbols represent *H. elioti* (triangles); *H. panamensis* (circles), and *H. kaylockae* (square). At this time, we know of no confirmed records of these species from neighboring Costa Rica or Colombia, and we posit that *H. fasciatus* Peters, 1862, does not occur in Panama, but more likely is restricted to Ecuador and perhaps part of Colombia.

Hemiphractus kaylockae new species

(Figs. 2, 4, 6, 8)

Hemiphractus panamensis Duellman 1970 [in part; for reference to specimens from eastern Prov. Darién, Panamá].

Hemiphractus fasciatus Trueb 1974 [in part; for reference to specimens from eastern Prov. Darién, Panamá]; Duellman 2001 [in part; for reference to specimens from eastern Prov. Darién, Panamá]; Crawford *et al.* 2012 and Castroviejo-Fisher *et al.* 2015 [in part, for samples from Cana, Prov. Darién, Panamá]; Köhler 2011 [in part; for map showing isolated populations in extreme eastern Panama].

Holotype. KU 107409, adult female, obtained at Panamá: Prov. Darién: N ridge of Cerro Cituro, Sierra de Pirre, N 07° 56', W 77° 42' (approx.), 900–1000 m on 17 January 1966, by Charles W. Myers.

Paratypes, Males: KU 107411, 107414 Panama: Darien: N ride Cerro Cituro, Serrania de Pirre, 1000 m; KU 107419 Panama: Darien: N ride Cerro Cituro, Serrania de Pirre, 900 m; KU 154992, Panama: Darien: S slope Cerro Cituro, Serrania de Pirre, 1100 m. Females: AMNH A92668, Panama: Darien: N ridge Cerro Cituro, Serrania de Pirre, 1100 m; KU 93506, Panama: Darien: SE Slope Cerro Pirre, 1440 m; KU 107413, Panama: Darien: N ridge Cerro Cituro, Serrania de Pirre, 1000 m; KU 93507, Panama: Darien, SE slope Cerro Pirre, 1440 m.

Diagnosis. *Hemiphractus kaylockae* may be distinguished from all species of *Hemiphractus* except *H. elioti*, *H. fasciatus*, *H. panamensis* and *H. scutatus* by not having a postorbital indentation (Fig. 2). *Hemiphractus kaylockae* may be distinguished from *H. scutatus*, an Amazonian species not occurring in Panama, by its smaller size (maximum SVL in males 52.5 mm vs. 57.4 mm in *H. scutatus*; females 64.7 mm vs. 80.5 mm in *H. scutatus*; data for *H. scutatus* from Trueb, 1974), and by having small expanded pads on the fingers and toes (absent in *H. scutatus*). *Hemiphractus kaylockae* differs from *H. elioti* by having neopalatine and vomerine odontoids narrowly separated (in contact in *H. elioti*; condition unknown in *H. scutatus*), whereas these rows of odontoids are widely separated in *H. panamensis* and *H. fasciatus* (Fig. 6). *Hemiphractus kaylockae* further differs from *H. panamensis* and *H. fasciatus* by having approximately seven vomerine odontoids (vs. approximately two in both *H. panamensis* and *H. fasciatus*). *Hemiphractus kaylockae* may be distinguished from *H. elioti*, *H. fasciatus*, and *H. panamensis* by having a distinct indentation on the paraoccipital horns, forming an angular margin of the paraoccipital horns (Figs. 2, 9); supraorbital ridges absent (evident, distinct in *H. fasciatus* and weakly developed in *H. panamensis*; Figs. 2, 9); canthal ridges evident, distinct (absent or weakly developed in *H. elioti*; Fig. 2). *Hemiphractus kaylockae* has a subtemporal fenestra approximately one-third diameter of the orbit in both males and females, approximately one-half diameter of orbit in females in *H. elioti* (very small in males; Fig. 2), approximately one-half diameter of the orbit in females of *H. fasciatus* (Fig. 9; males unknown), very large, approximately 1.5 x size of orbit, in females of *H. panamensis* (Fig. 9; males unknown); lateral margins of the quadratojugals extend to level of lateral tips of, or slightly less than, beyond the paraoccipital horns in dorsal view (extending far beyond the profile of the paraoccipital horns in *H. panamensis*; Figs. 2, 9).

Description of the holotype. An adult female: SVL 54.2 mm (not including proboscis); tibia length 28.4 mm (not including calcar); foot length 25.3 mm; head length 24.3 mm (not including proboscis); head width 26.5 mm; snout-paraoccipital process length 25.1 mm; tympanum ovoid, 6.6 mm high x 3.6 mm wide; eye diameter 6.5 mm; interorbital distance 10.2 mm; eye–tympanum distance 5.4 mm; body moderate; head large, wider than body, greatest width at level of pars articularis, bearing prominent paraoccipital processes; paraoccipital processes projecting posterolaterally in dorsal view, extending posterior to level of pars articularis; skin co-ossified over dorsal surface of skull; occipital ridge present, well-developed; paraoccipital ridges present, weakly developed; supraorbital, zygomatic, preorbital, and canthal ridges absent; canthus rostralis indistinct; loreal region flat; proboscis short, fleshy, pointed, laterally flattened in cross section; snout angling posteriorly at less than 45° from horizontal; nostrils ovoid, slightly protuberant, projecting dorsally; lips not flared. Top of head relatively flat; interorbital region 38 % of head width; eye diameter 25 % head width; tympanum vertically ovoid, oriented posteriorly and slightly laterally, visible below paraoccipital processes in dorsal view, greatest diameter equivalent to eye diameter; width of tympanum 1.6 times eye–tympanum distance; upper eyelid with one enlarged pointed projection and scattered smaller tubercles; interorbital tubercle absent; postorbital tubercle absent; skin over posterior surface of pars articularis bearing one small, fleshy tubercle. Tongue large, ovoid; vocal slits absent; mandible bearing serrations along entire length of lower jaw, with two prominent, tusk-like odontoids projecting from mentomeckelian bones. Axillary membrane absent; thoracic fold absent; dermal folds on wrists absent; fingers long, slender, bearing enlarged distal pads; finger pads about 1.8 times width of digits at penultimate phalange; relative lengths of fingers: III > IV > II > I; lateral fringe on fingers absent; outer metacarpal tubercle low, ovoid; inner metacarpal tubercle ovoid, diffuse; forearm with scattered tubercles, large, pointed, variously fused to produce an evident lateral fringe; webbing on hands absent. Heels of adpressed hind limbs overlap; tibiotarsal articulation extending to snout when hind limb extended; tarsal fold present, weakly developed; tibia length 52 % SVL; foot length 47 % SVL; outer metatarsal tubercle absent; inner metatarsal tubercle present, large, ovoid; toes IV and V with lateral fringe, prominent on Toe V; fringe of Toe V extending onto outer surface of base of tarsus; dorsal surface of hind limb relatively smooth, bearing irregular sets of tubercles along three transverse

bands on shank; calcar present, small; relative lengths of toes: IV > V > III > II > I; toe pads about 1.5 times width of penultimate phalange; webbing basal. Cloacal opening directed posteroventrally at midlevel of thigh. Dorsum smooth with scattered, low, diffuse tubercles; flanks smooth; ventral surfaces and throat smooth with scattered low, diffuse tubercles; sacral diapophyses projecting laterally, slightly narrower than posteriormost transverse processes of all vertebrae; lateral termini of transverse processes of presacral vertebrae VI–VIII not co-ossified with skin; five neural spines projecting dorsally, co-ossified with skin, visible externally. Pupil horizontal.

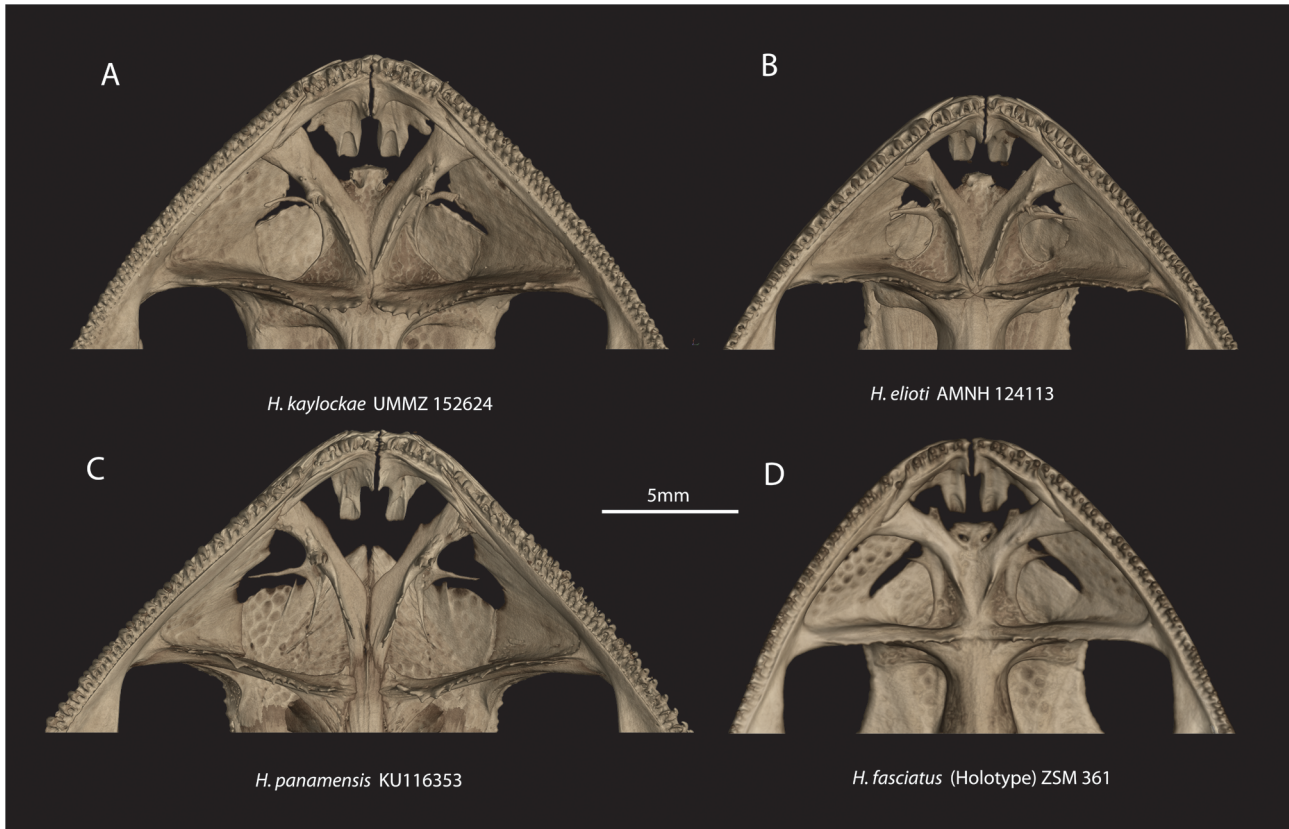


FIGURE 6. Condition of the vomer and neopalatine relationships of the *Hemiphractus* spp. considered in this paper. (A) adult male of *H. kaylockae* (UMMZ 152624), showing narrow separation between odontoids on vomers and neopalatines. (B) Adult male *H. elioti* AMNH 124113), showing contact between odontoids on vomers and neopalatines. (C, D) adult females of *H. panamensis* (KU 116353) and *H. fasciatus* (holotype), showing wide separation between odontoids on the vomers and palatines, as well as the reduced number of vomerine odontoids compared to *H. elioti* and *H. kaylockae*. Figures are presented in similar, but not fully equivalent scales.

All dorsal surfaces uniformly brown (Fig. 4). Thigh bearing two, shank bearing three indistinct transverse bands of irregular, brown mottling on dorsal surfaces, corresponding with three bands of tubercles on these bands; toes I and II are uniformly beige, toes III–V uniformly brown; forearm dark brown, bearing broad, brown, transverse band on dorsal surface; dorsal surface of manus more pale than forearm, ultimate and penultimate phalanges of fingers I and II beige, fingers III and IV dark brown. Upper and lower lips with narrow, transverse, dark brown bands, not extending onto proximal surfaces. Flanks beige with diffuse brown punctations; venter beige with scattered diffuse, fine brown markings; throat dark brown, extending onto pectoral region. Ventral surfaces of forearms beige with fine, brown mottling; ventral surfaces of hands beige. Ventral surfaces of hind limb and foot beige with fine, pale brown mottling.

Variation. Consistent sexual dimorphism in coloration or skin texture was not evident (Figs. 4, 8). Granulation on the throat in *Hemiphractus kaylockae* is variable among specimens examined, varying from smooth (e.g., KU 93506, 93507, 107411, 107417, 154992) to smooth with tubercles (e.g., AMNH 92668, KU 107419), smoothly granular with no tubercles (e.g., KU 107412, 107413), to smoothly granular with tubercles present (e.g., KU 107408, 107414, 107422, 107423, 154991, UMMZ 152624). Granulation of the venter ranges from smooth to uniformly granular (e.g., KU, 107411, 107422, 154992, UMMZ 152624); some specimens with smooth or uniformly granular venters also had variable numbers of discrete tubercles present (e.g., AMNH 92668, KU 93506,

93507, 107412, 107413, 107414, 107417, 107419, 107423, 154991). Throat coloration in most specimens is tan (e.g. KU 107417) to brown or dark brown (e.g., AMNH 92668, KU 93506, 107408, 107411, 107412, 107419, 107422, 154992) with some showing prominent white mottling, striping, and/or prominent labial barring (e.g. KU 93506, 107412, 107422, 154992) and KU 93507, 107413, 107414, 107417, 107423, 154991, UMMZ 152624 displaying stippling or speckling of brown and white. Ventral coloration in most specimens typically is a continuation of the gular coloration of dark brown or tan extending to approximately mid-abdomen where it abruptly changes to a beige coloration that typically contains variable amounts of darker brown stippling (e.g., AMNH 92668, KU 93507, 107408, 107411, 107414, 107417, 107419, 107423, 154992); KU 93506 and KU 107413 show a similar pattern however also display white mottling in the pectoral region while KU 107422 displays white spotting posteriorly. The dorsum of *H. kaylockae* is smooth or uniformly smoothly granular in all specimens with KU 93506, 107423, 154991, 154992, and UMMZ 152624 having some tubercles. Dorsal coloration in most is an overall tan or beige that may or may not include some level of darker brown stippling or mottling (e.g. KU 107408, 107412, 107413, 107417, 107419, 107422, 107423, 154991, 154992) while some specimens display an overall uniform brown color (e.g. AMNH 92668, KU 93506, 93507, 107411, 107414). Some specimens show a prominent dark band on the forearm (e.g. KU 107408, 107412, 107422, 107423, 154992). However, this band is diffuse or weakly developed in all other specimens. Two or three dark transverse bands are present on the femoral and tibial regions (absent or barely discernible on AMNH 92668, KU 93506, 107411, 107419, 154991), and a diffuse or very evident dark band or chevron present on the sacral region (e.g., KU 107408 [weakly developed], 107412, 107414, 107417, 107422, 154992, UMMZ 152624); in specimens KU 107422 and 154992 there are two chevrons present; in addition, specimens KU 107414, 107417, 107422, and 154992 have a dark irregular vertebral stripe extending from the sacral band connecting to a dark blotch at the occiput. The posterior surface of the thigh of KU 107412–14 and UMMZ 152624 bears a pattern of tan or brown mottled with white or beige while all other specimens bear a diffuse (e.g., KU 93506, 93507, 107411, 107422, 107423, 154991, 154992) or distinct white stripe along this surface (e.g., AMNH 92668, KU 107408, 107417, 107419).

Etymology. This species is named in honor and memory of Julia Kaylock. She was a colleague and friend, beloved by many, who was passionate about the conservation of the world's biodiversity, especially that of amphibians. She spent the latter part of her life working tirelessly to improve and document husbandry techniques for threatened Panamanian amphibians (e.g., Hill *et al.* 2012) maintained in *ex situ* facilities. She lost a lifelong battle with Type I Diabetes at the age of 28 on 12 June 2009. We graciously acknowledge her passion for amphibian conservation in the naming of this species of *Hemiphractus*. The specific epithet is the singular genitive case of the name Kaylock.

Distribution and ecology. Specimens of *Hemiphractus kaylockae* have been collected only in one region of far eastern Panama, in the Serranía de Pirre, Prov. Darien (Fig. 5). This region remains poorly documented biologically, and this species is expected to occur somewhat more broadly—at least until the recent invasion of the amphibian pathogen *Batrachochytrium dendrobatidis*. This frog has been found only in moist, lower montane forests at elevations from 900 to 1550 m (Myers 1966). Specimens collected at night at Cerro Pirre (Prov. Darien) by Myers (1966: 70) were observed "...on low perches (log, sticks, dead palm fronds) only one-half to 2 feet above ground, and two were on palm fronds 3 to 4 feet above the forest floor. Myers (1966) also provided in this account a description of a mouth gaping behavior in which the yellowish orange tongue is displayed followed by a painful bite with continued agitation as well as a "loud catlike squall emitted when removing an individual from a bag (Fig. 8C). It is likely that females of this species carry eggs on the back as has been documented for all other described species of *Hemiphractus*. As all documented observations have occurred at night, it is inferred that this species is most likely nocturnal.

Hemiphractus panamensis

(Figs. 3, 4, 6, 7, 9)

Cerathyla panamensis Stejneger 1917. Holotype: USNM 55320. Type locality: Signal Loma (Loma Peak) on the north coast of Panama, three miles [4.8 km] south of Santa Isabel, Prov. Colón, Panama.

Hemiphractus fasciatus Trueb 1974 [in part; for reference to specimens from Chagres Highlands, Panama]; Duellman, 2001 [in part; for reference to specimens from Chagres Highlands, Panama]; Crawford *et al.* 2012 [in part, for samples from Cerro Brewster, Prov. Panama, Panama]; Castroviejo-Fisher *et al.* 2015 [in part, for samples from Cerro Bruja and Cerro Brewster, Prov. Panama, Panama]; Köhler, 2011 [figs. 472, 473; in part; for map showing isolated populations in the

Re-description of the Holotype. Medium-sized adult female, SVL 59.3 mm (not including proboscis); tibia length 31.2 mm (not including calcar); foot length 27.3 mm; head length 26.6 mm (not including proboscis); head width 31.4 mm; snout–paraoccipital process length 25.8 mm; tympanum ovoid, 5.2 mm high x 2.6 mm wide; eye diameter 7.4 mm; interorbital distance 12.0 mm; eye–tympanum distance 3.3 mm; body moderate; head large, wider than body, greatest width at level of pars articularis, bearing prominent paraoccipital processes; paraoccipital processes projecting posterolaterally in dorsal view, extending posterior to level of pars articularis; skin co-ossified over dorsal surface of skull; occipital ridges indistinct, paraoccipital ridges present, weakly developed; supraorbital and canthal ridges slightly developed; zygomatic and preorbital ridges absent; canthus rostralis indistinct; loreal region flat; proboscis short, fleshy, pointed, triangular in cross section; snout angling posteriorly at approximately 45° from horizontal; nostrils ovoid, slightly protuberant, projecting dorsally, slightly laterally; lips not flared. Top of head relatively flat; interorbital region 38 % head width; eye diameter 24 % head width; greatest diameter 70 % times eye diameter; width of tympanum 84 % times eye–tympanum distance; upper eyelid appearing to bear only a single enlarged pointed projection, scattered smaller tubercles absent; interorbital, postorbital tubercles absent; skin over posterior surface of pars articularis bearing one large, fleshy tubercle. Tongue large, ovoid; mandible bearing serrations along entire length of lower jaw, with two prominent, tusk-like odontoids projecting from mentomeckelian bones. Axillary membrane absent; thoracic fold absent; dermal folds on wrists absent; fingers long, slender, bearing slightly enlarged distal pads; inner outer metacarpal tubercles present, but condition of specimen does not allow for accurate description; relative lengths of fingers: III > IV > II > I; lateral flanges appear to be absent on fingers; condition of specimen does not permit description, or determination of presence/absences of tubercles on forearms; webbing on hands absent. Heels of adpressed hind limbs overlap; tibiotarsal articulation not extending to snout when hindlimb extended; condition of specimen does not permit description of tarsal folds; tibia length 53 % SVL; foot length 46 % SVL; inner and outer metatarsal tubercles present, but condition is unclear; presence of condition of lateral fringe on toes unclear; calcar present, small; relative lengths of toes: IV > V > III > II > I; webbing basal. Cloacal opening directed posteroventrally at midlevel of thigh.

Texture and coloration of the skin, as well as the finer details of the hands and feet are unclear, as the type specimen is quite desiccated. Similarly, the desiccated nature of the holotype makes it unclear the level to which the transverse processes of the vertebrae are co-ossified with the skin. The pupil is not visible. In all major morphological features and measurements, Stejneger's (1917) description closely matches the current condition of the holotype (USNM 55330). Exceptions include coloration notes and textural details of the skin, various tubercles, and digital pads (Stejneger 1917: 32), all of which are now faded or physically distorted—evidently as a result of desiccation at some point in its history. Likewise, the indentations of eggs on the dorsal surface of this female that Stejneger (1917: 33) described no longer are evident.

Diagnosis. *Hemiphractus panamensis* may be distinguished from all species of *Hemiphractus* except *H. elioti*, *H. fasciatus*, *H. kaylockae*, and *H. scutatus* by not having a postorbital indentation (present in other species). *Hemiphractus panamensis* may be distinguished from *H. scutatus*, an Amazonian species not occurring in Panama, by its smaller size (maximum SVL in males 52.5 vs. 57.4, females 64.7 vs. 80.5; data for *H. scutatus* from Trueb 1974), and by having small expanded pads on the fingers and toes (absent in *H. scutatus*). *Hemiphractus panamensis* differs from *H. elioti* and *H. kaylockae* by having neopalatine and vomerine odontoids widely separated (vs. in contact in *H. elioti* and narrowly separated in *H. kaylockae*; Fig. 6). *Hemiphractus panamensis* appears to have only about two odontoids on each vomer, whereas *H. elioti* and *H. kaylockae* both have about seven (condition unknown in *H. scutatus*; Fig. 6). *Hemiphractus panamensis* may be distinguished from *H. kaylockae* by having a straight lateral margin of the paraoccipital horns (Figs. 2, 9); supraorbital ridges evident, weakly developed (absent or weakly developed in *H. elioti* and *H. kaylockae*; Figs. 2, 9); canthal ridges evident, distinct (absent or weakly developed in *H. elioti*; Figs. 2, 9). *Hemiphractus panamensis* has a very large subtemporal fenestra approximately 1.5 x size of the orbit in females (males unknown), subtemporal fenestra approximately one-third diameter of the orbit in both males and females in *H. kaylockae*, approximately one-half diameter of orbit in females of *H. elioti* (very small in males), approximately one-half diameter of the orbit in females of *H. fasciatus* (males unknown); lateral margins of the quadratojugal extending far beyond the profile of the paraoccipital horns in dorsal view (about to level of paraoccipital horns, or slightly beyond, *H. elioti*, *H. fasciatus*, and *H. kaylockae*).



FIGURE 7. Preserved holotype of *Cerathyla* (= *Hemiphractus*) *panamensis* Stejneger, 1917. Specimen (USNM 55320) is an adult female, SVL = 59.3 mm. Photographs courtesy of USNM curatorial staff.

Distribution and ecology. *Hemiphractus panamensis* is known from specimens collected from central Panama in the provinces of Colon and San Blas within or in proximity to what is now the Chagres National Park (Fig. 5). Specimens have been collected at ~750 m elevation in lower montane forests with high rainfall (Myers 1966). Trueb (1974) reported a large specimen (KU 93503) that contained "...an unidentified gastropod, a lizard (*Ptychoglossus*), and a dendrobatid frog (*Colostethus*) in the stomach. Myers (1966) reported *H. panamensis* to display mouth gaping behavior and biting when accosted (Fig. 3B). An individual collected by Myers in 1964 at

Altos de Pacora (Panama Province) was “on a stick lying on bare soil, in a roadside ditch at night. Two live specimens observed at night by T. Herman and colleagues (pers. comm.) at Cerro Brewster (Panam Province) were observed on vegetation < 1 m above ground level (Fig. 3A, C).

Remarks. While osteological characters of the skull would not seem to be useful diagnostic characters in the absence of skeletal specimens or radiography, we note that the distinctly enlarged subtemporal fenestra of *H. panamensis* can be detected by manual palpation and is also visible even in photographs of living specimens. Despite the relative proximity of the range of this species to Panama City, and infrastructural developments such as the Panama Canal and various Smithsonian field stations, relatively few specimens of this species appear to exist in museum collections. As a result, data regarding variation in coloration and morphometry are unavailable.

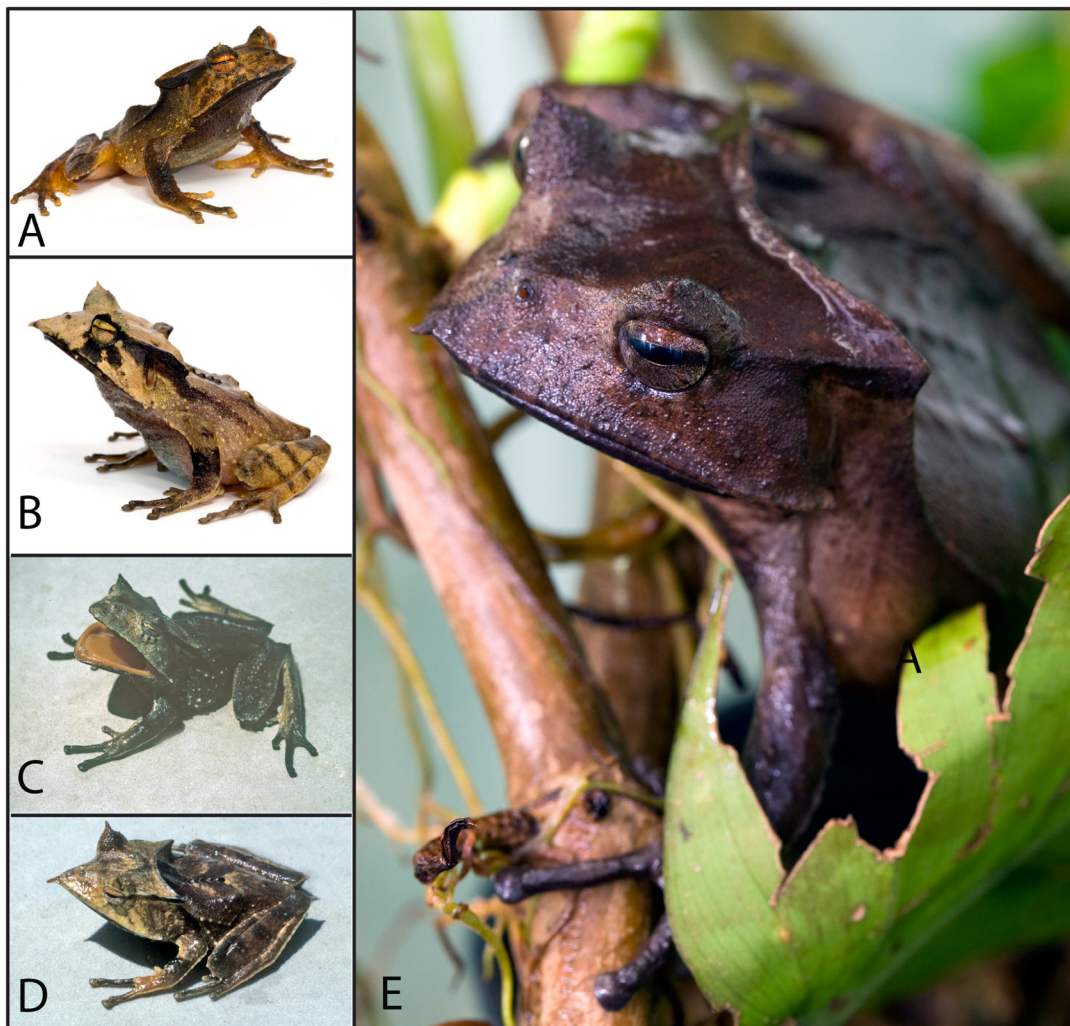


FIGURE 8. Live specimens of *Hemiphractus kaylockae*. (A, B) Adult specimens from vicinity of Cana, Darién, Panama (B. Wilson, courtesy of El Valle Amphibian Conservation Center): probable males, SVL unknown. (C) Photograph (KUDA 003746) of specimen KU 93506 (C.W. Myers) from Cerro Pirre, Darién, Panama; adult female, SVL = 54.2 mm. (D) Photograph (KUDU 003744) of specimen KU 93505 (C.W. Myers) from Cerro Pirre, Darién, Panama; adult female, SVL = 40.5 mm. (E) Adult specimen from vicinity of Cana, Darién, Panama (B. Wilson, courtesy of El Valle Amphibian Conservation Center): probably female, SVL unknown.

Comments on the status of *Hemiphractus fasciatus* Peters, 1862

While examining specimens from populations referred to *H. fasciatus* from Panama for this report, we became convinced that the taxon *H. fasciatus* does not occur in Panama. The skull characteristics of the holotype of *H. fasciatus* (Fig. 9) do not agree with those of the three species that we recognize herein as occurring in Panama (see

diagnoses above, and Figs. 2, 6, 9) We also note that the straight nature of the neopalatines is distinct from the variably arcuate nature of those elements in all the Panamanian species (Fig. 6). Trueb (1974) highlighted the uncertainty of the type locality, presumably from somewhere in Ecuador. Our sampling did not include sufficient numbers of specimens from Ecuador, nor Colombia, to provide a proper diagnosis for the species, nor a range delimitation. Consequently, a proper consideration of the characteristics and distribution of *H. fasciatus* extended beyond the scope of this report and remains a worthwhile project for consideration.

Our only germane contribution toward that goal is to highlight the distinctive skull morphology of a large specimen of *H. cf. fasciatus* (KU 200261; Fig. 9) from Prov. Nariño, Colombia, that does not appear to match the holotype of *H. fasciatus*, nor any of the material from Panama. It is possible that this specimen does not represent *H. fasciatus*, and we are unsure of its taxonomic status.

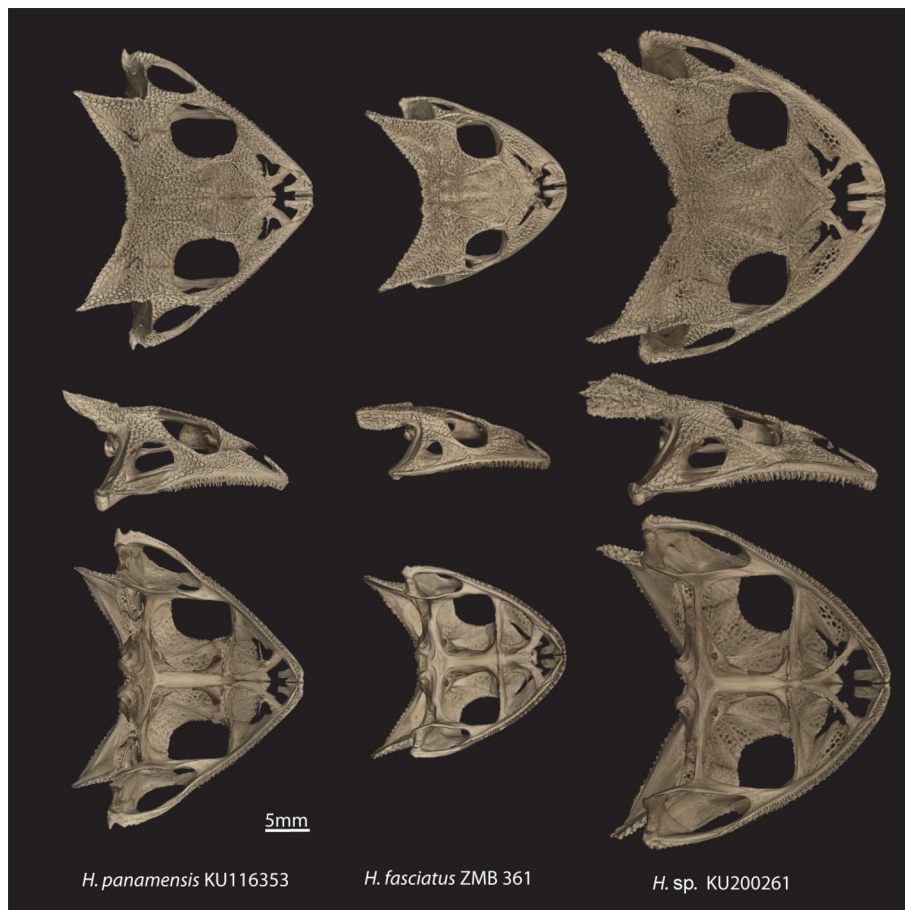


FIGURE 9. High-resolution Computed Tomography reconstructions of the skulls of *Hemiphractus panamensis*, the holotype of *H. fasciatus*, and an unidentified specimen of *Hemiphractus* from Prov. Nariño, Colombia (KU 200261). This latter specimen was initially identified and catalogued as *H. fasciatus*; we are unsure of its actual taxonomic identity because it resembles neither the holotype of *H. fasciatus* nor any of the material from Panama.

Acknowledgments

We are grateful for images, data, and loans of specimens from the following museums: ZSM, AMNH, KU, UMMZ, FMNH, CNHM, UTACV, and USNM. Photographs and assistance with digital files were generously offered by W. Duellman, L. Welton, B. Wilson, T. Herman, P. Crump, and E. Baitchman. M. Scherz and M. Franzen were especially helpful by providing CT scans and additional information on the holotype of *H. fasciatus*. David Blackburn arranged for access to the CT technology at Florida Natural History Museum. Daniel Mulcahy assisted with map images and A. Thompson assisted with images of specimens. Heidi Ross and Edgardo Griffith kindly provided access to living specimens in the collections of the El Valle Amphibian Conservation Center, as well as hospitality during our many visits there.

References

- Castroviejo-Fisher, S., Padial, J., de La Riva, I., Pombal Junior, J., da Silva, H., Rojas-Runjaic, F.J.M., Medina-Méndez, E. & Frost, D. (2015) Phylogenetic systematics of egg-brooding frogs (Anura: Hemiphractidae) and the evolution of direct development. *Zootaxa*, 4004 (1), 1–75.
<https://doi.org/10.11646/zootaxa.4004.1.1>
- Coloma, L., Ron, S., Jungfer, K., Solís, F., Ibáñez, R., Jaramillo, C., Fuenmayor, Q. & Bolaños, F. (2008) *Hemiphractus fasciatus*. The IUCN Red List of Threatened Species.
<https://doi.org/10.2305/IUCN.UK.2008.RLTS.T55367A11286659.en>
- Crawford, A., Cruz, C., Griffith, E., Ross, H., Ibáñez, R., Lips, K. & Crump, P. (2012) DNA barcoding applied to ex situ tropical amphibian conservation programme reveals cryptic diversity in captive populations. *Molecular Ecology Resources*, 13, 1005–1018.
- Duellman, W. (1970) The hylid frogs of Middle America. Vol. 1. *Monograph of the Museum of Natural History, University of Kansas*, 1, 1–427.
- Duellman, W. (2001) *The Hylid Frogs of Middle America. Vol. 2*. Society for the Study of Amphibians and Reptiles Contributions in Herpetology, Ithaca, New York, 1170 pp.
- Duellman, W., Maxson, L. & Jesiolowski, C. (1988) Evolution of marsupial frogs (Hylidae: Hemiphractinae): immunological evidence. *Copeia*, 1988, 527–543.
<https://doi.org/10.2307/1445371>
- Hill, R., Kaylock, J., Cuthbert, E., Griffith, E. & Ross, H. (2012) Observations on the captive maintenance and reproduction of the Cascade Glass Frog, *Sachatamia albomaculata*. *Herpetological Review*, 43, 601–604.
- Jiménez de la Espada, M. (1871) Faunae neotropicalis species quaedam nondum cognitae. *Journal of Science, Math, and Physics of the National Academy of Real Sciences*, 3, 57–65.
- Köhler, G. (2011) *Amphibians of Central America*. Herpeton Elke Köhler, Offenbach, 379 pp.
- Lips, K., Brem, F., Brenes, R., Reeve, J., Alford, R., Voyles, J., Carey, C., Livo, L., Pessier, A. & Collins, J. (2006) Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proceedings of the National Academy of Sciences, USA*, 103, 3165–3170.
<https://doi.org/10.1073/pnas.0506889103>
- Myers, C. (1966) The distribution and behavior of a tropical horned frog *Cerathyla panamensis* Stejneger. *Herpetologica*, 22, 68–71.
- Myers, C., Ibáñez, R., Grant, T. & Jaramillo, C. (2012) Discovery of the frog genus *Anomaloglossus* in Panama, with descriptions of two new species from the Chagres Highlands (Dendrobatidae: Aromobatidae). *American Museum Novitates*, 3763, 1–19.
<https://doi.org/10.1206/3763.2>
- Noble, G. (1926) An analysis of the remarkable cases of distribution among the Amphibia, with description of new genera. *American Museum Novitates*, 212, 1–24.
- Peters, W. (1862) Über de Batrachier-Gattung *Hemphractus*. *Monatsberichte de Königlichen Preussische Akademie de Wissenschaften zu Berlin*, 1862, 144–152.
- Sabaj-Perez, M. (2016) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 6.5 (16 August 2016). American Society of Ichthyologists and Herpetologists, Washington, D.C. Electronically accessible from: <http://www.asih.org/> (accessed 15 February 2017)
- Sheil, C. & Mendelson III, J. (2001) A new species of *Hemiphractus* (Anura: Hylidae: Hemiphractinae), and a redescription of *H. johnsoni*. *Herpetologica*, 57, 189–202.
- Sheil, C., Mendelson III, J. & da Silva, H. (2001) Phylogenetic relationships of the species of Neotropical horned frogs, genus *Hemiphractus* (Anura: Hylidae: Hemiphractinae), based on evidence from morphology. *Herpetologica*, 2, 203–214.
- Stejneger, L. (1917) A new species of horned tree-toad from Panama. *Proceedings of the Biological Society of Washington*, 301, 31–34.
- Trueb, L. (1974) Systematic relationships of Neotropical horned frogs, genus *Hemiphractus* (Anura: Hylidae). *Occasional Papers of the Museum of Natural History, University of Kansas*, 29, 1–60.
<https://doi.org/10.5962/bhl.part.11750>
- Wagler, J. (1828) Auzuge aus einem systema amphibiorem. *Isis von Oken*, 1828, 740–744.
- Wiens, J., Kuczynski, C., Duellman, W. & Reeder, T. (2007) Loss and re-evolution of complex life-cycles in marsupial frogs: does ancestral trait reconstruction mislead? *Evolution*, 61, 1886–1899.
<https://doi.org/10.1111/j.1558-5646.2007.00159.x>

APPENDIX. Specimens examined.

Hemiphractus elioti

PANAMA:

Females: Bocas del Toro: San Felix, 25 km [40.3 km] NNE Cerro Colorado, 1425–1500 m (USNM 297541). Chiriquí: continental divide above upper Quebrada de Arena, 1200–1300 m (AMNH 124114). Coclé: 6 mi [9.7 km] NNW El Cope, 600–800 m (UMMZ 152622).

Males: Bocas del Toro: north slopes of Cerro Colorado near continental divide, 1300–1600 m (AMNH A107955); San Felix, 25 km [40.3 km] NNE Cerro Colorado, 1425–1500 m (USNM 297542, 297543). Chiriquí: continental divide above upper Quebrada de Arena, 1200–1300 m (AMNH A124113, A124115). Coclé: 6 mi [9.7 km] NNW El Cope on continental divide, 600–800 m (UMMZ 167358); 6 mi [9.7 km] NNW El Cope on continental divide at sawmill, 600–800 m (UMMZ 153118); El Copé, N Parque Nacional General Omar Torrijos H., 650–850 m (USNM 572599–572601). Panamá: Río Maria, Altos de Maria, 875 m (UTACV A-64827, holotype).

Juveniles/Sex uncertain: Bocas del Toro: 30 mi [48.3 km] W Almirante, upper Río Chaugena Camp (CAS-SU 21772, CAS 93836). Chiriquí: continental divide above upper Quebrada de Arena, 1160–1220 m (AMNH A124112); continental divide above upper Quebrada de Arena, 1200–1300 m (AMNH A124116). Coclé: 6 mi [9.7 km] NNW El Cope on continental divide at sawmill, 600–800 m (UMMZ 153118, 152623); El Copé, N Parque Nacional General Omar Torrijos H., 650–850 m (USNM 572601). Veraguas: 6–12 km N Santa Fe N of Altopiedra and agricultural school in mountains area called Buenas Aires, 3000–3500 ft [915–1067 m] (UMMZ 167485–167486). Panamá: Río Maria, Altos de Maria, 875 m (UTA-EVP 008 [1 specimen], 078 [4 specimens]).

Hemiphractus fasciatus

COLOMBIA:

Females: Nariño: Reserva Natural La Planada, 7 km S Chucunes, 1650 m (KU 200261); Pastaza: Pastaza Valley (ZSM 36/0; holotype).

Juveniles/Sex uncertain: Antioquia: 8 km S Valdivia, 1450 m (FMNH 63850). ECUADOR:

Juveniles/Sex uncertain: Esmeraldas: near the upper Cachavi, system of the Esmeraldas, 250–350 m (CAS 122205); Pichincha: Mindo (UMMZ 55523).

Hemiphractus kaylockae

PANAMA:

Females: Darién: N ridge Cerro Cituro, Serrania de Pirre, 1000 m (KU 154990, 154991, 107413); SE slope Cerro Pirre, 1440 m (KU 93505–93507); N ridge Cerro Cituro, Serrania de Pirre, 900 m (KU 107419, 107417); north ridge Cerro Cituro, Serrania de Pirre, 1100 m (AMNH A92668).

Males: Darién: N ridge Cerro Cituro, Serrania de Pirre, 1000 m (KU 107408, 107411, 107412, 107414); N ridge Cerro Cituro, Serrania de Pirre, 900 m (KU 107419, 107423); S slope Cerro Cituro, Serrania de Pirre, 1100 m (KU 154992); Cerro Pirri 3.5 hr walk N Pirri marker Rancho Plastico, 1300 m (UMMZ 152624).

Juveniles/Uncertain sex: Darién: N ridge Cerro Cituro, Serrania de Pirre, 1000 m (KU 107422); SE slope Cerro Pirre, 1440 m (KU 93504, 93508); N ridge Cerro Cituro, Serrania de Pirre, 900 m (KU 107409, 107415, 107416, 107420, 107421); S slope Cerro Cituro, Serrania de Pirre, 1100 m (KU 154991, 154993).

Hemiphractus panamensis

PANAMA:

Females: Colón: Signal Loma 3 mi [4.8 km] S of San Isabel (USNM 55320, holotype). San Blas: Camp Summit, 400 m (KU 116353, 116354).

Males: Panama: Canal Zone, Cerro Azul, 900 m (KU 77017). San Blas: Camp Summit, 400 m (KU 116355).

Juveniles/Sex uncertain: Canal Zone: Carti Rd 13–14 km N Pan Am Hwy (UMMZ 152626). Colón: Signal Loma 3 mi [4.8 km] S of San Isabel (USNM 55321).