

Juvenile colouration, ontogenetic colour shifts, defensive behaviour, and frontal “hooding” threat display in Philippine coral snakes (Elapidae: *Hemibungarus*)

Rafe M. Brown^{1,*}, Justin M. Bernstein², Jason B. Fernandez³, Marites Bonachita Sanguila⁴, Camila G. Meneses⁵, Cameron D. Siler⁶, Kenneth Chin⁷, Luke J. Welton^{1,8}, and Maren Gaulke⁹

Abstract. The Philippine coral snakes of the genus *Hemibungarus* consist of three poorly known endemic species, constituting some of the most enigmatic elapid snakes in the world. Because of their secretive, subterranean, and heretofore undocumented microhabitat preferences, very little is known of these lineages. We present a synthetic description of aposematic colouration, ontogenetic colour changes, defensive anti-predator behaviour, and the first documentation of a full frontal “hooding” threat display in *Hemibungarus*, which is reminiscent of the elaborate threat displays of their highly aggressive, deadly venomous, close relative, the King Cobra (*Ophiophagus hannah*).

Keywords. Aposematic colours, Barred Coral Snakes, Cobras, Elapoidea, False Coral Snakes, Warning colouration

Introduction

Variation in defensive behavioural repertoires of snakes is extensive (Greene, 1988). Some postural defensive displays of snakes include dorsoventral flattening of the head and body (Dell’Aglío et al., 2012; Gray, 2015), tight defensive coiling (Greene, 1988), and body-bridging (Weldon and Burghardt, 1979).

Other taxa may engage in thanatosis (death-feigning) or concealment of the head under the posterior portions of their body, coupled with presentation of the tail to would-be predators (Greene, 1973). Some taxa (e.g., *Cylindrophis*, *Diadophis*) possess bright aposematic colouration, often involving the ventral surfaces of the tail or body. More aggressive defensive postures include elevation and/or inflation of anterior portions of the body (Cowles, 1938; Bustard, 1969; Carpenter and Gillingham, 1975), and/or erratic, jerky movements, or reversals of body orientation (Greene, 1988; Young, 2003; Gregory, 2016). Frontal, visual displays such as gaping, neck-flattening (Jara and Pincheira-Donoso, 2015), and hooding represent the most elaborate of snake defensive displays (Young et al., 1999a; Young and Kardong, 2010; Nasoori et al., 2016). When these are presented along with tail vibrating, rattling (e.g., *Crotalus*, *Pantherophis*, among many others), stridulating (e.g., *Dasypeltis scabra*: Pringle, 1944; Gans, 1974; Branch, 2014; *Echis carinatus* and *E. leucogaster*: Gans and Maderson, 1973), hissing, growling (Young, 1991), cloacal popping (Young et al., 1999b), and/or striking, these behaviours create a formidable and threatening display. In cobras (genera *Naja* and *Ophiophagus*), these derived combinations of posture and behaviour function as aggressive threat displays in two or more sensory modalities, and effectively ward off potential predators, even including those with no recent evolutionary history of sympatry with either taxon (Greene, 1997; Pokrant et al., 2017).

¹ KU Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, 1345 Jayhawk Boulevard, Lawrence, Kansas 66045, USA.

² Department of Biological Sciences, 206 Boyden Hall, Rutgers University-Newark, Newark, New Jersey 07102, USA.

³ 2 Purok 1, Barangay Biyabid, Municipality of Sison, Surigao del Norte, 8404 Philippines.

⁴ Biodiversity Informatics and Research Center, Father Saturnino Urios University, San Francisco Street, 8600 Butuan City, Philippines.

⁵ Museum of Natural History, University of the Philippines Los Baños, 4031 Los Baños, Laguna, Philippines.

⁶ Sam Noble Oklahoma Museum of Natural History and Department of Biology, University of Oklahoma, 2401 Chautauqua Avenue, Norman, Oklahoma 73072, USA.

⁷ Serangoon Central, Singapore.

⁸ BTG Specialty Pharmaceuticals, 615 Arapeen Drive, Suite 105, Salt Lake City, Utah 84108, USA.

⁹ GeoBio-Center, Ludwig-Maximilians-Universität, Richard-Wagner-Straße 10, 80333 München, Germany.

* Corresponding author. E-mail: rafe@ku.edu

The phylogenetic relationships of cobras and their relatives have begun to stabilize, with recent studies broadly agreeing on key evolutionary questions of interest, such as the numbers of origins of hooding, rifled hypodermic fang enlargement, and venom spitting (Wüster et al., 2007; Brown et al., 2018; Plettenberg Laing, 2018). The sister relationship between the largest venomous snake in the world, the king cobra (*Ophiophagus hannah*) and the strikingly dissimilar Philippine endemic false coral snakes (or barred coral snakes) of the genus *Hemibungarus* was entirely unexpected (Castoe et al., 2007), as these two taxa are almost diametrically opposed ecologically, behaviourally, and phenotypically (Leviton, 1964; Leviton et al., 2014; Weinell et al., 2019). More than a decade later, multilocus phylogenetic analyses continue to confirm this compelling relationship (Brown et al., 2018; Plettenberg Laing, 2018). Thus, the secretive behaviour, diet, ecology, and overall unknown fossorial biology of *Hemibungarus* has become of keen interest to evolutionary biologists and elapid snake systematists (Leviton et al., 1964, 2018; Meneses, 2020).

The taxonomic diversity of *Hemibungarus* is limited to three species: *H. calligaster* (Wiegmann, 1834) of the central-northern Luzon Island faunal subregion and possibly Mindoro Island; *H. mcclungi* (Taylor, 1922) of the southern Luzon-Quezon faunal subregion (the Bicol Peninsula, Polillo, and Catanduanes Islands); and *H. gemianulis* (Peters, 1872) of the West Visayan faunal region (central portions of the archipelago; Brown and Alcala, 1970; Leviton, 1964; Brown et al., 2018; Leviton et al., 2018), least-known of all, and represented poorly in collections and published literature (Sison et al., 1995; Ferner et al., 2001; Gaulke, 2011; Leviton et al., 2018).

Comparatively, the geographic range of *H. calligaster* is reasonably well known and documented from ten provinces on Luzon (Brown et al., 1996, 2000, 2012, 2013; McLeod et al., 2011; Siler et al., 2011; Leviton et al., 2018; Bernstein et al., 2021). However, almost nothing is known of its ecology, reproduction, or diet (but see Meneses, 2020). This species, and *H. mcclungi*, which was until just recently considered endemic to southern Luzon's Bicol faunal region (and its nearby land-bridge smaller islands of Polillo and Catanduanes; Leviton et al., 2014, 2018; Brown et al., 2018; Bernstein et al., 2021), have been hypothesized as models of an apparent mimicry system, involving their adult colour patterns and that of the brightly coloured, co-distributed moth caterpillar in the genus *Bracca* (Brown, 2006; Fig. 1; Siler and Welton, 2010). Consideration of the

caterpillar mimic has been discussed with reference to the presumed model, *Hemibungarus* adults, but has not yet been extended to the potential model colour patterns of juveniles, which have gone largely undocumented (but see Kucharzewski and Tillack, 2007; Gaulke, 2011; Leviton et al., 2018; Bernstein et al., 2021). Here we provide a synthesis of available documentation of juvenile colouration for *H. calligaster*, *H. gemianulis*, and *H. mcclungi*, all of which indicate ontogenetic shifts in several colour pattern elements in these species. We also document the first observations of defensive behaviour and frontal threat displays in these poorly known elapid snakes.

Materials and Methods

We conducted field work throughout the Philippines from 1990 until present, on all major landmasses where *Hemibungarus* occur (Leviton, 1963; 1964; Leviton et al., 2018; Brown et al., 2019). Semi-fossorial microhabitats were searched extensively, using various digging techniques (Brown et al., 2000; 2012; Gaulke, 2011; Siler et al., 2011), but nearly all records, encounters, data, and qualitative observations presented here were accumulated opportunistically. Most specimens, including all new juveniles collected at known localities and photographed in life, have been deposited in the University of Kansas herpetological collections (KU). In a comprehensive study of all publicly accessible voucher specimens ($n = 98$) from 14 natural history collections, Bernstein et al. (2021) redefined the ranges of *Hemibungarus* species under consideration of newly georeferenced occurrence data (specimen collection localities and observations) after revisiting and updating taxonomic identification of all specimens in the study, on the basis of morphological observations and multiple statistical procedures. Because this work (Bernstein et al., 2021) is the most comprehensive, recent, rigorous quantitative treatment of the group and includes both juveniles (10.6% of specimens) and adults, we adopt their refined diagnoses that incorporated earlier studies (Leviton, 1964; Leviton et al., 2014, 2018; Weinell et al., 2019) and also reported species-specified diagnostic character state differences for both juveniles and adults based on meristic and colour pattern characters. *Hemibungarus gemianulis* is phenotypically distinct (Leviton, 1964; Weinell et al., 2019) and allopatrically distributed in the West Visayan faunal region of the central Philippines (Leviton, 1964; Leviton et al., 2018). Thus, juveniles from the islands of Panay, Guimaras, Negros, and Cebu (Brown et al., 2018; Fig. 1; Bernstein et al., 2021; Fig. 1), where no other



Figure 1. Adult colouration of three species of *Hemibungarus* from the Philippines. (A) *H. mcclungi* from Laguna Province, central Luzon Island (KU 345469). (B) *H. mcclungi* from Sorsogon Province, southern Luzon Island (specimen not collected). (C) *H. calligaster* from Aurora Province, northern Luzon Island (KU 323337). (D) *H. gemianulis* from northwestern Panay Island (specimen not collected; inset: lateral view). Photos by JBF and RMB (A, C), CDS (B), and MG (D).

Hemibungarus species have ever been recorded, were confidently identified, and assigned to this species on the basis of its diagnostic characters (Figs. 2A–E, 3C; Leviton, 1964; Weinell et al., 2019) and the well-characterized geographic range derived from georeferenced occurrence data.

The identification of juvenile specimens from central Luzon Island, where the ranges of *H. calligaster* and *H. mcclungi* abut (parapatry) or partially overlap (sympatry), is somewhat more ambiguous. We based our identifications on (A) the distributions on adult specimens of the two species that have been reliably identified, properly vouchered, and subjected to rigorous statistical analyses of continuous, categorical, and meristic data (Bernstein et al., 2021), and (B) a few colour pattern characteristics that do not vary ontogenetically. The latter distil down to two key colour characters relevant to this study based on reliably identified juvenile specimens from near the contact zone between *H. calligaster* (generally treated as a central to northern Luzon Island species: Leviton, 1964; Leviton et al., 2014, 2018; Brown et al., 2018; Weinell

et al., 2019) and *H. mcclungi* (a Central Luzon to Bicol faunal region species, reported most frequently from Luzon’s Bicol Peninsula and the islands of Polillo and Catanduanes; Leviton et al., 2018; Brown et al., 2018: Fig. 1; Weinell et al., 2019; see Fig. 1 in Brown et al., 2018 and Fig. 1 in Bernstein et al., 2021 for maps of these hypothesized distributions). Because Bernstein et al. (2021) used ventral banding pattern, and temporal pigmentation, to distinguish these taxa, we focussed on these same characters to identify our juvenile specimens from Luzon Island to named species (or possible intergrades/hybrids; see Bernstein et al., 2021).

Results and Discussion

Although adults and juveniles of all *Hemibungarus* species (Figs. 1–5) possess the presumably aposematic, alternating red-and-black, ventral colouration, both adults and juveniles of *H. mcclungi* can be readily distinguished from those of *H. calligaster* by the distinct, bright white transverse bars (Figs. 1A–C, 2G–I, 5A) that interrupt black bands on ventral body surfaces (white bars absent

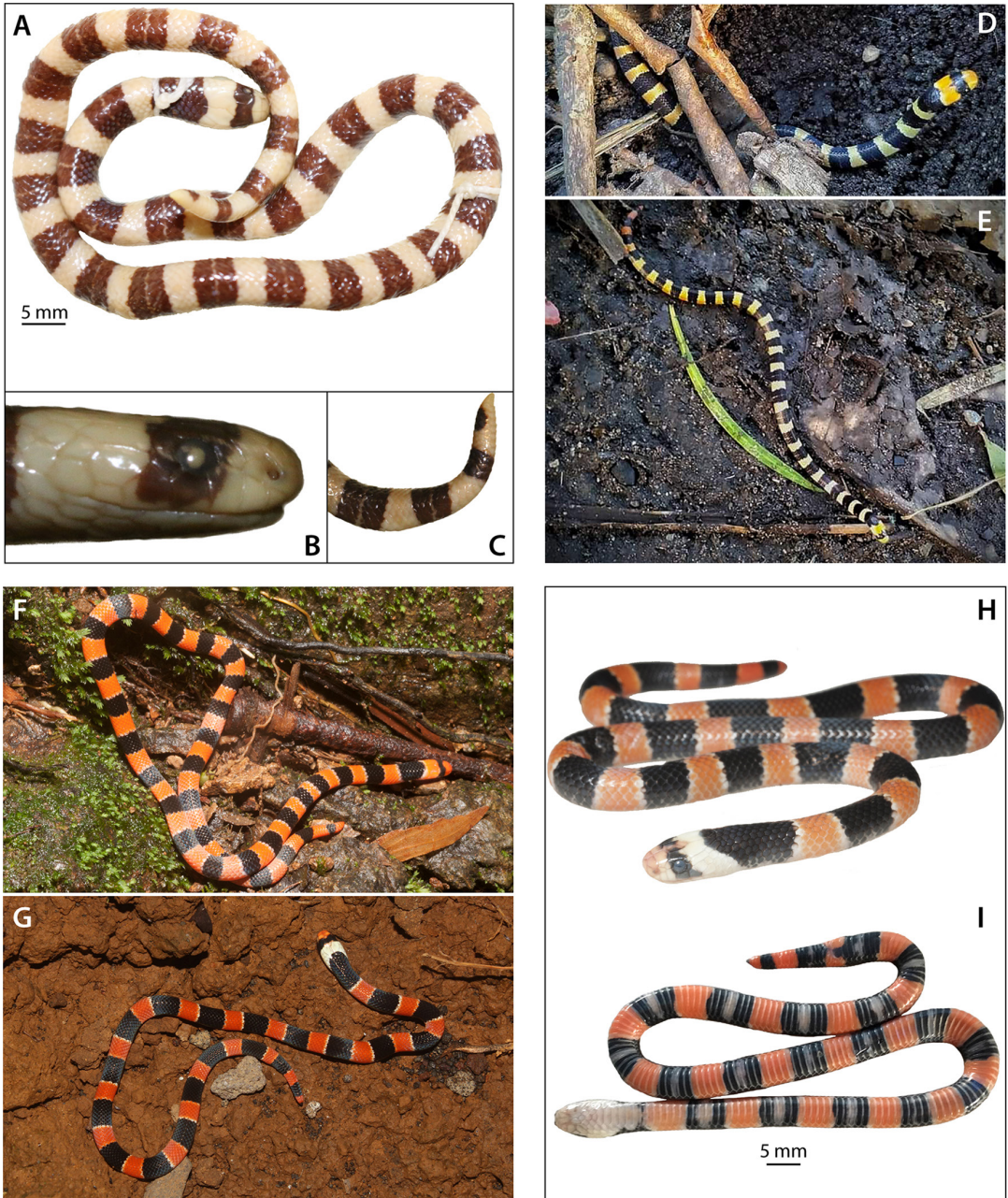


Figure 2. Photographs of *Hemibungarus gemianulis* from Cebu Island (CAS 15346), showing (A) a dorsal pattern with thin, intervening white bars within dorsal transverse black bands; (B) a lateral view of the head with transversal bar; and (C) a dorsal tail, with white bars visible within dorsal black tail bands; (D, E) live juvenile colouration in *H. gemianulis* (specimen not collected), from near Bacolod City, Negros Island; (F) live juvenile colouration in *H. calligaster* (KU 275815) from Luzon Island, Quezon Province, Infanta Municipality, Magsaysay Barangay; (G) *H. mcclungi* (KU 346508) from Luzon Island, Sorsogon Province, Bulusan Municipality, Salvacion Barangay; (H) dorsal and (I) ventral views of *H. mcclungi* juvenile (KU 348442) from Luzon Island, Sorsogon Province, Irosin Municipality, Cawayan Barangay (southern-most extent of the Bicol faunal region), exhibiting alternate, white-snouted pattern. Note the ventral white transverse bars, interrupting black bars (absent in *H. calligaster* adults [Fig. 1C] and juveniles [Fig. 4C]), a primary diagnostic feature of *H. mcclungi*; Leviton 1964). Photos by JMB (A–C), Ayong de la Torre and Jay Mavi Pagunsan (D, E), JBF and RMB (F–I).



Figure 3. Typical defensive behaviour of *Hemibungarus mcclungi* (A, B) from southern Luzon Island, and *H. gemianulis* (C) from northwestern Panay Island, involving concealment of the head, under anterior (A, C) or posterior (B) portions of the body, coupled with orientation of the tail towards a perceived threat, and usually coupled with lateral, side-to-side waving of the tail, and curling of the ventral tail surface dorsally, to expose bright orange-red aposematic colouration. Photos by RMB and LJW (A, B) and MG (C).

in *H. calligaster*, which has only simple, unbroken black bands alternating with red; Figs. 2F, 4A–C; see Bernstein et al., 2021: Fig. 1). Our juvenile specimens from Sorsogon Province, at the southern tip of Luzon Island, are clearly identified as *H. mcclungi* on the basis of this conspicuous character (Fig. 2I; vs. absent in *H. calligaster*: Fig. 4C) and by their bright white temporal region (Fig. 2G, H; vs. temporal region pigmented red in *H. calligaster*; Figs. 2F, 4A, B). Additionally, our *H. mcclungi* specimens originated at the extreme southern extent of the species' range, at the point farthest from its contact with *H. calligaster* (see Bernstein et al., 2021: Fig. 1). In contrast, our specimens of juvenile *H. calligaster* (Figs. 2F, 4A–C) were collected in Laguna and Quezon Provinces, to the north, in precisely the region of Luzon where the ranges of *H. calligaster* and *H. mcclungi* abut and may substantially overlap, and where intermediate colour phenotypes have been recorded (Bernstein et al., 2021: Fig. 1; thin, faded white ventral bars variably present, temporal pigmentation present). Nevertheless, both our juvenile and adult specimens from these intermediate localities lack any sign of colouration intermediacy (adult: Fig. 1C; juvenile: Figs. 2F, 4A–C), and we confidently refer them to *H. calligaster*.

Nonetheless, a previously undocumented ontogenetic colour shift in *Hemibungarus* involves the loss of bright (putatively aposematic) dorsal colouration in adults (Fig. 1); the dorsal red or yellow bands in juveniles (Fig. 2) appear to darken progressively and become nearly solid black with age (Fig. 1; see also Brown, 2006: Fig. 1; Siler and Welton, 2010: Fig. 2; Gaulke, 2011: Figs. 220, 221; Leviton et al., 2018: Figs. 92, 93). Adult *H. mcclungi* and *H. gemianulis* have dorsal white annuli interrupting dark dorsal bands (Figs. 1D, 3C), as well as ventral white bars within the black bands, which encircle the body (Fig. 5). These two species have alternating faint, vs. more prominent, dorsal white annuli (Fig. 1), leading to a higher dorsal annulus count (Leviton, 1964; Gaulke, 2011; Weinell et al., 2019). These annuli are variably faint but present in juveniles of *H. gemianulis* (based on one preserved specimen and one photographic voucher; Fig. 2A–E) but are absent in juveniles of *H. mcclungi* and *H. calligaster* (two and one live specimens, respectively; Fig. 2F–I). These fainter dorsal annuli are present in subadults and adults of *H. mcclungi* (eight live animals, 16 preserved specimens) and *H. gemianulis* (two live animals, four preserved specimens; Gaulke, 2011: Fig. 219) and absent in adults of *H. calligaster* (five live animals, 11 preserved specimens).

In *H. mcclungi* and *H. calligaster*, variable retention of dorsal white transverse markings, corresponding to the margins of black–red transverse band transitions, are retained from juvenile (Figs. 1, 2) to adult in most specimens examined by us. The diagnostic feature of the variably retained, indistinct white annulus on the dorsum, corresponding to a white transverse bar within the ventral black band, allows for species-level identification of juveniles (present in *H. mcclungi* and *H. gemianulis*; absent in *H. calligaster*; Figs. 1, 2, 4). Lateral head (temporal) colouration is variable.

Interestingly, ventral black transverse bands in juveniles of *H. mcclungi* (Fig. 2I) are interrupted by the intervening thin, transverse white bar, which corresponds to variable white dorsal annuli in adults (Fig. 1) but is absent from the dorsal black bands of juveniles (Fig. 2F–H). *Hemibungarus gemianulis* possesses a similar ventral pattern (transverse body bands interrupted by white bar), but this marking continues onto dorsal surfaces as retained annuli, interrupting black dorsal body bands in juveniles of this central Philippine endemic species (Figs. 1D, 2A–E, 3C). Finally, juveniles of *H. calligaster*



Figure 4. Defensive “hooding” posture and threat display in *Hemibungarus calligaster*. Lateral (A, B) and frontal (C) views of juvenile specimen (KU 275815), from east-central Luzon Island, Quezon Province, Infanta Municipality, Magsaysay Barangay. Note the absence of white transverse markings interrupting ventral black bars (typical of *H. calligaster*; Leviton, 1964; Weinell et al., 2019; Bernstein et al., 2021). Photos by JBF and RMB.

have a primarily red head colouration (Figs. 2F, 4A–C) with a single black transverse bar spanning the frontal scale, the posterior part of the prefrontals, and the dorsal ocular and preocular region, terminating at and spanning Supralabials 3–5 (and sometimes 6; Supralabial 1 adjacent to rostral scale; Fig. 2B), whereas *H. mcclungi* has a white or red snout (Fig. 2G–I), an immaculate white temporal region, and a variably fainter, at times less distinct (Fig. 2G, H) dark ocular bar in the same region as *H. calligaster* (Figs. 1, 2F, 4A, B). Nearly all dorsal red colouration is lost in adults, with the exception



Figure 5. Latter stages of hooding defensive threat display in *Hemibungarus gemianulis* (from Cebu Island, Moalboal Municipality; specimen not collected) in (A) anterior/frontal and (B) lateral views, showing the dorsoventral flattening of both anterior and posterior portions of the body (nuchal region compressed) and the subject's head held at sharp angle relative to anterior portion of body. Note the red pigmentation in the temporal region, which is diagnostic for the species (vs. temporal region with melanin in *H. calligaster* and *H. mcclungi*). (C) Initiation of threat display in *H. gemianulis* from northwestern Panay Island (specimen not collected). Note the uncompressed nuchal region, head not yet held at sharp angle to anterior portion of body. Photos by KC (A, B) and MG (C).

of the tip of the snout (Fig. 1; Siler and Welton, 2010; Fig. 2A) and the tail. In adults of *H. calligaster*, the last two ventral orange tail bands extend dorsally; the penultimate ventral orange band is still orange dorsally, but with variable amounts of black pigmentation.

Gaulke (2011) described ontogenetic colour change in the Panay Island population, emphasizing her observation of red bands persisting across the dorsum of juveniles and subadults (Gaulke, 2011: Fig. 220), which are later lost in adults (Gaulke, 2011: Fig. 219). Additionally, juvenile *H. gemianulis* also possess the transverse ocular bar that spans the frontal, posterior part of the prefrontals, and dorsal ocular and preocular scales, also terminating at Supralabial 3–5 (and sometimes 6; Fig. 2B). Because our initial information for *H. gemianulis* was based on preserved museum specimens (California Academy of Sciences, CAS 125364, 134225; Fig. 2A–E), which we assume gradually changed pattern intensity and faded colour and with time, we were uncertain of the colour of the pale regions on the head. However, recently captured images (by A. de la Torre and J.M. Pagunsan; Fig. 3) of a juvenile from Negros Island (Fig. 5B) make it clear that *H. gemianulis* does not have a red head colouration like *H. calligaster* but that its head is bright yellow in life (Fig. 2D, E; see also Gaulke, 2011: Fig. 220). Additionally, the dorsal transverse white annuli that interrupt dorsal black bands in adult *H. mcclungi* and *H. gemianulis* are likewise present in juvenile *H. gemianulis*, including distinctively so on the tail (dorsal white tail annuli absent in *H. mcclungi* and *H. calligaster*; Fig. 2F–I). Dorsal body and dorsal tail annuli may be a diagnostic character for juveniles of *H. gemianulis*; two additional specimens (identified as *H. gemianulis* but with no locality data: CAS 15345, 15346) also show this character. The adults of *H. gemianulis* are similar in colour and pattern to *H. mcclungi*, with the exception of the absence of melanin in the temporal region, which is red in *H. gemianulis* (Gaulke, 2011: Fig. 219).

Adult defensive behaviour. Adult defensive behaviour and threat displays in both sexes involve simultaneous dorso-ventral flattening of the body and tail, concealment of the head under posterior regions of the body, raising and laterally waving of the tail (in a side-to-side movement), and/or curling of the tail dorsally, thereby exposing the tail's brightly coloured, vibrant red ventral surface (observed on 3, 14, and 3 occasions for *H. calligaster*, *H. mcclungi*, and *H. gemianulis*, respectively; Figs. 4, 5); this display was described earlier for *H. gemianulis* (Gaulke, 2011). No cobra-like “hooding” had ever been reported in adult *Hemibungarus* of either sex, which, based on the

docile, fossorial, and highly secretive nature of these species, was unsurprising to elapid systematists (Alan Leviton, pers. comm.); there is virtually no history of envenomation of humans (Leviton et al., 2014).

The single account of envenomation is that of Gaulke (2011), who was envenomated by *H. gemianulis* and described localized tissue inflammation and blisters/blebs, swelling, and pain at the site of the bite, with pain spreading over the entire limb for several days, eventual fever and nausea, and a decline in these symptoms after one week (Gaulke, 2011: 321). Curiously, this symptomology lacks the tell-tale signs of a neurotoxicity (flaccid paralysis, tachycardia, ptosis, respiratory distress, fasciculations, etc.) that often result from *Ophiophagus* envenomation (Boquet, 1939; Tin-Myint et al., 1991; Warren, 2014; Norris, 2018). It should be noted that to date there have been no studies on the venoms of any species of *Hemibungarus*.

Juvenile defensive behaviour. During recent Philippine biodiversity inventory fieldwork on central-eastern Luzon Island, Quezon Province, Infanta Municipality, Magsaysay Barangay, Infanta-Marikina Highway, Southern Sierra Madre Mountain Range (14.6543°N, 121.5416°E; elevation 575 m; WGS 84), we encountered a seldom-observed (and infrequently collected) juvenile of *H. calligaster* (KU 275815; Figs. 2F, 4) on the surface of a gravel-strewn stream bed, in selectively logged and regenerating mid-montane forest at 18:15 h on 6 April 2016. Similarly, we encountered and collected two juvenile *H. mcclungi* specimens (Fig. 2G–I) at the southern tip of Luzon Island, one (KU 348442, Sorsogon Province, Irosin Municipality, Cawayan Barangay; 12.6994°N, 124.0737°E; elevation 320 m; WGS 84) on a dry stream bank where it was actively moving under an over-hanging root mass (16:50 h, 21 January 2017), and the other (KU 346508, Sorsogon Province, Bulusan Municipality, Salvacion Barangay; 12.7161°N, 124.1050°E; elevation 210 m, 16:15 h, 10 August 2017) was dislodged from its subterranean retreat by digging and raking in a coconut palm plantation, adjacent to regenerating secondary forest. We photographically documented juvenile defensive behaviour, and report a frontal, upright threat display (“hooding”), conspicuously reminiscent of shared common ancestry with *Ophiophagus* (Fig. 4). Photographs of the initiation of this display in an adult *H. gemianulis* (sex undetermined) from the central mountains of Panay Island (coordinates unrecorded), indicate that the raising of the anterior portion of the body occurs first (Fig. 5C), before the nuchal region compresses and the head is held at a sharp angle relative

to the body (Fig. 5A, B). Recently collected digital media of an adult *H. gemianulis* (sex undetermined; Moalboal Municipality, Cebu Island; 9.9562°N, 123.4025°E) also clearly demonstrates “hooding” behaviour (Fig. 5A), in conjunction with tail flattening.

The evolutionary history and anatomical mechanisms of hooding threat displays in *Hemibungarus* is completely unknown. Hooding in *Hemibungarus* is likely similar in some respects to that of its closest living relative, *Ophiophagus hannah*, and it would therefore appear that the common ancestor of these closely related lineages used such a threat display as well. Whether a hooding threat display evolved first in the common ancestor of *Hemibungarus* and *Ophiophagus* and, subsequently, was further developed into the broad, frontal threat display in *Ophiophagus* or has become secondarily minimized in these brightly coloured, subterranean species, is an open question. Apparently hooding in the docile, fossorial genus *Hemibungarus* is less common than in king cobras and its relatives. However, we also find it probable that the secretive, fossorial habits of *Hemibungarus* species have resulted in far fewer encounters with humans than for *Ophiophagus* or *Naja*, and thus, hooding and aggressive frontal threat displays may be present, but seldom observed in *Hemibungarus*. As such, the fossorial natural history, behaviour, diet, and general ecology of poorly known *Hemibungarus* species are topics that continue to provide practical opportunities for further research by Filipino field biologists, should these secretive, poorly-known, and docile snakes pique their interest.

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References

- Alcala, E.L., Alcala, A.C., Dolino, C.N. (2004): Amphibians and reptiles in tropical rainforest fragments on Negros Island, the Philippines. *Environmental Conservation* **31**: 254–261.
- Boquet, P. (1939): Sur le rôle de quantités infinitésimales de cuivre dans l'atténuation de venin de cobra (*Naja tripudians*) par l'eau oxygénée. *Comptes Rendus de l'Académie des Sciences, Biologies* **1939**: 1207–1209.
- Bernstein, J.M., Bautista, J., Diesmos, A.C., Clores, M.A., Cuesta, M.A., Sanguila, M.B., Brown R.M. (2021): Multivariate characterization of phenotypic variation from throughout the geographic ranges of Philippine false coral snakes: two species or four? *Ichthyology and Herpetology* **109**: 1036–1046.
- Branch, B. (2014): *A Photographic Guide to Snakes, Other Reptiles and Amphibians of East Africa*. Cape Town, South Africa, Penguin Random House.
- Brown, R.M. (2006): A case of suspected coral snake mimicry by lepidopteran larvae. *Raffles Bulletin of Zoology* **54**: 225–227.
- Brown, R.M., Ferner, J.W., Sison, R.V., Gonzales, P.C., Kennedy, R.S. (1996): Amphibians and reptiles of the Zambales Mountains of Luzon Island, Republic of the Philippines. *Herpetological Natural History* **4**: 1–22.
- Brown, R.M., McGuire, J.A., Ferner, J.W., Icarangal, N., Jr., Kennedy, R.S. (2000): Amphibians and reptiles of Luzon Island, II: preliminary report on the herpetofauna of Aurora Memorial National Park, Philippines. *Hamadryad* **25**: 175–195.
- Brown, R.M., Oliveros, C.H., Siler, C.D., Fernandez, J.B., Welton, L.J., Buenavente, P.A.C., et al. (2012): Amphibians and reptiles of Luzon Island (Philippines), VII: herpetofauna of Ilocos Norte Province, Northern Cordillera Mountain Range. *Check List* **8**: 469–490.
- Brown, R.M., Siler, C.D., Oliveros, C.H., Welton, L.J., Rock, A., Swab, J., et al. (2013): The amphibians and reptiles of Luzon Island, Philippines, VIII: the herpetofauna of Cagayan and Isabela Provinces, northern Sierra Madre Mountain Range. *ZooKeys* **266**: 1–120.
- Brown, R.M., Smart, U., Leviton, A.E., Smith, E.N. (2018): A new species of long-glanded coralsnake of the genus *Calliophis* (Squamata: Elapidae) from Dinagat Island, with notes on the biogeography and species diversity Philippine *Calliophis* and *Hemibungarus*. *Herpetologica* **74**: 89–104.
- Brown, W.C., Alcala, A.C. (1970): The zoogeography of the Philippine Islands, a fringing archipelago. *Proceedings of the California Academy of Science* **38**: 105–130.
- Castoe, T.A., Smith, E.N., Brown, R.M., Parkinson, C.L. (2007): Higher-level phylogeny of Asian and American coralsnakes, their placement within the Elapidae (Squamata), and the systematic affinities of the enigmatic Asian coralsnake *Hemibungarus calligaster* (Wiegmann, 1834). *Zoological Journal of the Linnean Society* **151**: 809–831.
- Cowles, R.B. (1938): Unusual defense posture assumed by rattlesnakes. *Copeia* **1938**: 13–16.
- Carpenter, C.C., Gillingham, J.C. (1975): Postural responses to kingsnakes by crotaline snakes. *Herpetologica* **31**: 293–302.
- Bustard, H.R. (1969): Defensive display behavior in the bandy-bandy, *Vermicella annulata* (Serpentes: Elapidae). *Herpetologica* **25**: 319–320.
- Dell'Aglio, D.D., Pacheco Toma, T.S., Muelbert, A.E., Sacco, A.G., Marques Tozetti, A.M. (2012): Head triangulation as anti-predatory mechanism in snakes. *Biota Neotropical* **12**: 1–3.
- Devan-Song, A., Brown, R.M. (2012): Amphibians and reptiles of Luzon Island, Philippines, VI: the herpetofauna of the Subic Bay Area. *Asian Herpetological Research* **3**: 1–20.
- Ferner, J.W., Brown, R.M., Sison, R.V., Kennedy, R.S. (2001): The amphibians and reptiles of Panay Island, Philippines. *Asiatic Herpetological Research* **9**: 34–70.
- Gans, C. (1974): *Biomechanics: an Approach to Vertebrate Biology*. Ann Arbor, Michigan, United States, University of Michigan Press.
- Gans, C., Maderson, P.F. (1973): Sound producing mechanisms in recent reptiles: review and comment. *American Zoologist* **13**: 1195–1203.
- Gaulke, M. (2011): *The Herpetofauna of Panay Island, Philippines*. Frankfurt am Main, Germany, Edition Chimaira.
- Gray, B.S. (2015): A study of the defensive behaviors of the free-ranging Dekay's Brownsnake, *Storeria dekayi* (Holbrook 1836). *The Journal of North American Herpetology* **1**: 43–52.
- Greene, H.W. (1973): Defensive tail display by snakes and amphisbaenians. *Journal of Herpetology* **7**: 143–161.
- Greene, H.W. (1988): Antipredator mechanisms in reptiles. In: *Biology of the Reptilia*, p. 1–152. Gans, C., Huey, R.B., Eds., New York, USA, Alan R. Liss.
- Greene, H.W. (1997): *Snakes: the Evolution of Mystery in Nature*. Berkeley, California, USA, University of California Press.
- Gregory, P.T. (2016): Responses of natricine snakes to predatory threat: a mini-review and research prospectus. *Journal of Herpetology* **50**: 183–195.
- Jara, M., Pincheira-Donoso, D. (2015): The neck flattening defensive behaviour in snakes: first record of hooding in the South American colubrid genus *Philodryas*. *Animal Biology* **65**: 73–79.
- Kucharzewski, C., Tillack, F. (2007): Redescription of the type specimen of *Naja (Hamadryas?) fasciata* Peters, 1861, a junior synonym of *Hemibungarus calligaster calligaster* (Wiegmann, 1834) (Reptilia, Squamata, Elapidae). *Mitteilungen aus dem Museum für Naturkunde in Berlin* **83**: 52–55.
- Leviton, A.E. (1963): Remarks on the zoogeography of Philippine terrestrial snakes. *Proceedings of the California Academy of Sciences* **42**: 112–145.
- Leviton, A.E. (1964): Contributions to a review of Philippine snakes, III. The genera *Maticora* and *Calliophis*. *Philippine Journal of Science* **92**: 523–550.
- Leviton, A.E., Brown, R.M., Siler, C.D. (2014): The dangerously venomous snakes of the Philippine Archipelago. In: *The Coral Triangle: the 2011 Hearst Biodiversity Philippine Expedition*, p. 473–530, Williams, G.C., Gosliner, T.M., Eds., San Francisco, California, USA, California Academy of Sciences.
- Leviton, A.E., Siler, C.D., Weinell, J.L., Brown, R.M. (2018): Synopsis of the snakes of the Philippines. *Proceedings of the California Academy of Sciences* **64**: 399–568.
- McLeod, D.S., Siler, C.D., Diesmos, A.C., Diesmos, M.L., Garcia, V.S., Arkonco, A.O., et al. (2011): Amphibians and reptiles of Luzon Island, V: the herpetofauna of Angat Dam watershed, Bulacan Province, Luzon Island, Philippines. *Asian Herpetological Research* **2**: 177–198.

- Meneses, C.G. (2020). Ophiophagy in the Philippine endemic Luzon False Coral Snake *Hemibungarus calligaster* (Wiegmann, 1834) on Gervais' Reed Snake *Calamaria gervaisii* Duméril, Bibron, and Duméril, 1854 and the importance of the Rabor collection in Philippine natural history. *Laksambuhay* **7**: 18–21.
- Nasoori, A., Shahbazzadeh, D., Tsubota, T., Young, B.A. (2016): The defensive behaviour of *Naja oxiana*, with comments on the visual displays of cobras. *The Herpetological Bulletin* **138**: 13–17.
- Norris, R.L. (2018): Cobra envenomation. *Medscape Drugs & Diseases*. Available at: <https://emedicine.medscape.com/article/771918-overview>. Accessed on 25 January 2021.
- Peters, W.C.H. (1872): Über drei neue Schlangenarten (*Calamaria bitorques*, *Stenognathus brevirostris* und *Hemibungarus gemianulis*) von den Philippinen. Königlich Preussische Akademie der Wissenschaften zu Berlin **1872**(Juli): 585–587.
- Plettenberg Laing, A. von (2018): A multilocus phylogeny of the cobra clade elapids. Unpublished PhD thesis, Bangor University, Wales.
- Pokrant, F., Kindler, C., Vamberger, M., Smith, K.T., Fritz, U. (2017): Grass snakes (*Natrix natrix*, *N. astreptophora*) mimicking cobras display a 'fossil behavior'. *Vertebrate Zoology* **67**: 261–269.
- Pringle, J.A. (1944): Stridulations in the South African egg-eating snake, *Daspeltis scaber*, Linn. *Nature* **154**: 709.
- Siler, C.D., Welton, L.J. (2010): Geographic variation in Philippine mimicry system: hypothesized widespread coral snake (*Hemibungarus calligaster*) mimicry by lepidopteran larvae (*Bracca* sp.) on Luzon Island, Philippines. *Herpetological Review* **41**: 427–430.
- Siler, C.D., Welton, L.J., Siler, J.M., Brown, J., Bucol, A., Diesmos, A.C., Brown, R.M. (2011): Amphibians and reptiles, Luzon Island, Aurora Province and Aurora Memorial National Park, northern Philippines: new island distribution records. *Check List* **7**: 182–195.
- Sison, R., Gonzales, P.C., Ferner, J.W. (1995): New records from Panay, Philippines. *Herpetological Review* **26**: 48–49.
- Supsup, C.E., Puna, N.M., Asis, A.A., Redoblado, B.R., Panaguinit, M.F.G., Guinto, F.M., et al. (2016): Amphibians and reptiles of Cebu, Philippines: the poorly understood herpetofauna of an island with very little remaining natural habitat. *Asian Herpetological Research* **7**: 151–179.
- Taylor, E.H. (1922): *The Snakes of the Philippine Islands*. Manila, Philippines, Bureau of Printing.
- Tin-Myint, Rai-Mra, Maung-Chit, Tun-Pe, Warrell, D.A. (1991): Bites by the king cobra (*Ophiophagus hannah*) in Myanmar: successful treatment of severe neurotoxic envenoming. *Quarterly Journal of Medicine* **80**: 751–762.
- Warrell, D.A. (2014): Venomous and poisonous animals. In: *Manson's Tropical Infectious Diseases*, 23rd Edition, p. 1096–1127, Farrar, J., Hotez, P.J., Junghanss, T., Kang, G., Lalloo, D., White, N.J., Saunders, W.B., Eds., Amsterdam, The Netherlands, Elsevier.
- Weinell, J.L., Hooper, E., Leviton, A.E., Brown, R.M. (2019): Illustrated key to the snakes of the Philippines. *Proceedings of the California Academy of Sciences* **66**: 1–49.
- Weldon, P.J., Burghardt, G.M. (1979): The ophiophage defensive response in crotaline snakes: Extension to new taxa. *Journal of Chemical Ecology* **5**: 141–151.
- Wiegmann, A.F.A. (1835). Amphibien, p. 185–268. In: *Beiträge zur Zoologie Gesammelt auf einer Reise um die Erde*. Siebente Abhandlung. Meyen, F.J.F., Ed., Halle, Germany, Nova Acta Physico-Medica Academia Caesarea Leopoldino-Carolina.
- Wüster, W., Crookes, S.I., Ineich, I., Mané, Y., Pook, C.E., Trape, J.F., Broadley, D.G. (2007): The phylogeny of cobras inferred from mitochondrial DNA sequences: evolution of venom spitting and the phylogeography of the African spitting cobras (Serpentes: Elapidae: *Naja nigricollis* complex). *Molecular Phylogenetics and Evolution* **45**: 437–453.
- Young, B.A. (1991): Morphological basis of "growling" in the king cobra, *Ophiophagus hannah*. *Journal of Experimental Zoology* **260**: 275–287.
- Young, B.A. (2003): Snake bioacoustics: toward a richer understanding of the behavioral ecology of snakes. *The Quarterly Review of Biology* **78**: 303–325.
- Young, B.A., Kardong, K. (2010): The functional morphology of hooding in cobras. *Journal of Experimental Biology* **213**: 1521–1528.
- Young, B.A., Lalor, J., Solomon, J. (1999a): The comparative biomechanics of an ophidian defensive behaviour: head triangulation in hognose snake (*Heterodon*) and an egg-eating snake (*Daspeltis*). *Journal of Zoology* **2**: 169–177.
- Young, B.A., Meltzer, K., Mersit, C., Abishahin, G. (1999b): Cloacal popping in snakes. *Journal of Herpetology* **33**: 557–566.