

# Multivariate Characterization of Phenotypic Variation from throughout the Geographic Ranges of Philippine False Coral Snakes: Two Species or Four?

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**The Philippine-endemic elapid genus *Hemibungarus* consists of three described species that are widely distributed across northern and central portions of the archipelago. *Hemibungarus calligaster*, *H. mcclungi*, and *H. gemianulis* were originally diagnosed, and remain recognized today, primarily based on differences in color pattern. Previous studies and faunal checklists suggest that these species occupy distinct geographic distributions within the Philippines. However, the relatively low numbers of specimens in collections and the misidentification of older specimens under outdated taxonomy have hampered a synthetic understanding of their actual distributional limits. Thus, an in-depth revisiting of the range of external morphological and color pattern variation within and among each species is still needed to clarify species boundaries and determine whether distributional limits change once properly documented. We provide a geographic assessment of morphological variation, using 98 specimens of *Hemibungarus* from institutional collections and public databases to reevaluate the range of phenotypic variation exhibited by each taxon and critically assess the geographic ranges of all three species of *Hemibungarus*. We use these data and multivariate statistics (principal coordinate and linear discriminant analyses) to demonstrate quantitatively how meristic data support the phenotypic distinctiveness of each species and to update the identifications of all accessible specimens. Georeferencing all specimens reidentified with morphological data indicates that *H. calligaster* is limited to central and northern regions of Luzon Island, whereas *H. gemianulis* is restricted to islands in central Philippines (Visayas). *Hemibungarus mcclungi*, previously considered restricted to the Bicol Peninsula in southern Luzon, appears to be more widely distributed—extending north into central and northern Luzon. We also identify a population of *Hemibungarus* that is intermediate in morphology between the parapatric *H. calligaster* and *H. mcclungi*, which raises the question of species boundaries and should be the focus of future study. Overall, our results provide a much-needed reconsideration of the identities of all available specimens in the world's biodiversity repositories, which use newly summarized data to elucidate the geographic distributions of the members of this enigmatic elapid genus, identify future directions for research on this group, and highlight the importance of returning to verified species occurrence data from the source (museum specimens) when considering biogeographical questions, species boundaries, and all related natural history studies.**

THE Indo-Australian Archipelago is one of the most widely studied geographic realms and is recognized as an ideal model study system for classic biogeographic and speciation theory (Wallace, 1869; Wilson and MacArthur, 1967). This region and its 20,000+ islands were formed through a complex mosaic of geological processes, such as Quaternary sea-level changes, tectonic uplift, and volcanism (Hall, 2009; Lohman et al., 2011; Husson et al., 2020). These events and the resulting heterogeneous landscapes have led to a wide array of flora and fauna, much of which is endemic, with complex evolutionary histories (Woodruff, 2010; Brown et al., 2013; de Bruyn et al., 2014). Some of the most well-studied groups that reflect the biogeographic complexity in Southeast Asia include agamid lizards (Klabacka et al., 2020), ranid frogs (Chan et al., 2020), homalopsid snakes (Bernstein et al., 2021), zenarchopterid fishes (de Bruyn et al., 2013), and planorbisid snails (Gauffre-Autelin et al., 2021). However, despite continuing advances in DNA sequencing technology and computational analyses, several reptilian groups remain

understudied due to their secretive habits and inadequacy of sampling efforts in their distributional ranges.

False coral snakes (genus *Hemibungarus*) are a small, enigmatic group of elapid snakes endemic to the Philippines. Little is known about their natural history and biology (Leviton, 1964), and specimens are generally rare in museum collections from many countries. The genus is comprised of three proteroglyphous species (Brown et al., 2018), which utilize venom like the closely related and highly venomous elapids *Dendroaspis* and *Ophiophagus*, the latter of which is sister to *Hemibungarus* (Castoe et al., 2007; Pyron et al., 2013; Brown et al., 2018; von Plettenberg Laing, 2018). However, the potency of this venom is unknown, as bites are seldom reported (but see Gaulke, 2011). Some published accounts have found that sympatric lepidopteran larvae (*Bracca* sp.) closely resemble *Hemibungarus* in color and pattern, potentially indicating that *Hemibungarus* may be a model system for mimicry (Brown, 2006; Siler and Welton, 2010). This group's taxonomy and evolution also remain to be studied

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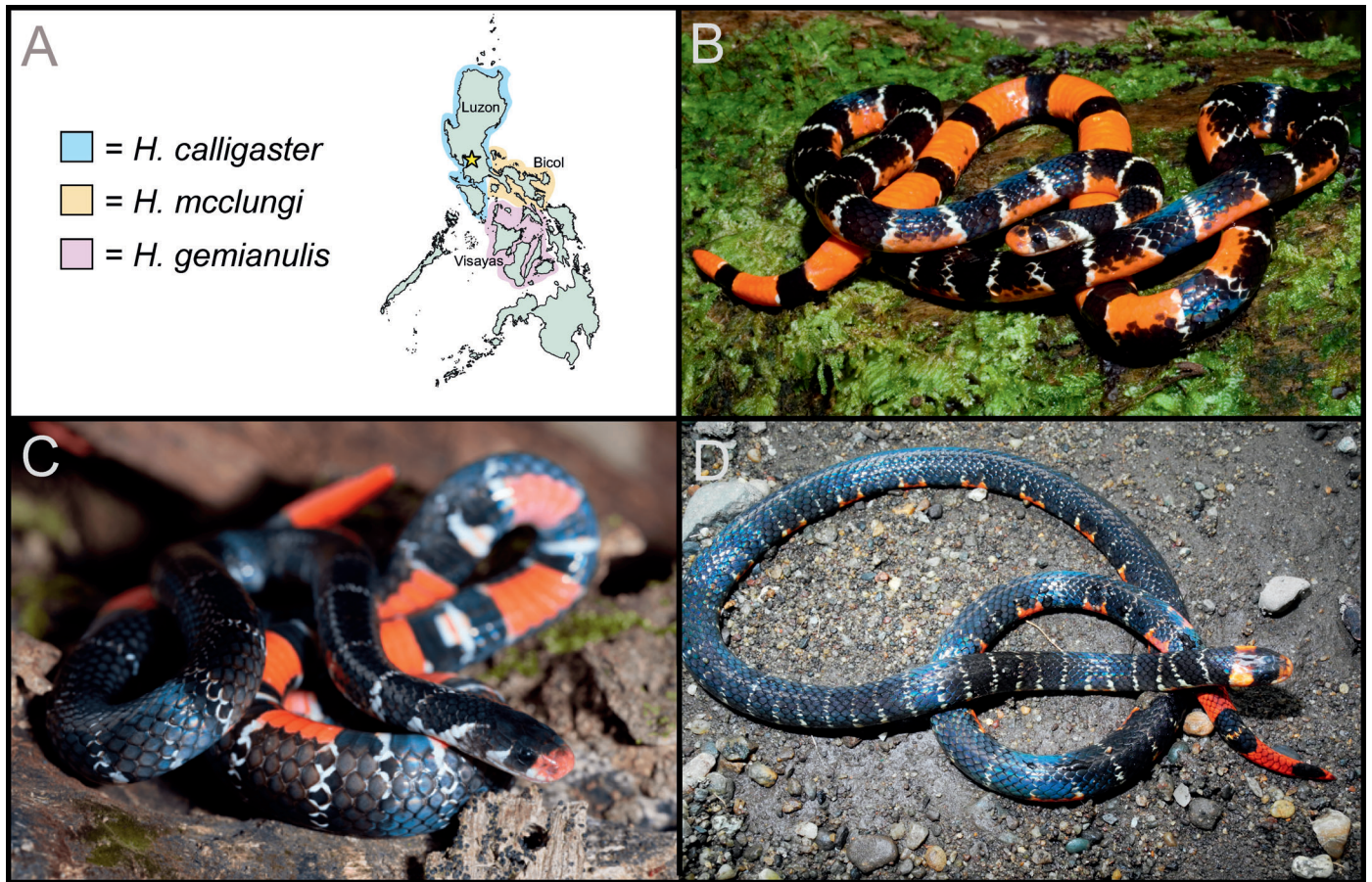
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**Fig. 1.** The three currently recognized species of *Hemibungarus*, all of which are endemic to the Philippines. (A) Hypothesized distribution of *H. calligaster* (blue: central and northern Luzon), *H. mcclungi* (orange: central and southern Luzon), *H. gemianulis* (purple: West Visayan islands and Masbate); star (★) represents Manila on Luzon Island. *In situ* photographs of live *H. calligaster* (B; KU 323337; photo: © C. Siler), voucher specimen of *H. mcclungi* (C; OMNH 45930; photo: © N. Huron), and *H. gemianulis* (D; specimen not collected; photo: © M. Gaulke).

and has changed little since Leviton's (1964) taxonomic review, except that subspecies were elevated to species (Leviton et al., 2014, 2018). Currently, each species is diagnosed based on its color pattern and geographic distribution. It is thought that *H. gemianulis* is restricted to the islands in the West Visayan region of central Philippines, *H. calligaster* to northern and central Luzon, and Brown et al. (2018) hypothesized that *H. mcclungi* is restricted mainly to the Bicol Peninsula of southern Luzon, which, together with nearby smaller islands of Polillo and Catanduanes, constitutes a distinct faunal subregion with considerable endemism (Brown et al., 2018; Leviton et al., 2018; Fig. 1A). This arrangement has not been critically examined, with accompanying data, and the identifications of the three species (Weinell et al., 2019) still essentially rely on Leviton's (1964) color pattern character states and geographic distribution (Brown et al., 2018).

All known species of *Hemibungarus* have a black dorsum with thin, white annuli and a blood orange venter with thick, black bands (Weinell et al., 2019). *Hemibungarus mcclungi* differs from *H. calligaster* (Fig. 1B, C) by possessing dorsal white annuli which extend into the black ventral bands as an intervening white bar (absent in *H. calligaster*); *H. gemianulis* (Fig. 1D) differs from its congeners by a lack of temporal pigmentation (pigmented with melanin in *H. calligaster* and *H. mcclungi*).

Although the current knowledge of this group acts as a starting point for investigating systematic, ecological, and biogeographic hypotheses, their cryptic habits and distribution in poorly sampled, hard-to-reach regions and virtually unstudied subterranean habitats preclude the acquisition of natural history information to test such hypotheses. Historically, this has led to reduced sample sizes when identifying *Hemibungarus* and uncertainty regarding species boundaries. Furthermore, few specimen-associated genetic resources are available for species of *Hemibungarus* (a critical limiting factor for studying natural history; Monfils et al., 2017; Meineke et al., 2019). Institutional collections have few specimens and/or identifications have not been updated under current taxonomy (i.e., our surveys of accessible collections found numerous specimens identified as "*Calliophis* sp.," "*Maticora* sp.," or the nominal species *H. calligaster* was applied to specimens we eventually reidentified as *H. mcclungi* or *H. gemianulis*; see Results and Discussion). Thus, given the widespread confusion, and our concern for the downstream inferences to be based on the fundamental principles of specimen identification and specimen-based, properly validated geographical occurrences, we started with a brute force approach to reidentify all accessible museum specimens. We then collected, georeferenced, and summarized each species' geographical distribution. Finally, we collected external morphological data to perform quantitative multivariate

analyses on 98 specimens of *Hemibungarus* from 14 natural history collections. In this study, we use our newly obtained data to (1) statistically reconsider the morphological distinctiveness of the three described species of *Hemibungarus* to facilitate proper identification of specimens in future work, and (2) characterize the geographic distributions of *H. calligaster*, *H. mcclungi*, and *H. gemianulis*, based on species occurrences, validated with correctly identified specimens, and specimen-associated locality information.

## MATERIALS AND METHODS

### Data Collection

**Specimens and morphological data.**—Data from specimens were obtained from 14 natural history collections (Supplemental Table S1 [see Data Accessibility]; institutional abbreviations follow Sabaj, 2020) and one newly salvaged dead-on-road specimen, encountered during a 2019 field expedition in the Caramoan Peninsula (Camarines Sur Province, Municipality of Caramoan, Luzon; see Acknowledgments for permit details). We prioritized obtaining data from specimens that were associated with locality information (minimum level = provincial). However, we obtained meristic data and morphological measurements from specimens lacking associated locality information so as to objectively (independently) evaluate identifications of species lodged in the world's natural history collections. Because the taxonomy of *Hemibungarus* is currently based on temporal pigmentation and dorsal and ventral banding patterns, we also used photographs of museum vouchers (when specimens could not be accessed in-person by JMB) because these characters can be conveniently captured photographically. Thus, initial identifications relied on color pattern characters, and subsequently, on additional diagnostic characters from external morphology. Morphological data included: scale type (keeled vs. smooth), apical pits (present vs. absent), snout-vent length, tail length, dorsal scale rows at mid body, ventral scale count (not including cloacal plate) using the methods of Dowling (1951), subcaudal scale type (complete vs. divided), subcaudal scale count (excluding the terminal spine), head length (from rostral scale to end of mouth gape), head width (at level of anterior margin of the parietal scales), body width (average of three measurements at midbody), number of scales bordering left parietal outer margin, number of scales bordering right parietal outer margin, mental scale contacting anterior chin shields (adjacent vs. separate), white ventral annuli bordering ventral black bands (present vs. absent), white annuli within ventral black bands (present vs. absent), number of white dorsal annuli (dorsal black bands counted for juveniles), number of ventral black bands, number of upper labials, number of lower labials, number of ventral scales per orange ventral band, number of ventral scales per black ventral band (includes white annuli in *H. mcclungi* and *H. gemianulis*), temporal region pigmented with melanin (present vs. absent), annuli on dorsal black bands of tail (present vs. absent), state of ventral annuli (absent vs. faded/partial/blurry vs. distinct/complete), upper temporal scale divided (present vs. absent), dorsal white annuli present in juveniles (present vs. absent). Continuous data measurements were recorded using a Mitutoyo digital caliper or measuring tape; continuous data from photographs were obtained by calibrating the measure tool in FIJI (Fiji Is Just Image; Rueden et al., 2017) with a scale bar.

**Multivariate statistics.**—Continuous and categorical morphological measurements were analyzed using multivariate statistics in R v.4.0.2 (R Core Team, 2020) using the following packages: *MASS* (Venables and Ripley, 2002), *mice* (van Buuren and Groothuis-Oudshoorn, 2011), *ggbiplot* (Vu, 2011), *car* (Fox and Weisberg, 2019), *labdsv* (Roberts, 2019), *caret* (Kuhn, 2020), *vegan* (Oksanen et al., 2020), *stats* (R Core Team, 2020), and *dplyr* (Wickham et al., 2020). All values were log transformed prior to analyses. We used multidimensional scaling (principal coordinates analysis [PCoA]; *vegan* and *labdsv* packages) to assess the distribution of our data in morphospace, and we preliminarily sorted our samples into four groups: *H. calligaster*, *H. mcclungi*, *H. cf. mcclungi*, and *H. gemianulis*. The third category ("*H. cf. mcclungi*") was adopted because multiple individual specimens exhibited color and scale pattern phenotypes intermediate between *H. calligaster* and *H. mcclungi* (see Results: Morphological investigation). Because some of our data were not normally distributed and are categorical in form (and PCoA analysis ignores classification), we also analyzed our data using supervised machine learning classification (linear discriminant analysis [LDA]; *caret* package). The *caret* package creates a confusion matrix to assess the prediction accuracy of the LDA. Categorical data were converted to numerical values representing discrete states. Because juveniles have a different color pattern and will inevitably skew continuous data measurements (e.g., length, width, etc.), we excluded these from the PCoA and LDA analyses. Additionally, linear measurements (e.g., head length, head width) were not standardized by body size, as this would cause overrepresentation of body size data, ultimately leading to potential bias and overcomplexity in our analysis. While we briefly mention the results of our PCoA, we focus on the results of the LDA in more detail, as the latter analysis allows us to estimate accuracy using a confusion matrix (see Results). We also excluded specimens in which photographs or specimen quality did not yield complete trait data, such as if all ventral scales or number of color bands were not visible in a photograph; invariant traits (scale type, apical pits, subcaudal division) were not included in the analyses, but we include them in this study for completeness and future investigations.

**Geographic distributions.**—All voucher and photographed specimens were identified as *H. calligaster*, *H. mcclungi*, *H. cf. mcclungi*, or *H. gemianulis* based on their current delimitation using temporal region pigmentation and dorsal and ventral banding pattern. Polygon shape and elevation map files for the Philippines were downloaded from DIVA-GIS (<https://www.diva-gis.org/>). We used QGIS v3.4.3 Madeira (QGIS.org, 2020. QGIS Geographic Information System. QGIS Association, <https://www.qgis.org>) to provide coordinates for specimens with minimal locality. We included specimens only if they were associated with original collector information at least to the level of the province in which a specimen was collected. If coordinates were not available, we used centroids of the smallest locality level as our best approximation of coordinates for that specimen. Specimens that could not be identified to the species level were not included. We also included four observations from iNaturalist (Ueda, 2020), when images were of sufficient quality to facilitate species-level identification based on criteria used in this study. These four observations were not



**Fig. 2.** *In situ* photographs of a juvenile *Hemibungarus mcclungi* (A, KU 348442) and an adult (B, specimen deposited at KU, not yet cataloged), both from Sorsogon Province, southern Luzon Island. Note red and black bands, encircling entire body of juvenile, which lacks melanistic temporal (lateral head) pigmentation; in contrast, adult red coloration is restricted to venter and has melanistic temporal region. Photos: © J. B. Fernandez and RMB.

included in the statistical analyses but are identified at the species level based on temporal pigmentation and banding pattern. Some specimens used in the morphological examination had no or limited locality data; thus, they could not be included in the test of geographic distributions.

## RESULTS

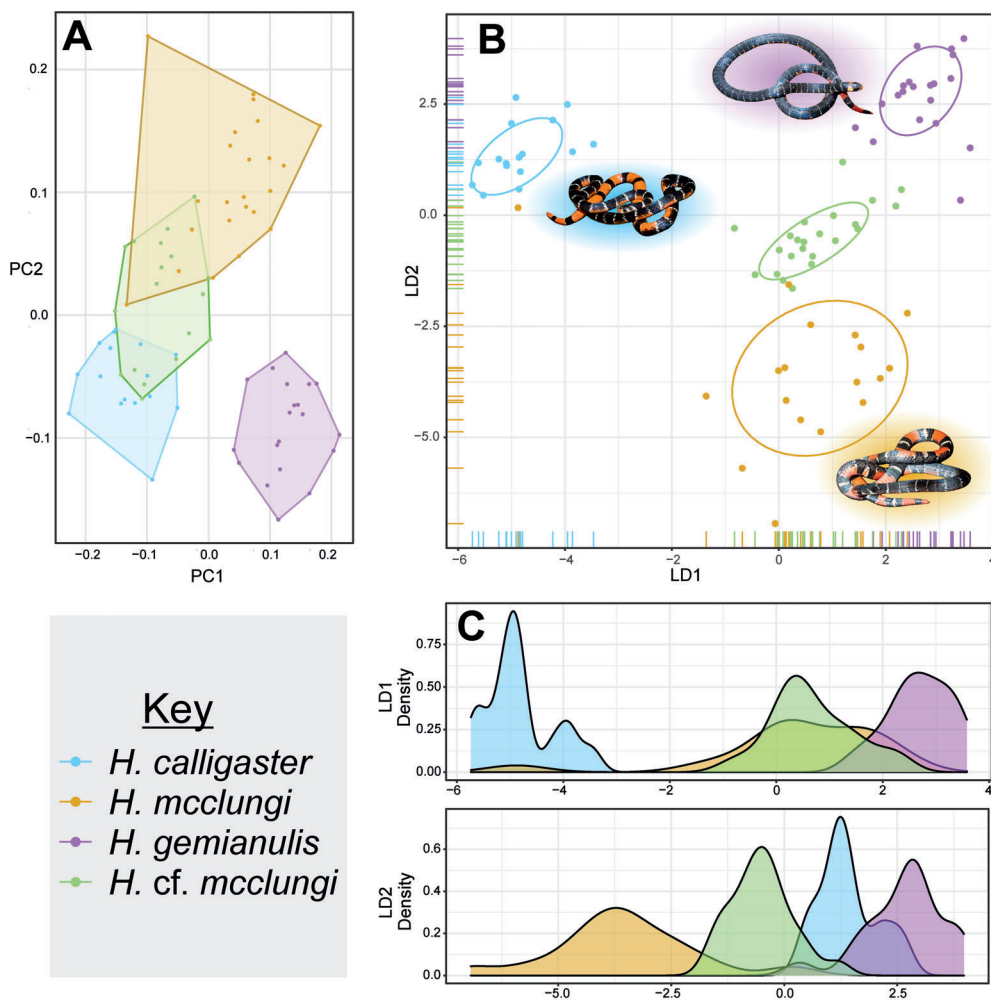
**Morphological investigation.**—A total of 94 specimens were examined, ten of which were juveniles. We found that a large number of specimens (~42%) in natural history museums were misidentified (usually as “*H. calligaster*”). Diagnostic characters reliably distinguishing the groups in this study agree with those provided by previous works (Leviton, 1964; Leviton et al., 2018; Weinell et al., 2019) and include temporal pigmentation, ventral banding pattern, and dorsal band pattern on the tail (juveniles only, Brown et al., in press). *Hemibungarus calligaster* is readily differentiated from *H. mcclungi* by the lack of a white bar within the black ventral bands (present in *H. mcclungi*) and from *H. gemianulis* by the presence of melanistic pigmentation in the temporal regions of the head (absent in *H. gemianulis*, which have red/blood orange temporal regions). Juveniles of all three species have black and red/blood orange bands that completely encircle

the body (red/orange scales only on venter in adults), and head pigmentation amongst the juveniles of the three species are similar, with all of them lacking melanin in the temporal regions, unlike in adults (Fig. 2; Brown et al., in press). However, juveniles can still be distinguished at the species level by the following characteristics: *H. calligaster* with white bar within ventral black bands absent (present in *H. mcclungi* and *H. gemianulis*); *H. mcclungi* with thin dorsal white annuli within dorsal black bands absent (absent in *H. calligaster*; present in *H. gemianulis*); *H. gemianulis* with thin dorsal white annuli within dorsal black tail bands present (absent in *H. calligaster* and *H. mcclungi*). The dorsal thin white annuli that connect to the white bar on the ventral black bands do not appear until later in life for *H. mcclungi*, but appear to be present from birth in *H. gemianulis* (Brown et al., in press; this study). Of the 94 samples examined, we confidently/unambiguously identified 20 *H. calligaster*, 28 *H. mcclungi*, and 24 *H. gemianulis*, respectively.

Additionally, 22 specimens were found to be intermediate between *H. calligaster* and *H. mcclungi*, and were tentatively labeled “*H. cf. mcclungi*” for subsequent consideration. These specimens had a ventral white bar present, but appeared faded or broken (distinct in *H. mcclungi*), or their ventral scale counts or average body width were placed between the ranges of these characters reported by previous studies (Leviton, 1964; Weinell et al., 2019). The four observations from iNaturalist were identified as *H. calligaster*, *H. mcclungi*, *H. gemianulis*, and *H. cf. mcclungi*. A summary of morphological data for all specimens examined is provided in the Supplemental Table S2 (see Data Accessibility).

**Multivariate statistics.**—A total of 77 adult *Hemibungarus* were included in our PCoA and LDA. Our PCoA shows evidence of multiple groups of *Hemibungarus* (Fig. 3A). Along the first principal coordinate (PC1), *H. gemianulis* is distinct from *H. calligaster* and *H. cf. mcclungi*, and slightly overlaps with *H. mcclungi* (Fig. 3A). *Hemibungarus calligaster*, *H. cf. mcclungi*, and *H. mcclungi* broadly overlap along PC1. Along the second principal coordinate (PC2), *H. calligaster* and *H. gemianulis* occupy a very similar morphospace (Fig. 3A). Whereas *H. calligaster* and *H. mcclungi* form two different groups, *H. cf. mcclungi* bridges the morphospace between these two species (Fig. 3A).

The confusion matrix of our LDA was 98.7% accurate, with only one specimen tentatively identified as *H. mcclungi* being recovered as *H. calligaster*; all other specimens were correctly classified by their taxonomic designations using the machine learning methods. Linear discriminants 1 and 2 (LD1, LD2) contain 48% and 36.8% of the variation, respectively (LD3 15.2%, not discussed). Our LDA showed different patterns compared to the PCoA, but provides evidence of four morphologically distinct groups (Fig. 3B). *Hemibungarus calligaster* is distinct from the other three groups along LD1; the variation of *H. cf. mcclungi* along LD1 is encompassed by the variation observed in *H. mcclungi*. *Hemibungarus gemianulis* slightly overlaps with *H. mcclungi* and *H. cf. mcclungi* along LD1. All four groups are distinct along LD2 (Fig. 3B). Traits that contributed to high levels of variation in LD1 were the number of ventrals, body width, the presence of white bars in the ventral black bands, and the number of dorsal annuli; for LD2, the traits that contributed the most variation were the number of ventrals, the presence of white bars in the ventral black bands, the number of dorsal annuli, and the



**Fig. 3.** Multivariate analyses of *Hemibungarus calligaster*, *H. mcclungi*, *H. gemianulis*, and *H. cf. mcclungi*. (A) Multivariate ordination principal components, with each point corresponding to a single specimen. (B) Linear discriminant analysis with 68% Gaussian data ellipses. Density rugs (colored lines) on axes correspond to plotted points in morphospace. (C) Density plots for linear discriminant axes 1 (LD1; top) and 2 (LD2; bottom). Photograph credits: *H. calligaster* (KU 323337, © C. Siler), *H. mcclungi* (© J. B. Fernandez and RMB), and *H. gemianulis* (© M. Gaulke).

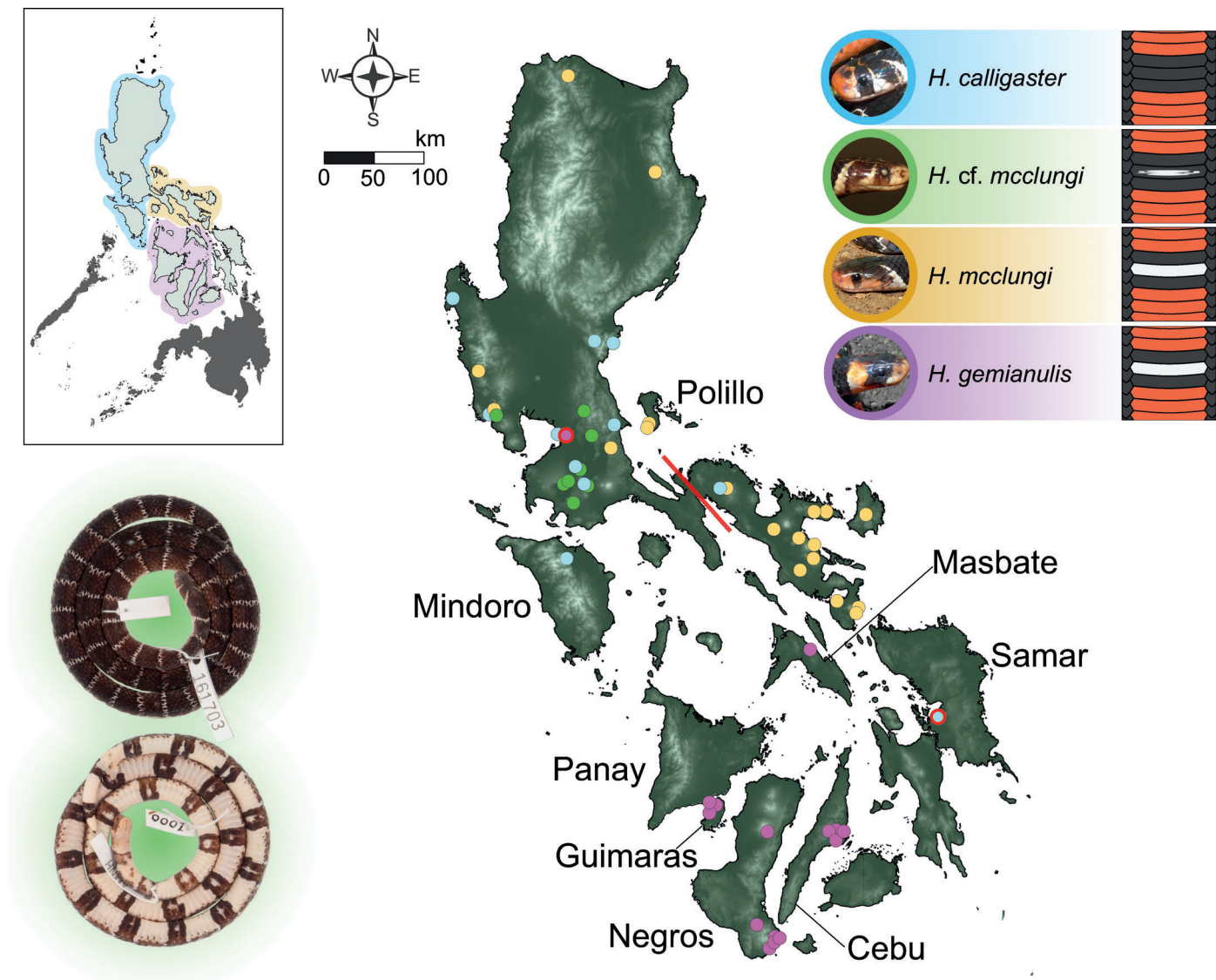
highest number of orange scales in ventral bands. The same LDA was performed with the removal of characters that strongly deviated from normal distributions; the confusion matrix results and accuracy were identical, and the only difference in morphospace was *H. calligaster* was encompassed in the morphospace of *H. mcclungi* (in comparison to *H. cf. mcclungi*; results not shown).

**Geographic distributions.**—We plotted georeferenced localities for 75 individuals on a map of the Philippines (Fig. 4). Based on our reidentifications of the species and their specimen-associated locality records, true *H. calligaster* appears to be found in northern and central regions of Luzon, and on Mindoro, located only ~10 km south of Luzon (Fig. 4). One record in our dataset has a locality of ‘Samar’ which we suspect is an error (see Discussion; Kucharzewski and Tillack, 2007). Most *H. mcclungi* are from central to south Luzon, and Polillo Island (Quezon Province). Surprisingly, several reidentified specimens confirm records of *H. mcclungi* from northern Luzon for the first time (Fig. 4). The range of *H. gemianulis* is restricted to the islands of Negros, Panay, Guimaras, Cebu and Masbate, which are all part of the same Pleistocene Aggregate Island Complex (Brown and Diesmos, 2002, 2009) in the central Philippines (Fig. 4). One record exists from ‘Manila,’ on the island of Luzon, which is likely in error (see Discussion). Coordinate localities of all specimens used for geographic

distributions are provided in Supplemental Table S3 (see Data Accessibility).

## DISCUSSION

We provide an extensive morphological dataset for the endemic snake genus *Hemibungarus*, consisting of three recognized species from the Philippines: *H. calligaster*, *H. mcclungi*, and *H. gemianulis*. Our new data highlight what is currently known and unknown about the species’ distributions and morphological distinctiveness. This exercise brings the global collection resources for *Hemibungarus* and their specimen-associated locality records up-to-date and identifies several key next steps for investigating the species boundaries and natural history of these poorly known snakes. Other than a few studies related to potential mimicry systems (Brown, 2006; Siler and Welton, 2010), taxonomy (Leviton et al., 2014; Brown et al., 2018), and occurrence accounts and checklists (Gaulke, 2011; Leviton et al., 2018; Weinell et al., 2019), little is known of these elapid snakes, which is surprising given their close relationships to king cobras (Castoe et al., 2007). Our multivariate analyses of morphological data reinforce the identifications, diagnoses, and morphological distinctiveness of the three described forms and includes both continuous and categorical data. However, the differential results obtained from PCoA versus those from LDA (Fig. 3A, B; analysis strategies differing primarily by their means of dimensionality reduction) preclude firm conclu-



**Fig. 4.** Map depicting 75 unambiguously identified and newly georeferenced specimens of *Hemibungarus* (see text for details) in relation to the entire archipelago (upper left inset). See Supplemental Table S3 for additional details (see Data Accessibility). Red line = portion of Philippine “mobile belt” fault. Color-coded species occurrence points correspond to key (upper right), depicting head pigmentation and ventral color pattern for each putative taxon (note: only general color pattern shown; scale counts and exact details in line art not based on morphological data or specimen photos). Occurrence points with red outline in Manila and on Samar represent specimens with questionable locality data. Lower left inset: dorsal and ventral photograph of *H. cf. mcclungi* (AMNH 161703) illustrating faded white bars in ventral black bands (specimen photos: © K. McCartha).

sions or any possible taxonomic recommendations at present, particularly concerning the phenotypically intermediate specimens of “*H. cf. mcclungi*.” Although the possibilities hint at possible taxonomic solutions ranging from two species to four species, we hold taxonomic changes in abeyance until molecular data are available and modern statistical species delimitation analyses can be performed.

Interestingly, the PCoA and LDA analyses (both with and without non-normally distributed characters) depict *H. cf. mcclungi* generally occupying its own morphospace—but whether this result is best interpreted as a possible new species, or intraspecific variation of a single, widespread Luzon species, cannot be concluded without molecular data and broader geographic sampling. Alternatively, the intermediate morphology of *H. cf. mcclungi* could indicate a population of secondary contact between *H. calligaster* and *H. mcclungi*. About 120 km east of the southernmost records of

*H. cf. mcclungi* is an active fault system corresponding to the Philippine mobile belt (Barrier et al., 1991; Rangin, 1991; Tsutsumi and Perez, 2013). Here, the two primary components of Luzon collided ~3–5 million years ago (Hall, 2002; Esselstyn and Brown, 2009), resulting in the formation of the largest island in the archipelago (Fig. 4). With our current sampling, most records of *H. mcclungi* are east and south of this part of the Philippine fault (the Guinayangan fault), while most specimens of *H. calligaster* are west and north of this line (with the exclusion of the Mindoro and Samar records, discussed below). Although snake hybrid zones have seldom been studied in great detail, intermediate phenotypes have been suggestive of secondary contact (Martínez et al., 2006; Martínez-Freiría et al., 2009; Tarroso et al., 2014), especially in areas recognized as contemporary or historic biogeographic barriers (Burbrink et al., 2020). Other studies that have used dimensionality reduction methods on

putative hybrids have recovered similar patterns to those observed in this study (e.g., Asztalos et al., 2020). Additionally, the observation of *H. mcclungi* and *H. cf. mcclungi* west of the Guinayangan fault, coupled with the apparent lack of records of most *H. calligaster* east of the fault (except one specimen), may be evidence of a unidirectional movement of these snakes. If so, this observation may be related to the narrow landscape (17 km wide) of the Tayabas isthmus, just west of the Philippine fault, which may have limited bidirectional movement of these populations (Kindler et al., 2017). However, without molecular data, we cannot distinguish between such hypotheses. The mechanisms that isolate populations (i.e., geographical vs. ecological) and impact hybrid zone dynamics require complex analyses based on large sample sizes, dense geographic coverage, and multi-locus or genomic data. Until such sampling becomes available, and the phylogenetic relationships and historical population demography of *Hemibungarus* can be studied, the scenarios for possible gene flow, phenotypic characterization of hybrids, position and width of clines, and an accurate measure of species richness, remain unknown.

Some of the specimens in our study show distributions that are anomalous and which we find biogeographically unlikely. In particular, these involve a specimen of *H. calligaster* from Samar and a record of *H. gemianulis* from Manila. Specimen localities listed as 'Manila' in museum databases may be artifactually related to documents accompanying specimens, documenting the port of shipment when specimens were sent to European museums (Brown and Alcala, 1978; Crombie, 1992; Brown et al., 2002). It is uncertain at this point if other records, such as *H. calligaster* from Samar (Kucharzewski and Tillack, 2007), are true extralimital occurrences or represent transcription errors. Islands in the East Visayas and in southern Philippines are comparatively underexplored compared to northern portions of the archipelago, and biodiversity surveys continue to reveal surprising discoveries (Sanguila et al., 2016; Brown et al., 2018; Diesmos et al., 2020).

In this study, we synthesized and expanded on the current knowledge of identification and distribution of *Hemibungarus* species, which remain understood only at a cursorial level. These snakes may hold medical significance due to their venom (Waheed et al., 2017) and play an essential role in their fossorial environments, whether as a potential mimicry system (Brown, 2006; Siler and Welton, 2010) or as subterranean/terrestrial predators (Meneses, 2020). Our study demonstrates the importance of returning to voucher specimens in the natural history collections of museums and incorporating records from public databases (e.g., iNaturalist) for elucidating the natural history of enigmatic groups like these elapid snakes. In addition, a more detailed examination of populations in the vicinity of the Philippine fault zone may have biogeographic implications (such as filter or hybrid zones) that, to date, are poorly explored (Welton et al., 2010).

In the last few decades, our knowledge of the archipelago's herpetological diversity has expanded with the discovery of new genera and species (Linkem et al., 2011; Linkem and Brown, 2013; Weinell and Brown, 2018; Barley et al., 2020; Brown et al., 2020; Weinell et al., 2020), fine-scale documentation of their distributions (Siler et al., 2014; Sanguila et al., 2016; Clores et al., 2021), and inference of the evolutionary patterns and processes that shape this diversity (e.g.,

Esselstyn and Brown, 2009; Brown et al., 2013; Oaks et al., 2013, 2019). The region has become a model archipelago for a variety of organismal groups (Brown et al., 2013), but these recent works make it clear that much remains to be learned regarding diversity within poorly studied clades (Brown et al., 2016, 2017, 2020; Barley et al., 2020; Diesmos et al., 2020; Meneses et al., 2020; Wood et al., 2020). In the case of Philippine false coral snakes, eventual molecular data from increased sampling efforts may open up research opportunities capable of identifying species boundaries and the species' natural histories underlying evolutionary and ecological components. Studies utilizing genome-wide sampling of nuclear loci (e.g., double digest DNA restriction-site associated DNA, ultraconserved elements, anchored phylogenomics), as well as mitochondrial DNA, have successfully identified hybrid zones or found evidence of migration, introgression, or other processes affecting demographic histories of populations, ultimately providing insight into the evolutionary phenomena that shape species and aiding the determination of species limits (i.e., delimitation; Kindler et al., 2017; Schield et al., 2018; Mason et al., 2019; Burbrink et al., 2020; Slager et al., 2020; Chan et al., 2021). Although these opportunities may not materialize in the immediate future, our updated summaries of morphological and georeferenced species occurrence data from all publicly available global scientific specimen repositories provide a framework for the next level of inquiry, once sufficient collections and genetic resources are made available in the public domain.

#### DATA ACCESSIBILITY

Supplemental material is available at <https://www.ichthyologyandherpetology.org/h2021035>. All specimen data used for statistical analyses and georeferencing in this study can be found in Supplemental Tables S1–S3. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

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