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A New, Miniaturized Genus and Species of Snake (Cyclocoridae) from the Philippines

Jeffrey L. Weinell¹, Daniel J. Paluh², Cameron D. Siler³, and Rafe M. Brown¹

The Philippine archipelago is an exceptionally biodiverse region that includes at least 112 species of land snakes from 41 genera and 12 families. Recently, Cyclocoridae (formerly Lamprophiidae: Cyclocorinae) was proposed as a distinct, Philippine-endemic family, containing four genera: *Cyclocorus*, *Hologerrhum*, *Myersophis*, and *Oxyrhabdium*. Here, we describe an additional cyclocorid genus and species, *Levitonius mirus*, new genus and species, from Samar and Leyte Islands, Philippines. Molecular data support *Levitonius*, new genus, to be most closely related to *Myersophis* and *Oxyrhabdium*, and it shares multiple skeletal characteristics with these genera; *Levitonius*, new genus, differs from all of these taxa in body size, scalation, and other characters. Skeletal and other phenotypic data suggest that *Levitonius*, new genus, is fossorial and likely has a diet that is specialized on earthworms. *Levitonius mirus*, new genus and species, has a maximum total length of 172 mm and is at present the smallest known species in Elapoidea. Our results highlight the need for future work on Samar and Leyte Islands, which have received relatively little attention from systematists, in part because of a prevailing biogeographic paradigm that predicted (not necessarily correctly) that these islands would simply have a nested faunal subset of the Mindanao faunal region land vertebrates. The discovery of a strikingly distinct and phylogenetically divergent snake lineage on these landmasses joins numerous related studies calling for a wholesale reconsideration of the Pleistocene Aggregate Island Complex model (the PAIC paradigm of diversification) biogeographic framework.

THE terrestrial snake fauna of the Philippines includes 112 species from 12 families (Acrochordidae, Colubridae, Cyclocoridae, Elapidae, Gerrhopilidae, Homalopsidae, Lamprophiidae, Pareidae, Pythonidae, Typhlopidae, Viperidae, and Xenopeltidae) and 41 genera, including five genera that are endemic to the archipelago (Leviton et al., 2018; Uetz et al., 2020). The Philippine-endemic snake genera include the coral snakes of the genus *Hemibungarus* (Elapidae) and all members of Cyclocoridae, which contains *Cyclocorus* (Triangle-spotted Snakes), *Hologerrhum* (Stripe-lipped Snakes), *Oxyrhabdium* (Philippine Burrowing Snakes), and *Myersophis* (Philippine Mountain Snakes; Brown et al., 2018; Leviton et al., 2018; Weinell and Brown, 2018; Zaher et al., 2019). Cyclocoridae was only recently recognized as a distinct evolutionary lineage and currently includes four Philippine-endemic genera, seven species, and three subspecies (Weinell and Brown, 2018; Zaher et al., 2019).

Within Cyclocoridae, *Oxyrhabdium* contains two species, *Oxyrhabdium leporinum* and *O. modestum*, and occurs on multiple islands within the Luzon, Mindanao, and Western Visayas Pleistocene Aggregate Island Complexes (PAICs), the Babuyan Island Group, and the islands of Camiguin Sur, Lubang, Mindoro, and Siquijor (Fig. 1; Leviton et al., 2018; Weinell and Brown, 2018). *Cyclocorus* includes two species, *Cyclocorus lineatus* and *C. nuchalis*, and is distributed throughout the geographic range of *Oxyrhabdium*, as well as the islands of Sibuyan and Tablas (Leviton et al., 2018; Pili and del Prado, 2018). *Hologerrhum* includes two species, *Hologerrhum philippinum* and *H. dermali*, and is restricted to the islands of the Luzon PAIC (Luzon, Marinduque, Catanduanes, and Polillo), one island of the West Visayan PAIC (Panay), and a single island (Sibuyan) of the Romblon Island Group (Leviton et al., 2018). Currently, the genus *Myersophis*

includes a single, poorly known species, *Myersophis alpestris*, known only from the mountains of northern and central Luzon Island (Leviton et al., 2018). Recently, Weinell and Brown (2018) identified an unnamed cyclocorid lineage from Samar Island (then represented phylogenetically by a single individual that had been misidentified as a member of the genus *Calamaria*). We discovered two additional specimens of this unnamed lineage, which had been misidentified as members of the genus *Pseudorabdion*, from Samar and Leyte Islands. Members of *Calamaria* and *Pseudorabdion* (Colubridae: Calamariinae) are fossorial and superficially similar in appearance to the unnamed cyclocorid lineage (Leviton and Brown, 1959; Inger and Marx, 1965; Brown et al., 1999; Weinell and Brown, 2018).

Here, we describe a new genus and new species to accommodate the previously identified unnamed lineage, considering its distinctive morphology and deep phylogenetic divergence from the other members of the Cyclocoridae. We provide additional genetic, meristic, mensural, color pattern, and CT-surveyed osteological data (skeletal anatomy) for the new genus and species as well as representative species of the genera *Cyclocorus*, *Hologerrhum*, *Myersophis*, and *Oxyrhabdium*. In addition, we discuss these data with respect to their inferred phylogenetic relationships, diet, and ecological niche.

MATERIALS AND METHODS

Tissues, DNA extraction, PCR, and sequencing.—We obtained ethanol-preserved liver or muscle tissue samples from individuals that we collected, or that were collected by colleagues (including E. L. Rico, A. C. Diesmos, J. Fernandez, C. Infante, and C. Linkem) during multiple field expeditions in the Philippines between 2006 and 2012 and deposited in

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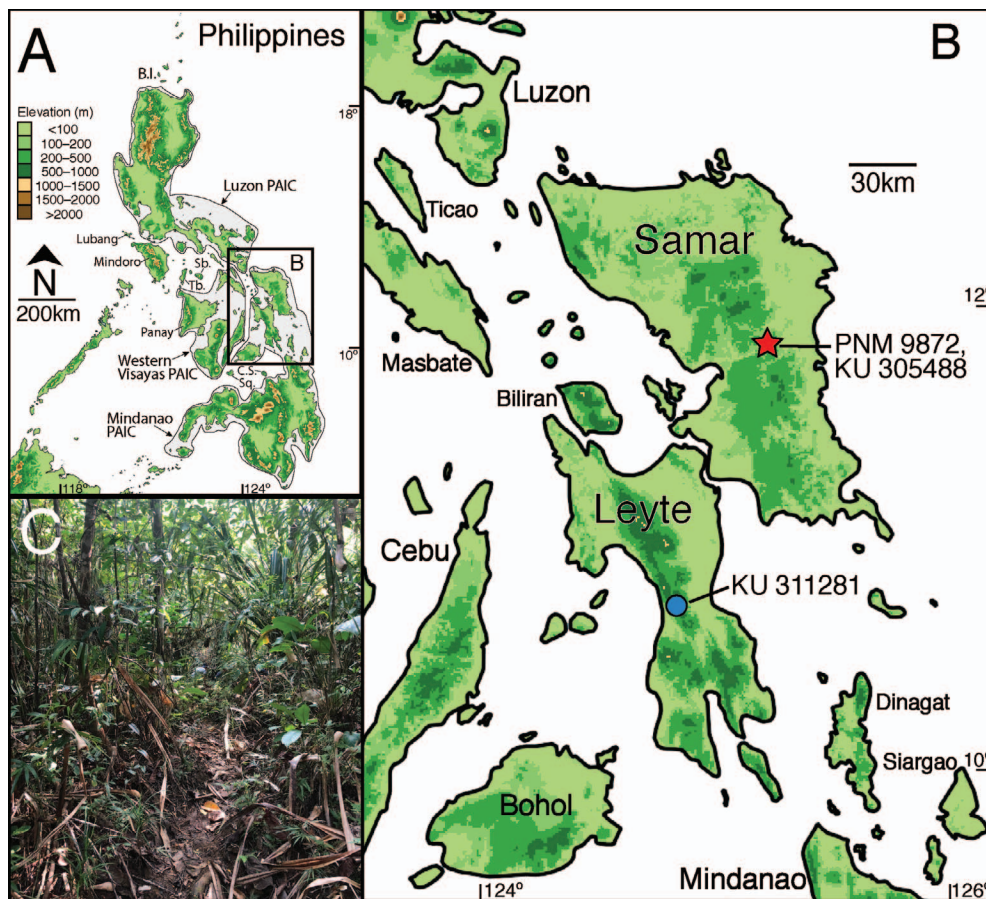


Fig. 1. (A) Elevation map of the Philippines, showing location of islands and PAICs mentioned in this article; B.I. = Babuyan Island Group, Sb. = Sibuyan Island, Sq. = Siquijor Island, C.S. = Camiguin Sur, Tb. = Tablas. (B) Samar, Leyte, and nearby islands; red star indicates the type locality of *Levitonius mirus*, new genus and species; blue circle indicates a second occurrence locality; (C) karst rainforest habitat at the *L. mirus*, new genus and species, type locality (Barangay San Rafael, Municipality of Taft, Samar Island).

the University of Kansas Biodiversity Institute herpetological collection. To extract and purify genomic DNA, we lysed tissues with Proteinase K and then used a Maxwell® Rapid Sample Concentrator Instrument with the Maxwell® 16 Tissue DNA Purification Kit (Promega Corporation). Polymerase chain reaction (PCR) was used to amplify either ~380 or ~1,350 base pairs (bp) of the mitochondrial gene Cytochrome-b (Cyt b) and ~580 bp of the nuclear, protein-coding gene oocyte maturation factor mos (CMOS). To amplify and sequence Cyt b, we used either novel primers or primers from Burbrink et al. (2000). Novel Cyt b primers (337F.23: 5'-TTCTGAGCAGCAACAGTAATCAC-3' and 732R.21: 5'-YTCTGGTTAATGTGTTGKGG-3') were designed using the Primer3 v0.4.0 (Untergasser et al., 2012) as implemented in Geneious® v6.1 and a Cyt b alignment that contained a broad diversity of snakes. To amplify and sequence CMOS, we used primers designed by Lawson et al. (2005). For each pair of primers, PCR involved 34 cycles of denaturation, annealing at 49°C (±1–3°C), and elongation. Amplified products were visualized using gel electrophoresis on 1.5% agarose gels. Purification of PCR product, cycle sequencing, cycle sequencing cleanups, and nucleotide sequence determination were conducted with standard GeneWiz® protocols.

Taxon sampling.—We collected new DNA sequence data from five individuals and four species, including one individual of *Psammodynastes pulverulentus*, *Oxyrhabdium leporinum*, and *O. modestum*, and two individuals of the new species described herein. The new species was included previously in a phylogenetic study and was referenced as “unnamed lineage”

(Weinell and Brown, 2018). In addition to our new sequence data, we included sequences from GenBank for 23 individuals (20 species, 18 genera) from Elapoidae and Colubridae (Table 1).

DNA assembly, variation, and divergence.—To *de novo* assemble and edit sequences, we used Geneious® v6.1, and we used the MUSCLE plugin in Geneious to align sequences (Edgar, 2004; Kearse et al., 2012). To calculate the number of variable sites, parsimony informative sites, and percent genetic distance between each pair of individuals, we used R v3.5.2 and packages ape v5.3 and Biostrings v2.50.2 (Paradis and Schliep, 2018; R Core Team, 2018; Pagès et al., 2019).

Phylogenetic inference.—We used IQ-TREE v1.6.4 (Nguyen et al., 2014) implemented on the web server W-IQ-TREE (Trifinopoulos et al., 2016) to infer a multi-locus maximum likelihood (ML) tree that includes representative species from Colubridae, Elapidae, and Lamprophiidae. We treated each locus as a separate partition, and we used the automatic model-selection feature (Chernomor et al., 2016) to identify and assign the best-fit substitution model for each partition during tree inference. We performed 1,000 ultrafast bootstraps to assess heuristic support for inferred clades, and we considered ultrafast bootstrap support values (UFboot) ≥ 95 to strongly support the monophyly of a group (Minh et al., 2013).

External morphology and color pattern.—We examined meristic, mensural, and color pattern characters for all known individuals ($n = 3$) of the new species. Meristic characters

Table 1. Species, catalog numbers, localities, and GenBank numbers for the individuals sampled in this study. Novel DNA sequences generated for this study are shown in bold; cells with dashes indicate missing data. Institutional abbreviations follow Sabaj (2020), with the following additions: CMRK = Christopher M. R. Kelly field numbers; GPN = E. O. Wilson Biodiversity Center herpetological collection, Gorongosa National Park.

| Species | Catalog # | Locality | Cytb | CMOS |
|--|--|--|-----------------------|---------------------------|
| <i>Aparallactus capensis</i> | GPN 134 | Gorongosa National Park, Mozambique | MG746886 | MG775883 |
| <i>Atractaspis bibronii</i> | PEM R15835 | Chibuto, Gaza Province, Mozambique | AY612023 | AY611932 |
| <i>Buhome depressiceps</i> | IRSNB 16404 | Itsiba, Boumi-Louetsi Department, Ngounié Province, Gabon | AY612042 | AY611951 |
| <i>Cyclocorus lineatus</i> | KU 328836 | Municipality of Buhi, Albay Province, Luzon Island, Philippines | MG458749 | MG458759 |
| <i>Cyclocorus lineatus</i> | KU 329413 | Municipality of Doña Remedios Trinidad, Bulacan Province, Luzon Island, Philippines | MG458750 | — |
| <i>Cyclocorus nuchalis</i> | KU 315163 | Municipality of Pasonanca, Zamboanga City Province, Mindanao Island, Philippines | MG458753 | MG458763 |
| <i>Cyclocorus nuchalis</i> | KU 321700 | Municipality of Pasonanca, Zamboanga City Province, Mindanao Island, Philippines | MG458754 | MG458764 |
| <i>Hologerrhum philippinum</i> | KU 330056 | Municipality of Gonzaga, Cagayan Province, Luzon Island, Philippines | MG458757 | MG458766 |
| <i>Hologerrhum philippinum</i> | KU 330752 | Municipality of Los Banos, Laguna Province, Philippines | MG458758 | MG458767 |
| <i>Lamprophis fiskii</i> | PEM R5764 | Northern Cape Province, South Africa | DQ486354 | DQ486178 |
| <i>Levitonius mirus</i> , new genus and species | KU 305488 | Barangay San Rafael, Municipality of Taft, Eastern Samar Province, Samar Island, Philippines | MN166284 | MN166281 |
| <i>Levitonius mirus</i> , new genus and species | PNM 9872 (KU 337269) | Barangay San Rafael, Municipality of Taft, Eastern Samar Province, Samar Island, Philippines | MG458751 | MG458760 |
| <i>Levitonius mirus</i> , new genus and species | KU 311281 | Municipality of Baybay, Leyte Province, Leyte Island, Philippines | MN166285 | MN166282 |
| <i>Micrelaps muelleri</i> | R 16944 | Ein Hod, Israel | MG746784 | MG775897 |
| <i>Myersophis alpestris</i> | KU 308684 | Municipality of Quezon, Nueva Vizcaya Province, Luzon Island, Philippines | MG458752 | MG458762 |
| <i>Naja kaouthia</i> | ¹ unknown; ² CAS 206602 | ¹ unknown; ² Ayeyarwady Region, Myanmar | ¹ FR693728 | ² AY058938 |
| <i>Ophiophagus hannah</i> | ¹ unknown; ² unknown | ¹ unknown; ² Bali, Indonesia | ¹ FR693730 | ² AZIM01001917 |
| <i>Oxyrhabdium leporinum</i> | KU 325975 | Municipality of Quezon, Nueva Vizcaya Province, Luzon Island, Philippines | MG458755 | MG458765 |
| <i>Oxyrhabdium leporinum</i> | KU 303287 | Barangay Vigo, Municipality of Lubang, Lubang Island, Occidental Mindoro Province, Philippines | MN166286 | MN166283 |
| <i>Oxyrhabdium modestum</i> | KU 326678 | Barangay Malagos, Municipality of Calinan, Davao City Province, Mindanao Island, Philippines | MG458756 | — |
| <i>Oxyrhabdium modestum</i> | KU 321722 | Municipality of Pasonanca, Zamboanga City Province, Mindanao Island, Philippines | MN166287 | — |
| <i>Pantherophis guttatus</i> | — | — | JTLQ01873845 | JTLQ01113106 |
| <i>Prosymna janii</i> | PEM R12072 | Kosi Bay Nature Reserve, KwaZulu- Natal, South Africa | FJ404319 | FJ404293 |
| <i>Psammodynastes pulverulentus</i> | KU 309922 | Barangay Pandan, Municipality of Mambajao, Camiguin Sur Island, Camiguin Province, Philippines | MN166288 | MG458761 |
| <i>Psammophis mossambicus</i> | CMRK 125 | Nyagatare, Rwanda | DQ486383 | DQ486185 |
| <i>Pseudaspis cana</i> | PEM R17084 | Western Cape Province, South Africa | AY612080 | AY611989 |
| <i>Thamnophis sirtalis</i> | ¹ isolate: 37914A; ² isolate: EDBJR-23777 | — | ¹ AF420193 | ² LFLD01144685 |

Table 2. Meristic and mensural data collected for the holotype and paratypes of *Levitonius mirus*, new genus and species; scale counts: longitudinal dorsal scale rows (anterior body: midbody: posterior body); ventral scales; subcaudal scales; supralabial scales; and infralabial scales.

| Catalog # | PNM 9872 (KU 337269) | KU 305488 | KU 311281 |
|------------------------|-------------------------|-----------|-----------|
| Type | holotype | paratype | paratype |
| Sex | male | male | female |
| Dorsals | 15:15:15 | 15:15:15 | 15:15:15 |
| Ventrals | 107 | 124 | 122 |
| Subcaudals | 30 | 31 | 17 |
| Supralabials | 5 | 5 | 5 |
| Infralabials | 6 | 6 | 6 |
| Head length [mm] | 7.3 | 7.6 | 6.3 |
| Head width [mm] | 3.7 | 3.6 | 4.2 |
| Head height [mm] | 2.6 | 2.8 | 2.9 |
| Snout–vent length [mm] | 136.0 | 137.7 | 156.0 |
| Tail length [mm] | 29.5 | 25.3 | 16.1 |
| Total length [mm] | 165.5 | 163 | 172.1 |
| Eye diameter [mm] | 0.7 | 1.2 | 0.8 |

included counts of the following scales: ventral scales (Dowling, 1951a), subcaudal scales (not including the terminal scute), supralabial scales, infralabial scales, loreal scales, preocular scales, supraocular scales, postocular scales, primary and secondary temporal scales, pairs of anterior and posterior chin shields, medial gular scales (between chin shields and first ventral scale), and longitudinal dorsal body scale rows (Dowling, 1951b).

We assessed the following patterns of scalation: subcaudal scale pattern (divided or undivided); anal scale pattern (divided or undivided); nasal scale pattern (completely divided, incompletely divided, or undivided); infralabial-mental pattern (first infralabials in contact medially vs. not in contact medially and separated by the mental scale); infralabial-chin shield pattern (which infralabials contact first pair of chin shields); loreal pattern (which scales contact the loreal scale); internasal scale pattern (pair of internasals absent or present); parietal pattern (pair of parietals absent or present); anterior chin shields pattern (in contact medially or not in contact medially); posterior chin shields pattern (in contact medially or not in contact medially); type of dorsal and ventral body scales (smooth or keeled); apical pits on dorsal scales (present or absent); arrangement of dorsal body scale rows (horizontal or oblique rows); vertebral body scale pattern (enlarged or not enlarged, relative to other dorsal body scales); vertebrocaudal scale pattern (vertebrocaudal scales enlarged or not enlarged, relative to other dorsocaudal scales); reduction of dorsal body scale rows (Dowling, 1951b); and reduction of dorsocaudal scale rows (Dowling, 1951b). We also recorded which supralabial scales contact each of the following: prefrontal, orbit, postocular, temporals, and nasal scales.

Mensural characters were measured as either relative or absolute sizes. Specifically, we examined the relative shape or size of the following: pupil (post-mortem); rostral scale (taller than wide or wider than tall); mental scale (longer than wide or wider than long); frontal scale (longer than wide or wider than long); and relative sizes (lengths) of anterior versus posterior chin shield pairs. We measured the following characters with calipers or a flexible ruler to the nearest 0.1

mm: snout–vent length (SVL); tail length from the vent to the tip of the tail; head length from the tip of the snout to the posterior tip of the mandible; head width at the widest section of the head; head height at the tallest section of the head; and maximum orbit diameter along the horizontal axis. Meristic and mensural character data are summarized in Tables 1–2. We used Köhler's (2012) color catalogue when describing the color pattern of ethanol-preserved specimens. Color pattern characters included ground color and markings on dorsal, lateral, and ventral surfaces of the head, body, and tail.

For comparison to the new species, we examined specimens of Philippine snake species represented in the University of Kansas Biodiversity Institute (KU) collection. For Philippine snake species not represented within the KU collection, we compared data for the new species to earlier species accounts (Taylor, 1922a, 1922b; Leviton, 1963, 1964a, 1964b, 1964c, 1964d, 1965a, 1965b, 1965c, 1967, 1968, 1970a, 1970b, 1979, 1983; Inger and Marx, 1965; Brown et al., 1999, 2001).

Osteology.—We collected high-resolution computed tomography (microCT) data from formalin-fixed specimens of five species (one adult individual per species): *Oxyrhabdium leporinum* (KU 323386), *Myersophis alpestris* (KU 203012), *Hologerrhum philippinum* (KU 330056), *Cyclocorus lineatus* (KU 329413), and the new species (PNM 9872, described below; formerly KU 337269 and misidentified as *Calamaria gervaisii*). The scanning was performed at the University of Florida's Nanoscale Research Facility, using a Phoenix v|tome|x M scanner (GE Measurement and Control, Boston), with a 180 kV X-ray tube containing a diamond-tungsten target and the following settings: 70–90 kV, 180–200 mA, 0.2 s detector capture time, and 24–66 μ m voxel resolution. The raw X-ray data were processed using datos|x v2.3 and resulting microCT volume files were segmented and visualized using VG StudioMax v3.2.4 (Volume Graphics, Heidelberg, Germany). We deposited TIFF stacks and 3D mesh files in MorphoSource. Although Palci and Caldwell (2013) suggested that the postorbital bone *sensu* Cundall and Irish (2008) may be homologous to the jugal bone of other lizards, we used the terminology of Cundall and Irish (2008) when discussing cranial bones. CT data can be accessed through MorphoSource (Table 3).

RESULTS

DNA sequences.—The concatenated DNA alignment included sequences for two loci for 27 individuals (up to 1,580 base pairs [bp]; total missing data = 7.3%), from 20 species (seven cyclocorid species and 13 outgroup species; Table 1). Selected outgroup taxa included species from Atractaspididae, Colubridae, Elapidae, Lamprophiidae, Prosymnidae, Psammophiidae, Pseudaspidiidae, Pseudoxyrhophiidae, and from the elapoid *incertae sedis* genera *Buroma*, *Micrelaps*, and *Psammodynastes* (Table 1). Specifically, our DNA alignment included sequences at the mitochondrial protein-coding gene Cyt b (1,012 bp; 562 variable and 467 parsimony informative sites) and the nuclear protein-coding gene CMOS (568 bp; 108 variable and 53 parsimony informative sites) for 27 (100%) and 24 (89%) of the sampled individuals, respectively. GenBank accession numbers for all DNA sequences used in this study are listed in Table 1.

Table 3. Osteological data for the holotype of *Levitonius mirus*, new genus and species, and for representative species of other cyclocorid genera. Brackets indicate number of additional teeth suspected missing; question marks indicate uncertainty in the number of missing teeth. DOI = Digital Object Identifiers for CT scan files.

| | <i>Levitonius mirus</i> , new genus and species | <i>Cyclocorus</i> <i>lineatus</i> | <i>Hologerrhum</i> <i>philippinum</i> | <i>Oxyrhabdium</i> <i>leporinum</i> | <i>Myersophis</i> <i>alpestris</i> |
|---|---|--------------------------------------|--|--|---------------------------------------|
| Catalog # | PNM 9872 | KU 329413 | KU 330056 | KU 323386 | KU 203012 |
| DOI | 10.17602/M2/ M123949 | 10.17602/M2/ M123950 | 10.17602/M2/ M123947 | 10.17602/M2/ M75896 | 10.17602/M2/ M53482 |
| Sex | male | female | male | male | female |
| Predloacal vertebrae (<i>n</i>) | 114 | 166 | 150 | 166 | 174 |
| Cloacal + caudal vertebrae (<i>n</i>) | 30 | 43 | 54 | 58 | 31 |
| Dentary teeth: left, right (<i>n</i>) | 27, 26 | 20[5], 19[6] | 21[6], 22[6] | 27[1], 23[4] | 18, 18 |
| Maxillary teeth: left, right (<i>n</i>) | 25, 25 | 17[4], 16[7] | 12[9], 13[9] | 19[11], 21[9] | 15, 15 |
| Palatine teeth: left, right (<i>n</i>) | 16, 14 | 9[8], 9[7] | 8, 9[1] | 15[3], 17[2] | 11, 11 |
| Pterygoid teeth: left, right (<i>n</i>) | 29, 30 | 13, 13 | 17[11?], 18[11?] | 25[7], 26[6] | 24, 23 |

Phylogenetic relationships.—We recovered strong support for the monophyly of Cyclocoridae and for the monophyly of each of the cyclocorid species and genera (Fig. 2). However, we observed low support values at nodes describing relationships among sampled genera. Within Cyclocoridae, analyses support a clade containing the sampled species with

relatively broad heads and a second clade containing the sampled species with relatively narrow heads (Fig. 2). The broad-headed clade includes members of the genera *Cyclocorus* and *Hologerrhum*, whereas the narrow-headed clade includes species of *Myersophis* and *Oxyrhabdium*, and the new species described herein. Within the narrow-headed clade,

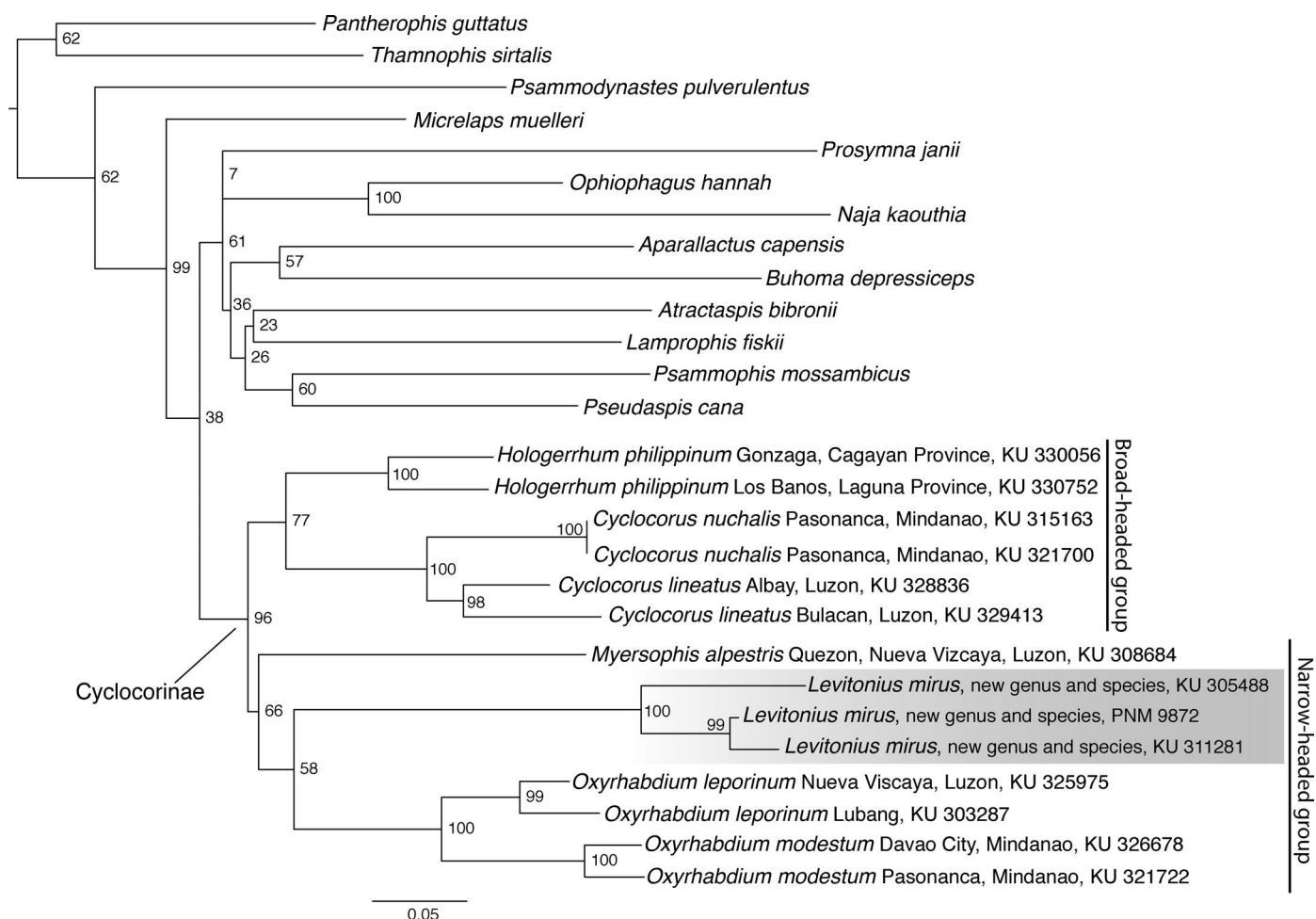


Fig. 2. IQ-TREE phylogeny of Cyclocorinae inferred from Cyt b and CMOS genes; *Levitonius mirus*, new genus and species, samples highlighted in gray; values at internal nodes indicate ultrafast bootstrap support, and values ≥ 95 were considered strong support; branch lengths indicate substitutions/site. See Data Accessibility for tree file.



Fig. 3. Dorsal (left column), lateral (center column), and ventral (right) views of the skulls of representative cyclocorine species. White scale bars = 1 mm.

we recovered *Myersophis* as the sister group to a subclade containing *Oxyrhabdium* and the new species (Fig. 2).

External morphology, color pattern, and osteology.—The new genus and species differs from the other cyclocorid species with respect to multiple mensural and meristic characters, in color pattern, whereas relatively few differences exist among the three individuals of the new genus and species (Tables 1–2). Osteological differences also differentiate the new species and genus from other cyclocorid taxa (Table 3). Morphologically the new species and genus is more similar to species of *Oxyrhabdium* and *Myersophis* than to species of *Cyclocorus* or *Hologerrhum* (Tables 1–3; Figs. 3–8).

Levitonius, new genus

urn:lsid:zoobank.org:act:BBD9F92A-41D1-424B-B084-03EB-C68345AA

Dwarf Burrowing Snakes
Figures 1–8, Tables 1–3

Type species.—*Levitonius mirus*, new species.

Diagnosis.—Members of the genus *Levitonius* can be distinguished by the possession of five supralabial scales, 15 longitudinal rows of dorsal scales throughout the length of the body, and subcaudal scales unpaired.

Description.—See description of *Levitonius mirus*, new species.

Content.—*Levitonius* includes a single species, *Levitonius mirus*, new species.

Etymology.—The new generic appellation *Levitonius* is a masculine noun and a patronym in the genitive singular, honoring the numerous contributions and life-long dedication of Alan E. Leviton to the study of the systematics of Philippine snakes.

Levitonius mirus, new species

urn:lsid:zoobank.org:act:27901547-0A54-4733-8F8D-63FEEF810971

Waray Dwarf Burrowing Snake
Figures 1–8, Tables 1–3

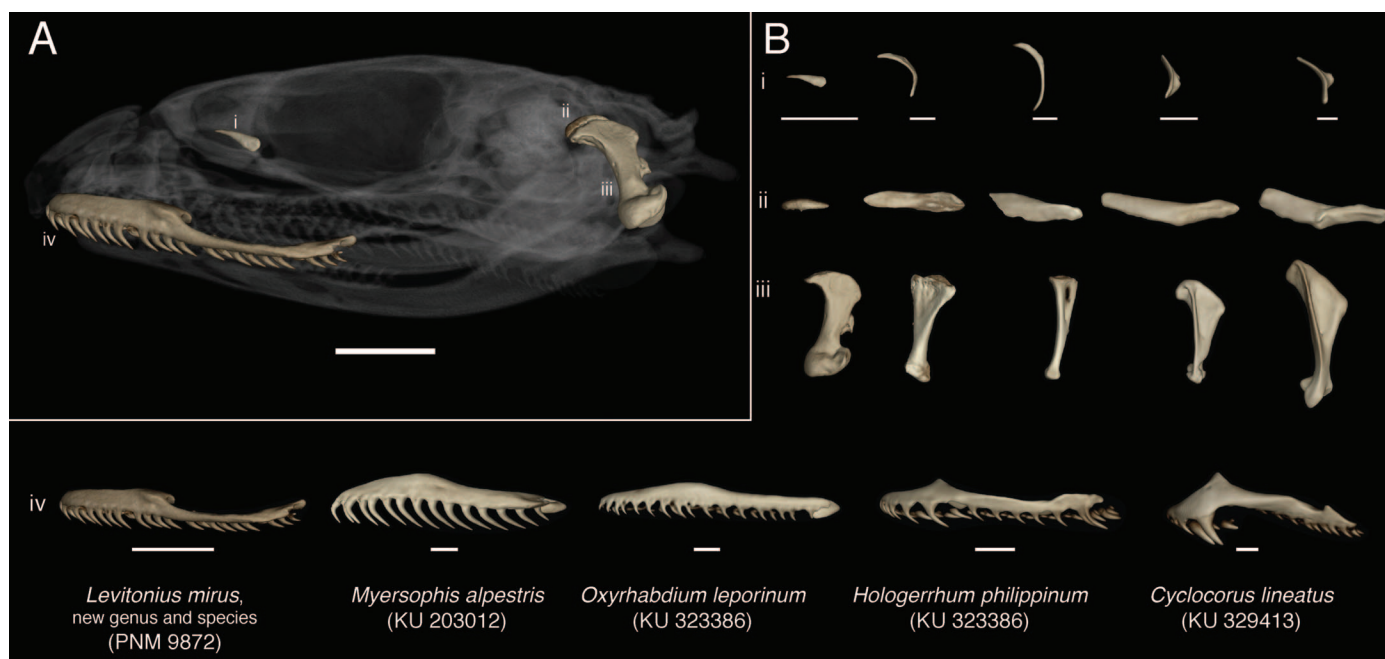


Fig. 4. Comparison of selected cranial bones of cyclocorid species. (A) Skull of *Levitonius mirus*, new genus and species, showing the position of bones i–iv; from left to right: bones of *L. mirus*, new genus and species, *Myersophis alpestris*, *Oxyrhabdium leporinum*, *Hologerrhum philippinum*, and *Cyclocorus lineatus*; i = postorbital bone, ii = supratemporal bone, iii = quadrate bone, and iv = maxilla. White scale bars = 1 mm.

Holotype.—PNM 9872 (formerly KU 337269; field tag number RMB 19087), adult male (Figs. 7A, 8), Barangay San Rafael, Taft, Eastern Samar Province, Samar Island, Philippines, elevation 187 m above sea level (asl), 11.832°N, 125.276°E, Kerry Cobb and Rafe M. Brown, 1900–2100 hrs, 17 June 2014.

Paratypes.—KU 305488 (field number CDS 1846), adult male (Fig. 7C), Taft Forest, Barangay San Rafael, Taft, Eastern Samar Province, Samar Island, Philippines, elevation 188 m asl, 11.832°N, 125.283°E, Cameron D. Siler and Charles Linkem, 16 June 2006; KU 311281 (field number CDS 3403), adult female (Fig. 7B), Pilim, Barangay San Vicente, Baybay, Leyte Province, Leyte Island, Philippines, elevation 490 m asl, 10.741°N, 124.842°E, Cameron D. Siler, approximately 1200 hrs, 1 January 2007.

Diagnosis.—*Levitonius mirus* can be distinguished from all other SE Asian snake species by having the following combination of characters: small size (largest total length known 172.1 mm); five supralabial scales; 15 longitudinal rows of dorsal scales throughout length of body; subcaudal scales unpaired; pair of internasal scales present; anterior temporal scale present; preocular scale absent; loreal scale present, not in contact with eye; mental scale broadly in contact with anterior chin shields; scales smooth, iridescent; dorsum ground color may be light brown to nearly black; one pale transverse band present on posterior of head, crosses parietals, temporals, and posterior supralabials; pale midventral line present or absent.

Description of holotype.—Adult male; snout–vent length 136 mm; tail length 29 mm; 107 smooth ventral scales; 30 unpaired subcaudal scales; anal scale undivided. Head length 7.3 mm; head width 3.7 mm; head height 2.6 mm. Eye diameter 0.7 mm; pupils subcircular. Supralabials five,

third in contact with prefrontal, third and fourth in contact with eye, fourth in contact with postocular, fourth and fifth in contact with primary temporal, fifth in contact with lower secondary temporal. Infralabials six, first pair separated from each other by mental scale, first three contact first chin shield, third and fourth contact second chin shield. Rostral scale slightly taller than wide. Nasal scale divided, surrounds small nostril, in contact with first and second supralabials. Single loreal scale, elongate, not in contact with eye, in contact with nasal, second and third supralabials, prefrontal, and internasal. Preocular and subocular scales absent; one supraocular; one postocular. One large primary temporal; two secondary temporals (one upper, one lower). Dorsal surface of head includes two internasals in contact with each other medially, two prefrontals in contact with each other medially and in contact with eye, two supraoculars separated by frontal scale, and two parietals in contact with each other medially. Mental scale wider than long and wider than rostral. First pair of chin shields in contact with mental scale, each other medially, and twice as long as second pair; second pair of chin shields separated from each other by first genial scale. Five enlarged genial scales anterior to first ventral scale. Ventral scales smooth. Dorsal scales smooth, without apical pits, in 15 parallel (rather than oblique) longitudinal rows throughout length of body; vertebral scales not enlarged compared to other dorsal body scales; posterior vertebrocaudal scales enlarged compared to other dorsocaudal scales; dorsocaudal scale row reduction formula: $10_{2+3(2)} \frac{9^{1+2(4)} 7^{3+4(16)} 5^{2+3(28)} 3(30)}{1+2(4) \ 3+4(16) \ 2+3(27)}$.

Skull highly ossified and basicranium is fused (Fig. 3); descending processes of parietal bone short; supratemporal and postorbital bones highly reduced (Figs. 3, 4); prefrontal bone anteriorly extended around septomaxilla; anterior-lateral edge of parietal bone extends around lateral edge of

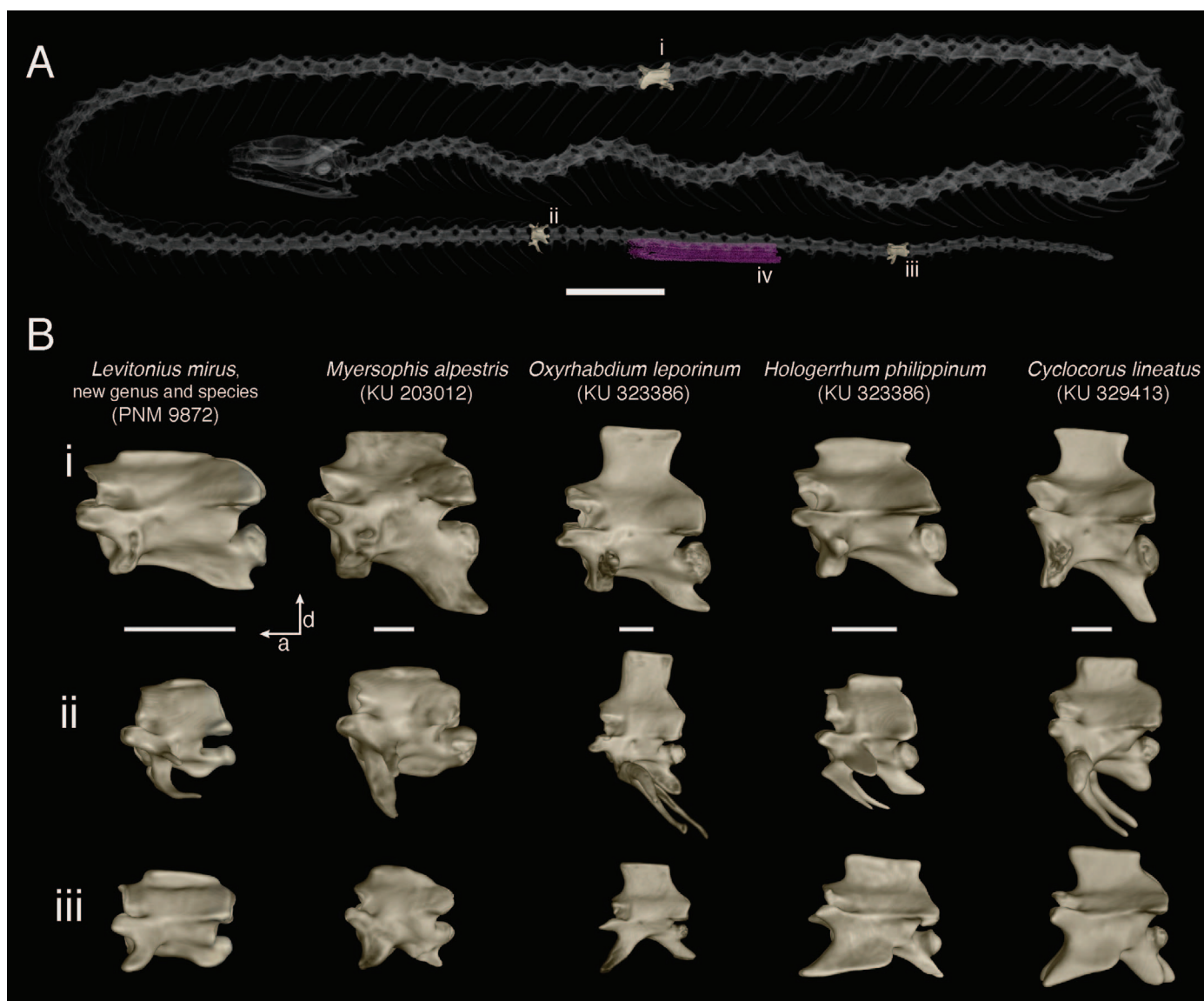


Fig. 5. Comparison of vertebrae of *Levitonius mirus*, new genus and species, and other cyclocorid species. (A) Whole skeleton (transparent) of *L. mirus*, new genus and species, showing the position of structures i–iv; (B) from left to right: *L. mirus*, new genus and species, *Myersophis alpestris*, *Oxyrhabdium leporinum*, *Hologerrhum philippinum*, and *Cyclocorus lineatus*; (A–B) i = prelocaal vertebra at midbody, ii = cloacal vertebra, iii = caudal vertebra midway along tail; (A) iv = hemipenes. White scale bar = 5 mm (A), 1 mm (B).

frontal bone; stapes mostly enclosed by crista circumfenestralis; vertebrae 144 (114 prelocaal, 30 caudal; Fig. 5A). Dentary teeth 27 (left), 26 (right), subequal in size; maxillary teeth 25 (left and right), subequal in size; palatine teeth 16 (left) and 14 (right), subequal in size; pterygoid teeth 29 (left) and 30 (right), subequal in size.

Coloration of the holotype in preservative.—After formalin-fixation and preservation in ethanol, ground color of dorsal and lateral surfaces of head, body, and tail fuscous (color 283; Köhler, 2012); each scale mottled with tiny unpigmented patches barely visible without optical magnification. Incomplete pale (unpigmented) transverse bar present on head posterior to eyes, crossing parietals, anterior temporal, and fourth and fifth supralabials (Fig. 7). Anterior-ventral surface of head fuscous with small, irregular shaped unpigmented markings (Fig. 7). Posterior-ventral surface of head with small

irregular shaped fuscous markings, otherwise unpigmented (Fig. 7). Ventral body scales medially unpigmented, some fuscous flecks; laterally fuscous (Fig. 7).

Variation.—The paratypes differ from the holotype in the following ways: KU 311281: six medial gular scales between posterior chin shields and first ventral; ventrals 122; subcaudals 17; fifth infralabial contacts third and fourth chin shields (vs. third); dorsocaudal scale row reduction formula: $9\frac{2+3(3)}{2+3(3)}7\frac{3+4(9)}{3+4(10)}5\frac{1+2(16)}{1+2(16)}3(17)$. Dorsal and lateral surfaces of head, body, and tail raw sienna (color 32; Köhler, 2012; vs. fuscous; Fig. 7B).

KU 305488: ventrals 124; subcaudals 31; dorsocaudal reduction formula: $13\frac{2+3(2)}{2+3(2)}11\frac{5+6(4)}{2+3(4);5+6(4)}82 + 3(5)7\frac{3+4(17)}{3+4(16)}5\frac{2+3(27)}{2+3(27)}3(31)$. Dorsal and lateral surfaces of head, body, and tail russet (Köhler, 2012; vs. fuscous; Fig. 7C); ventral surfaces

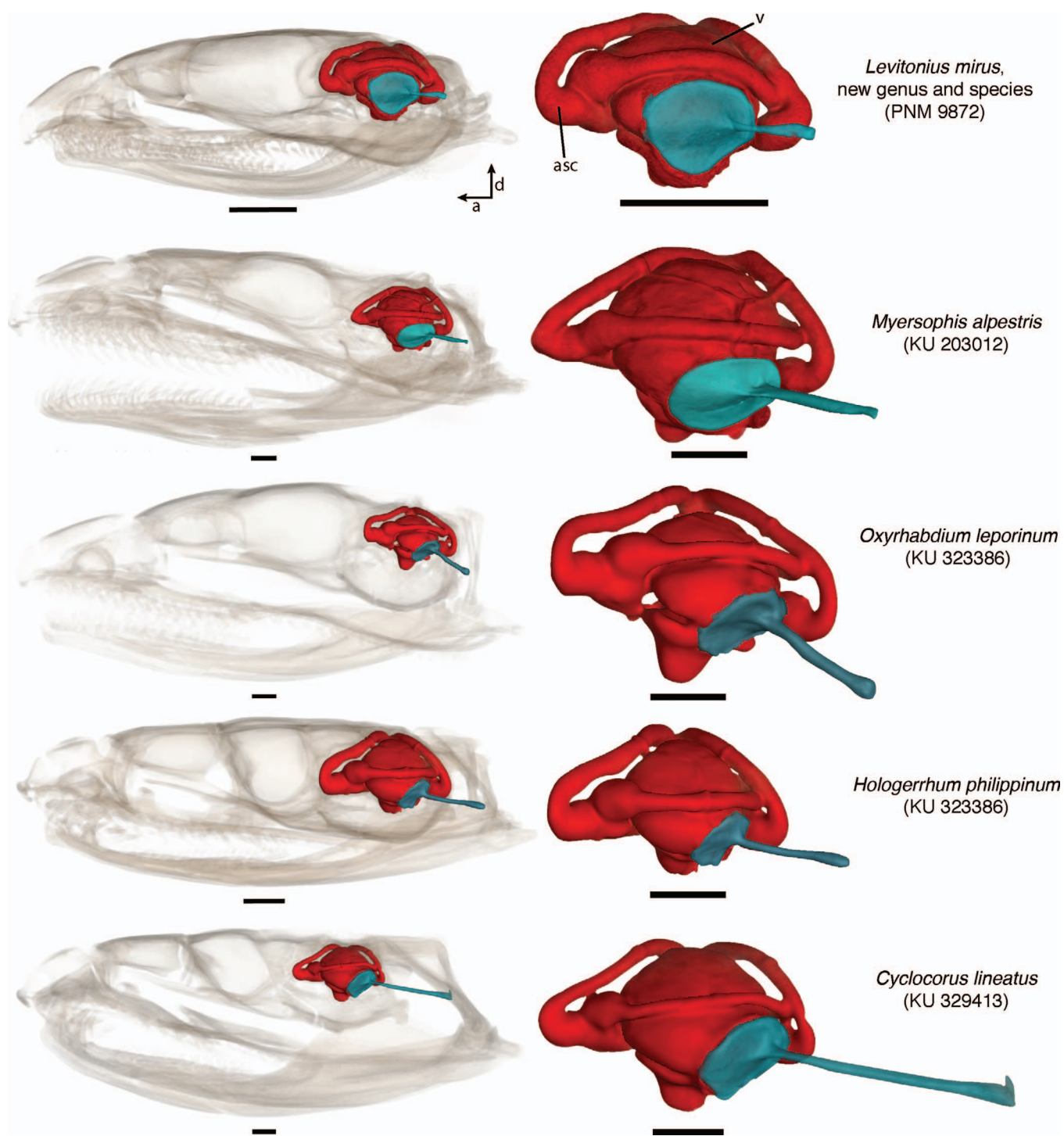


Fig. 6. Shape and position of the inner ear endocasts within the skulls (transparent) of representative cyclocorid species; asc = anterior semicircular canal; v = vestibule; red = bony labyrinth; blue = stapes; black scale bars = 1 mm.

of head, body, and tail russet (vs. fuscous with unpigmented midventral stripe; Fig. 7C).

Percent genetic distance (p-distance) is lowest between the holotype and the paratype from Leyte Island (PNM 9872 vs. KU 311281: p-distance = 3.95 % at Cyt b and 0 % at CMOS), intermediate in amount between the holotype and Samar Island paratype (PNM 9872 vs. KU 305488: p-distance = 14.34 % at Cyt b and 0.18 % CMOS), and highest between the two paratypes (KU 311281 vs. KU 305488: p-distance = 16.83 % at Cyt b and 0.19 % at CMOS).

Comparisons.—This new species is most likely to be confused with juveniles of the genera *Cyclocorus*, *Hologerrhum*, *Myersophis*, and *Oxyrhabdium*, as well as adults and juveniles of *Calamaria* and *Pseudorabdion*. *Levitonius mirus* can be distinguished from all species of *Calamaria*, *Myersophis*, *Oxyrhabdium*, and *Pseudorabdion* by having unpaired subcaudals (vs. paired). Additionally, from species of *Oxyrhabdium*, the new species can be distinguished by its much smaller adult body size, by having a pale transverse bar on the head that is centered over the parietals (vs. on the nuchals or absent), five

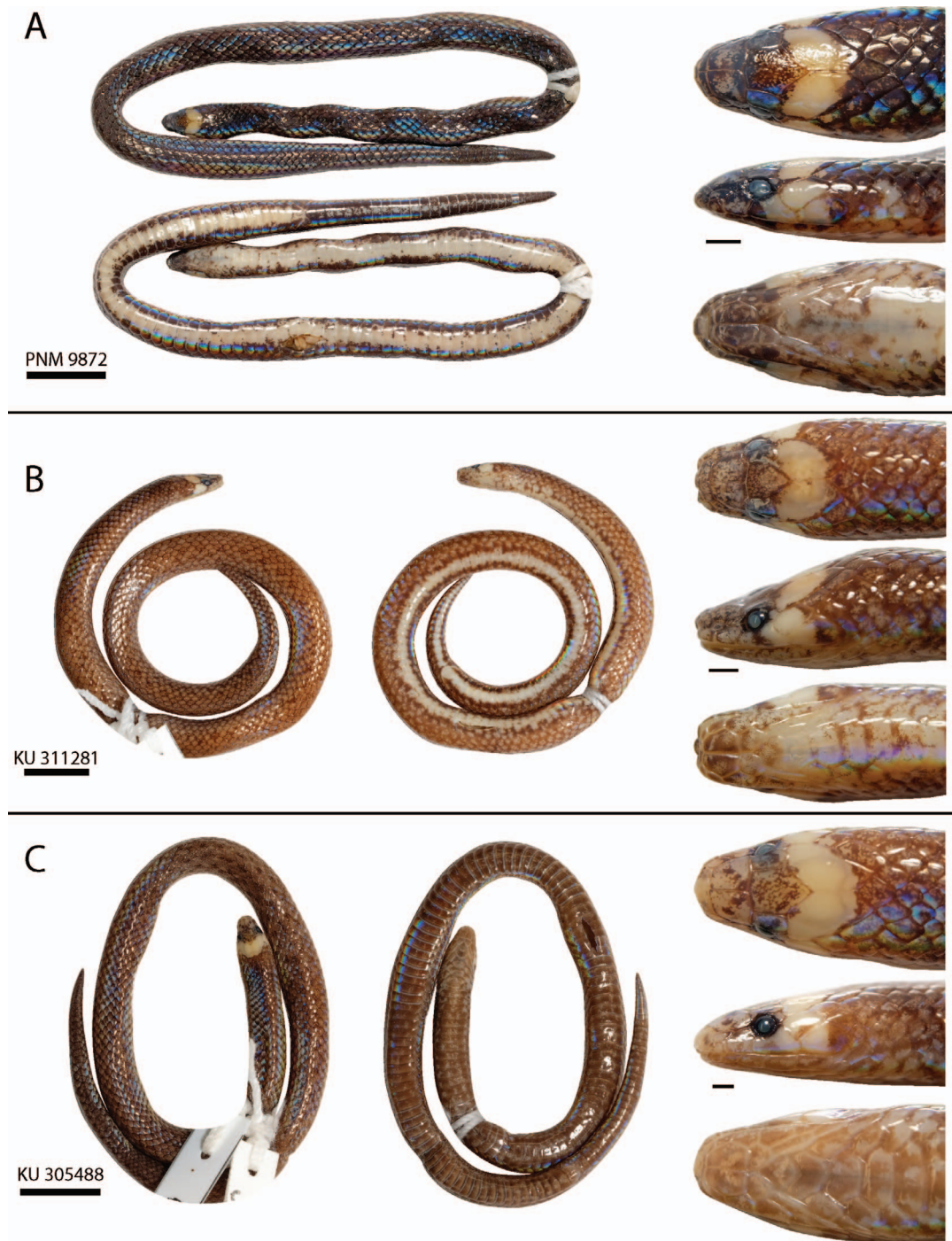


Fig. 7. Photographs of *Levitonius mirus*, new genus and species, type specimens (alcohol preserved): holotype PNM 9872 (A), and paratypes KU 311288 (B) and KU 305488 (C). Dorsal view of body (A, top left; B–C, left); ventral view of body (A, bottom left; B–C, center); dorsal view of head (A–C, top right); lateral view of head (A–C, center right); ventral view of head (A–C, bottom right). Thick black scale bars = 10 mm; thin black scale bars = 1 mm.

supralabials (vs. 6–8), 107–124 ventrals (vs. >150), and by having 17–31 subcaudals (vs. 33–70); from members of *Calamaria* and *Pseudorabdion* by having parietals separated from the supralabials by a large anterior temporal scale (vs. parietals in contact with the supralabials); from all species of *Calamaria* by having 15 longitudinal rows of dorsal scales (vs. 13); from all species of *Cyclocorus* and *Hologerrhum* by its much smaller adult body size, and by having a narrow snout

(vs. relatively broad), five supralabials (vs. seven or eight), and by having 15 longitudinal rows of dorsal scales (vs. 17).

Natural history.—The three specimens were all collected between 187–490 m asl. The field notes for the paratype KU 311281 state that it was collected “in secondary forest in a decaying log.” Specimens were all collected by raking fossorial habitats (loose soil beneath rotting logs, woody

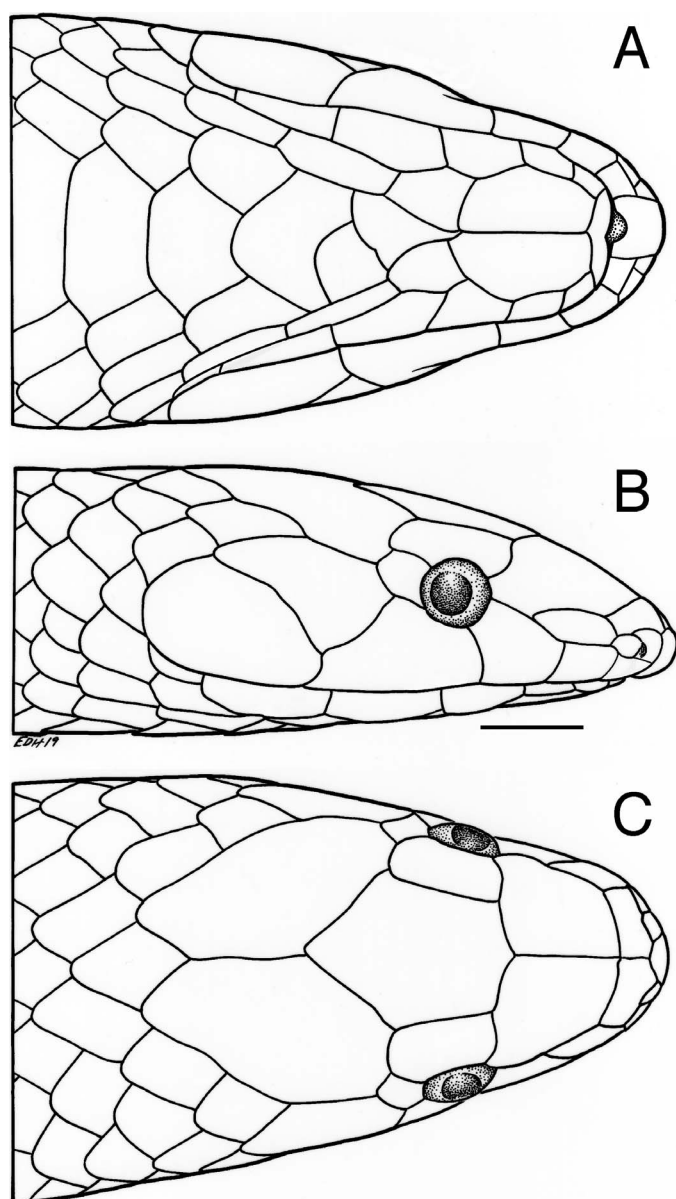


Fig. 8. Head scalation of *Levitonius mirus*, new genus and species, holotype (PNM 9872); (A) ventral, (B) lateral, and (C) dorsal views of head. Illustrations by Errol D. Hooper (2019). Black scale bar = 1 mm.

forest floor debris, leaf litter, etc.). Additionally, the new species' small size, reduced number of scales on the head, heavily ossified skull, smooth and iridescent scales, small eyes and nostrils, small neural spine of vertebrae, and additional cranial characteristics (see Discussion) all suggest that *Levitonius mirus* is fossorial (Gower, 2003; Cundall and Irish, 2008; Yi and Norell, 2015; Palci et al., 2017). In addition to the new species, 33 snake species are known to occur on Leyte or Samar Islands, including seven that are either fossorial or semi-fossorial: *Calamaria gervaisii*, *C. lumbricoidea*, *Calliophis philippina*, *Cyclocorus nuchalis taylori*, *Malayotyphlops ruber*, *Ramphotyphlops marxi*, and *Ramphotyphlops olivaceus* (Leviton et al., 2018). Notably, species of *Pseudorabdion* have not been recorded from either Leyte or Samar, despite the presence of this genus on nearby islands such as Mindanao (Leviton et al., 2018), suggesting that *L. mirus* may replace *Pseudorabdion* in occupying a portion of

the fossorial snake niche in Samar and Leyte. More specimens of *L. mirus* are needed to understand the ecology, distribution, phenotypic diversity, and genetic diversity of this species.

Distribution.—The new species is currently only known from Samar and Leyte Islands, southeastern Philippines.

Etymology.—The species epithet *mirus* is a Latin adjective, meaning unexpected finding or surprise—a fitting specific epithet for the miniaturized, phylogenetically unique evolutionary lineage represented by the new genus and species described here. The suggested common name, the Waray Dwarf Burrowing Snake, honors the Waray-waray people of the eastern Visayas, in particular the Samareños who live in vicinity of the type locality, among the forested mountains of Samar Island, and the Leyteños who inhabit the new genus' only other documented locality in the montane forests of Leyte Island.

Remarks.—Our finding that PNM 9872 from San Rafael, Samar Island is much more closely related to the Leyte Island individual than to the other Samar individual is unexpected (Fig. 2), and suggests that additional species-level diversity may exist within *Levitonius* on Samar Island. The presence of a pale mid-ventral stripe on both PNM 9872 and KU 311281 (which is absent on KU 205488) is consistent with this multiple-species hypothesis (Fig. 7). However, we conservatively treat the three individuals of *Levitonius* as a single species until additional specimens and genetic samples can be analyzed.

DISCUSSION

Phylogenetic relationships.—Weinell and Brown (2018) showed that *Cyclocorus*, *Hologerrhum*, *Levitonius* (then called “unnamed Samar-Leyte lineage”), *Myersophis*, and *Oxyrhabdium* form a strongly supported, Philippine-endemic clade; this study confirms those earlier findings. Earlier taxonomists suggested a close relationship between *Myersophis* and *Oxyrhabdium* (Taylor, 1963; Leviton, 1983) and a close relationship between *Cyclocorus* and *Hologerrhum* (Leviton, 1967; Brown et al., 2001), but these four genera were thought to be distantly related until molecular data demonstrated that they form an ancient, Philippine-endemic clade, with a nearly archipelago-wide distribution (Brown et al., 2001; Cundall and Irish, 2008; Weinell and Brown, 2018; Deepak et al., 2019). We found strong support for the monophyly of Cyclocoridae, and we recovered a sister relationship between the two broad-headed genera *Cyclocorus* and *Hologerrhum*. Additionally, we inferred *Levitonius* to be a member of the clade containing the narrow-headed species (i.e., species of *Levitonius*, *Myersophis*, and *Oxyrhabdium*), rather than sister to a clade containing all other cyclocorid taxa (Weinell and Brown, 2018). Additional, genome-wide sampling of DNA sequences are needed to resolve relationships among the cyclocorid genera, to confirm the monophyly of the broad-headed and narrow-headed groups, and to resolve the position of Cyclocoridae within Elapoidea.

Leviton (1957) discussed the striking morphological similarity between *Oxyrhabdium* and the Indian-endemic genus *Xylophis* and suggested that the similarity is due to convergence, rather than a close phylogenetic relationship. This convergence hypothesis was supported by Deepak et al.

(2019), who showed that *Xylophis* is not closely related to *Oxyrhabdium* but instead represents an old lineage (Xylophiinae) within Pareidae. Although we consider it unlikely, we cannot entirely rule out the possibility that the narrow-headed cyclocorids (i.e., *Oxyrhabdium*, *Levitonius*, and *Myersophis*) and *Xylophis* represent the plesiomorphic body morphology of Colubroidea. Resolving relationships within Cyclocoridae, and the position of this clade within Elapoidea, will likely improve our ability to infer trait evolution within Colubroidea as a whole.

Miniaturization in snakes.—With a maximum total length (SVL + tail length) of 172.1 mm, *Levitonius mirus* is the smallest species in Elapoidea. The smallest known elapid is *Simoselaps minimus* (maximum total length of 217 mm) and the previously reported smallest elapoid is *Compsophis vinckei* (Pseudoxyrhophiidae; maximum total length of 195 mm; Feldman et al., 2016). Within Alethinophidia, only 18 species (17 colubrids and 1 pareid) are known to be smaller than *L. mirus*, of which *Pseudorabdion sirambense* (Colubridae: Calamariinae) is the smallest (98 mm total length; Feldman et al., 2016). *Levitonius mirus* possesses 144 vertebrae (114 precloacal and 30 caudal), the fewest known for any elapoid species and among the fewest known for any snake species (Hoffstetter and Gasc, 1969; Gower and Winkler, 2007). *Xylophis captaini* (Pareidae) has the lowest number of vertebrae of any snake (135 total, 113 precloacal and 22 caudal; Gower and Winkler, 2007), and this species is also miniaturized with a maximum total length of 145 mm (Feldman et al., 2016). Reduction of vertebral number in miniaturized alethinophidian snakes is likely a consequence of body size reduction, as previous work has demonstrated that body size and vertebral number are generally correlated in snakes (pleomerism; Lindell, 1994; Head and Polly, 2007). Wake (1986) similarly documented that *Idiocranium* and *Grandisonia*, two miniaturized caecilian genera, have the fewest number of vertebrae within Gymnophiona. Reduction in body size may not always be associated with a loss of vertebrae, however, as Griffith (1990) found that miniaturized *Plestiodon* skinks have a higher number of vertebrae and an elongated body form compared to the largest species in the genus. *Levitonius* possesses many unique cranial features within the Cyclocoridae that are also present in the miniaturized, fossorial uropeltid snakes (Olori and Bell, 2012) and *Aprasia* pygopodids (Daza and Bauer, 2015), including a highly ossified skull, fused basicranium, relatively enlarged sensory regions of the brain and inner ear, reduced supratemporal and postorbital bones, and an anteriorly shifted quadrate and suspensorium. These convergent traits are likely widespread in small, burrowing squamates and are the result of shared constraints related to size reduction and selective pressures related to a fossorial lifestyle (Lee, 1998).

Ecological niche and diet in Cyclocoridae.—Osteological data support a fossorial to semi-fossorial life history for all cyclocorid species, and much of the variation in skull morphology is likely explained by variation in diet. Numerous studies have investigated the relationship between osteological form and function in snakes, especially with respect to the bones of the skull (Savitzky, 1983; Cundall and Irish, 2008; Yi and Norrel, 2015; Klaczko et al., 2016; Sherratt et al., 2019; Watanabe et al., 2019). For all species that we

examined, the inner ears have a relatively large, spheroid vestibule, and the anterior semicircular canal is not strongly curved ventrally (Fig. 6), suggesting that these species are fossorial or semi-fossorial and are not strong climbers (Yi and Norell, 2015). Furthermore, the relatively short vertebral neural spines (Fig. 5A; *H. philippinum*, *L. mirus*, and *M. alpestris*), iridescent scales (Fig. 7; all cyclocorids), and pigment reduction (*L. mirus*) are all characters associated with fossoriality in snakes (Gower, 2003; Cundall and Irish, 2008), consistent with the few ecological notes that have been published for these species (Taylor, 1922a, 1922b; Leviton, 1957, 1967; Brown et al., 1999, 2001, 2012, 2013). Among the features that Cundall and Irish (2008) considered to be associated with a long-headed burrower ecomorph, most are present in *Levitonius*, *Myersophis*, and *Oxyrhabdium*, but absent in both *Cyclocorus* and *Hologerrhum*, including: short postorbital bones, short supratemporal bones, elongation of the prefrontal bone over the dorsolateral process of the septomaxilla, extension of the anterior-lateral edge of the parietal bones along the lateral edge of the frontal bone, and increased enclosure of the stapes by the crista circumfenestralis (Fig. 3). The small postorbital bone of *L. mirus* (Figs. 3, 4) may also be an adaptation for increased fossoriality, or the result of body size miniaturization (Hanken, 1993; Cundall and Irish, 2008; Da Silva et al., 2018).

Cyclocorid species can be sorted into one of two groups based on the shape of the skull: the narrow-headed group and broad-headed group (Fig. 3), and skull shape differences are likely the result of differences in diet. Compared to the broad-headed species, the narrow-headed species have shorter quadrates, shorter supratemporals, and a shorter mandible relative to the length of the head. As a result, both mouth gape and prey diameters are expected to be smaller in the narrow-headed group (Cundall and Irish, 2008; Hampton and Moon, 2013), which is consistent with what is known about the trophic ecology of species of *Oxyrhabdium*—both *Oxyrhabdium modestum* and *O. leporinum* exclusively eat earthworms (Thompson, 1913; Taylor, 1922a, 1922b; Leviton, 1965a; Weinell, pers. obs.). Although nothing is known about the diets of *Myersophis alpestris* or *Levitonius mirus*, their skulls are similar to that of *O. leporinum*, suggesting that they also eat slender-bodied prey, such as earthworms. The narrow-headed species additionally possess pterygoid teeth that extend from anterior–posterior tips of the pterygoid bone, a trait that may facilitate the swallowing of slender-bodied prey. An elongated row of pterygoid teeth is present in other snake species that specialize on slender-bodied prey (Paluh, pers. obs., determined by examining skull shape files on MorphoSource), such as *Brachyorrhos*, *Carphophis*, and *Geophis* (worm-eaters), and *Farancia* (elongate salamander and eel specialists; Clark, 1970; Cundall and Greene, 2000; Murphy et al., 2011; Murphy and Voris, 2013), supporting this hypothesis.

In contrast to the narrow-headed species, the broad-headed species *Cyclocorus lineatus* and *Hologerrhum philippinum* both have a skull morphology that allows them to consume moderate to large prey (such as limbed vertebrates). These species are characterized by having elongated quadrates and supratemporals, laterally expanded parietals and maxillae, robust lower jaws, and enlarged teeth on the anterior region of the maxilla and dentary (Fig. 3). *Cyclocorus* has additional adaptations for eating relatively hard-bodied prey (such as

scincids), including enlarged anterior maxillary teeth followed by a diastema and a strongly angled maxilla (Savitzky, 1983; Jackson and Fritts, 2004). Scincivory is also supported by stomach content data: both *C. lineatus* and *C. nuchalis* primarily eat scincid lizards, but may also eat small burrowing snakes, and reptile eggs (Taylor, 1922a, 1922b; Leviton, 1967; Weinell, pers. obs.). The diets of the other broad-headed species, *H. philippinum* and *H. dermali*, are unknown, but we expect that they also eat moderate to large prey. However, unlike *C. lineatus*, the maxilla of *H. philippinum* is not strongly angled and its anterior maxillary teeth are not particularly enlarged, which suggests that *H. philippinum* may eat relatively soft-bodied prey. Gunther (1873) reported that the posterior maxillary teeth of *H. philippinum* are enlarged and grooved, which our results confirm (Fig. 3); the presence of grooved, fang-like teeth suggests that it may use venom to subdue its prey. Additional data on the diets of cyclocorid species are needed to understand the evolutionary transitions in diet within the group. Furthermore, considering that Cyclocoridae is a relatively old group (>20 Ma), studies that compare the timing of arrival and diversification of potential prey taxa into and throughout the Philippines are needed to understand the evolution of diet and ecology of these snakes.

Biogeography.—The known geographic distribution of *Levitonius* reinforces a need for reconsideration and augmentation of a pure PAIC model (*sensu* Inger, 1954; Heaney, 1985) of Philippine biogeography (Brown and Diesmos, 2009). Although this simple, elegant diversification model has heuristic value for its ability to generate hypotheses that can be tested in phylogenetic, phylogeographic, and quantitative biogeographical studies (Brown and Guttman, 2002; Esselstyn and Brown, 2009; Siler et al., 2010; Oaks et al., 2013; Brown, 2016), exceptions to PAIC predictions have been numerous. These exceptions have proved to be the most informative for understanding the multitude of ways that Philippine land vertebrates have responded to colonization of the archipelago's geographic template, contingency, species interactions, and ecological opportunity (Esselstyn et al., 2011; Siler et al., 2011a; Brown and Siler, 2013; Blackburn et al., 2013; Brown et al., 2013, 2016; Alexander et al., 2017; Oaks et al., 2019).

The uncritical way in which specimens of *Levitonius* were formerly misidentified as *Calamaria* and *Pseudorabdion* can be blamed, in part, on the unrealistic expectation that the snake fauna of Samar and Leyte is a nested subset of the Mindanao snake fauna. Many earlier studies have found fine-scale (species-level) differentiation, as well as microendemism and patterns suggesting ecological differentiation among reptiles of the southern Philippines (Welton et al., 2010, 2016; Siler et al., 2011b; Sanguila et al., 2016; Brown et al., 2018). Mindanao faunal region exceptions to a pure PAIC model of Philippine biogeography provide compelling opportunities for future research.

Conclusion.—The new genus *Levitonius* and new species *L. mirus* are known from both Samar and Leyte Islands, southeastern Philippines. At present, only three vouchered specimens of this species exist, and additional fieldwork aimed at understanding the ecology of this new species is needed to organize conservation strategies. We confirm that *Levitonius* is a member of Cyclocoridae and likely a close

relative of *Myersophis* and *Oxyrhabdium*, which also share multiple skeletal features including adaptations for eating slender-bodied prey. The skeletal morphology and dentition of *L. mirus* suggests that it is fossorial and probably eats earthworms or other limbless invertebrates, although direct evidence is needed to confirm these hypotheses. A resolved species and genus-level phylogeny of Cyclocoridae is needed to test hypotheses about the evolution of skull shape, diet, and ecological niches within this group.

DATA ACCESSIBILITY

Supplemental material is available at <https://www.copeiajournal.org/ch2020110>.

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LITERATURE CITED

- Alexander, A., Y.-C. Su, C. H. Oliveros, K. V. Olson, S. L. Travers, and R. M. Brown. 2017. Genomic data reveals potential for hybridization, introgression, and incomplete lineage sorting to confound phylogenetic relationships in an adaptive radiation of narrow-mouth frogs. *Evolution* 71:475–488.
- Blackburn, D. C., C. D. Siler, A. C. Diesmos, J. A. McGuire, D. C. Cannatella, and R. M. Brown. 2013. An adaptive radiation of frogs in a Southeast Asian island archipelago. *Evolution* 67:2631–2646.
- Brown, R. M. 2016. Biogeography of land vertebrates, p. 211–220. *In*: Encyclopedia of Evolutionary Biology, Edition 1. R. M. Kliman (ed.). Academic Press/Elsevier Inc., Cambridge, Massachusetts.
- Brown, R. M., and A. C. Diesmos. 2009. Philippines, Biology, p. 723–732. *In*: Encyclopedia of Islands. R.

- Gillespie and D. Clague (eds.). University of California Press, Berkeley, California.
- Brown, R. M., and S. I. Guttman.** 2002. Phylogenetic systematics of the *Rana signata* complex of Philippine and Bornean stream frogs: reconsideration of Huxley's modification of Wallace's Line at the Oriental-Australian faunal zone interface. *Biological Journal of the Linnean Society* 76:393–461.
- Brown, R. M., A. E. Leviton, J. W. Ferner, and R. V. Sison.** 2001. A new snake of the genus *Hologerrhum* (Reptilia; Squamata; Colubridae) from Panay Island, Philippines. *Asiatic Herpetological Research* 9:9–22.
- Brown, R. M., A. E. Leviton, and R. V. Sison.** 1999. Description of a new species of *Pseudorabdion* (Serpentes: Colubridae) from Panay Island, Philippines with a revised key to the genus. *Asiatic Herpetological Research* 8:7–12.
- Brown, R. M., C. H. Oliveros, C. D. Siler, J. B. Fernandez, L. J. Welton, P. A. C. Buenavente, M. L. L. Diesmos, and A. C. Diesmos.** 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., and C. D. Siler.** 2013. Spotted stream frog diversification at the Australasian faunal zone interface, mainland versus island comparisons, and a test of the Philippine 'dual-umbilicus' hypothesis. *Journal of Biogeography* 41:182–195.
- Brown, R. M., C. D. Siler, C. H. Oliveros, L. J. Welton, A. Rock, J. Swab, M. V. Weerd, J. van Beijnen, E. Jose, D. Rodriguez, E. Jose, and A. C. Diesmos.** 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., U. Smart, A. E. Leviton, and E. N. Smith.** 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 of Philippine *Calliophis* and *Hemibungarus*. *Herpetologica* 74: 89–104.
- Brown, R. M., Y.-C. Su, B. Barger, C. D. Siler, M. B. Sanguila, A. C. Diesmos, and D. C. Blackburn.** 2016. Phylogeny of the island archipelago frog genus *Sanguirana*: another endemic Philippine radiation that diversified 'Out-of-Palawan'. *Molecular Phylogenetics and Evolution* 94: 531–536.
- Burbrink, F. T., R. Lawson, and J. B. Slowinski.** 2000. Mitochondrial DNA phylogeography of the polytypic North American Rat Snake (*Elaphe obsoleta*): a critique of the subspecies concept. *Evolution* 54:2107–2118.
- Chernomor, O., A. von Haeseler, and B. Q. Minh.** 2016. Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology* 65:997–1008.
- Clark, D. R., Jr.** 1970. Ecological study of the worm snake *Carphophis vermis* (Kennicott). University of Kansas Publications, Museum of Natural History 19:85–194.
- Cundall, D., and H. W. Greene.** 2000. Feeding in snakes, p. 293–333. *In: Feeding: Form, Function, and Evolution in Tetrapod Vertebrates.* K. Schwenk (ed.). Academic Press, London.
- Cundall, D., and F. Irish.** 2008. The snake skull, p. 249–692. *In: Biology of the Reptilia.* Vol. 20. The Skull of Lepidosauria. C. Gans, A. S. Gaunt, and K. Adler (eds.). Society for the Study of Amphibians and Reptiles, Ithaca, New York.
- Da Silva, F. O., A.-C. Fabre, Y. Savriama, J. Ollonen, K. Mahlow, A. Herrel, J. Müller, and N. Di-Poi.** 2018. The ecological origins of snakes as revealed by skull evolution. *Nature Communications* 9:376.
- Daza, J. D., and A. M. Bauer.** 2015. Cranial anatomy of the pygopodid lizard *Aprasia repens*, a gekkotan masquerading as a scolecophidian, p. 303–350. *In: All Animals Are Interesting: A Festschrift in Honour of Anthony P. Russell.* O. R. P. Bininda-Emonds, G. L. Powell, H. A. Jamniczky, A. M. Bauer, and J. Theodor (eds.). BIS Verlag, Oldenburg, Germany.
- Deepak, V., S. Ruane, and D. J. Gower.** 2019. A new subfamily of fossorial colubroid snakes from the Western Ghats of peninsular India. *Journal of Natural History* 52: 2919–2934.
- Dowling, H. G.** 1951a. A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology* 1:97–99.
- Dowling, H. G.** 1951b. A proposed method of expressing scale reductions in snakes. *Copeia* 1951:131–134.
- Edgar, R. C.** 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32:1792–1797.
- Esselstyn, J. A., and R. M. Brown.** 2009. The role of repeated sea-level fluctuations in the generation of shrew (Soricidae: *Crocodyra*) diversity in the Philippine Archipelago. *Molecular Phylogenetics and Evolution* 53:171–181.
- Esselstyn, J. A., S. P. Maher, and R. M. Brown.** 2011. Species interactions during diversification and community assembly in an island radiation of shrews. *PLoS ONE* 6:e21885.
- Feldman, A., N. Sabath, R. A. Pyron, I. Mayrose, and S. Meiri.** 2016. Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara. *Global Ecology and Biogeography* 25:187–197.
- Gower, D. J.** 2003. Scale microornamentation of uropeltid snakes. *Journal of Morphology* 258:249–268.
- Gower, D. J., and J. D. Winkler.** 2007. Taxonomy of the Indian snake *Xylophis beddome* (Serpentes: Caenophidia), with description of a new species. *Hamadryad* 31:315–329.
- Griffith, H.** 1990. Miniaturization and elongation in *Eumeces* (Sauria: Scincidae). *Copeia* 1990:751–758.
- Günther, A. C. L. G.** 1873. Notes on some reptiles and batrachians obtained by Dr. Adolf Bernhard Meyer in Celebes and the Philippine islands. *Proceedings of the Zoological Society of London* 1873:165–172.
- Hampton, P. M., and B. R. Moon.** 2013. Gape size, its morphological basis, and the validity of gape indices in Western Diamond-backed Rattlesnakes (*Crotalus atrox*). *Journal of Morphology* 274:194–202.
- Hanken, J.** 1993. Adaptation of bone growth to miniaturization of body size, p. 70–104. *In: Bone.* Vol. 7. Bone Growth–B. B. K. Hall (ed.). CRC Press, Boca Raton, Florida.
- Head, J. J., and P. D. Polly.** 2007. Dissociation of somatic growth from segmentation drives gigantism in snakes. *Biology Letters* 3:296–298.
- Heaney, L. R.** 1985. Zoogeographic evidence for middle and late Pleistocene land bridges to the Philippines. *Modern Quaternary Research of SE Asia* 9:127–143.
- Hoffstetter, R., and J.-P. Gasc.** 1969. Vertebrae and ribs of modern reptiles, p. 201–310. *In: Biology of the Reptilia.*

- Vol. 1. Morphology A. C. Gans, A. d'A. Bellairs, and T. S. Parsons (eds.). Academic Press, New York.
- Inger, R. F.** 1954. Systematics and zoogeography of Philippine Amphibia. *Fieldiana* 33:181–531.
- Inger, R. F., and H. Marx.** 1965. The systematics and evolution of the oriental colubrid snakes of the genus *Calamaria*. *Fieldiana: Zoology* 49:1–304.
- Jackson, K., and T. H. Fritts.** 2004. Dentitional specialisations for durophagy in the common Wolf snake, *Lycodon aulicus capucinus*. *Amphibia-Reptilia* 25:247–254.
- Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, T. Thierer, B. Ashton, P. Meintjes, and A. Drummond.** 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28:1647–1649.
- Klaczko, J., E. Sherratt, and E. E. Z. F. Setz.** 2016. Are diet preferences associated to skulls shape diversification in xenodontine snakes? *PLoS ONE* 11:e0148375.
- Köhler, G.** 2012. Color Catalogue for Field Biologists. Herpeton, Offenbach, Germany.
- Lawson, R., J. B. Slowinski, B. I. Crother, and F. T. Burbrink.** 2005. Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 37:581–601.
- Lee, M. S. Y.** 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. *Biological Journal of the Linnean Society* 65:369–453.
- Leviton, A. E.** 1957. A review of the Philippine snakes of the genus *Oxyrhabdium* (Serpentes: Colubridae). *The Wasmann Journal of Biology* 15:285–303.
- Leviton, A. E.** 1963 [1962]. Contributions to a review of Philippine snakes, I. The snakes of the genus *Oligodon*. *Philippine Journal of Science* 91:459–484.
- Leviton, A. E.** 1964a [1963]. Contributions to a review of Philippine snakes, II. The snakes of the genera *Liopeltis* and *Sibynophis*. *Philippine Journal of Science* 92:367–381.
- Leviton, A. E.** 1964b. Contributions to a review of Philippine snakes, IV. The genera *Chrysopelea* and *Dryophiops*. *Philippine Journal of Science* 93:131–145.
- Leviton, A. E.** 1964c. Contributions to a review of Philippine snakes, V. The snakes of the genus *Trimeresurus*. *Philippine Journal of Science* 93:251–276.
- Leviton, A. E.** 1964d [1963]. Contributions to a review of Philippine snakes, III. The genera *Maticora* and *Calliophis*. *Philippine Journal of Science* 92:523–550.
- Leviton, A. E.** 1965a [1964]. Contributions to a review of Philippine snakes, VI. The snakes of the genus *Oxyrhabdium*. *Philippine Journal of Science* 93:407–422.
- Leviton, A. E.** 1965b [1964]. Contributions to a review of Philippine snakes, VII. The snakes of the genera *Naja* and *Ophiophagus*. *Philippine Journal of Science* 93:531–550.
- Leviton, A. E.** 1965c. Contributions to a review of Philippine snakes, VIII. The snakes of the genus *Lycodon*. *Philippine Journal of Science* 94:117–140.
- Leviton, A. E.** 1967 [1965]. Contributions to a review of the Philippine snakes, IX. The snakes of the genus *Cyclocorus*. *Philippine Journal of Science* 94:519–533.
- Leviton, A. E.** 1968 [1967]. Contributions to a review of Philippine snakes, X. The snakes of the genus *Ahaetulla*. *Philippine Journal of Science* 96:73–90.
- Leviton, A. E.** 1970a. Contributions to a review of Philippine snakes, XI. The snakes of the genus *Boiga*. *Philippine Journal of Science* 97:291–314.
- Leviton, A. E.** 1970b [1968]. Contributions to a review of Philippine snakes, XII. The Philippine snakes of the genus *Dendrelaphis* (Serpentes: Colubridae). *Philippine Journal of Science* 97:371–399.
- Leviton, A. E.** 1979 [1977]. Contributions to a review of Philippine snakes, XIII. The snakes of the genus *Elaphe*. *Philippine Journal of Science* 106:99–128.
- Leviton, A. E.** 1983. Contributions to a review of Philippine snakes, XIV. The snakes of the genera *Xenopeltis*, *Zaocys*, *Psammodynastes* and *Myersophis*. *Philippine Journal of Science* 112:195–223.
- Leviton, A. E., and W. C. Brown.** 1959. A review of the snakes of the genus *Pseudorabdion* with remarks on the status of the genera *Agrophis* and *Typhlogeophis* (Serpentes: Colubridae). *Proceedings of the California Academy of Sciences, Series 4* 29:475–508.
- Leviton, A. E., C. D. Siler, J. L. Weinell, and R. M. Brown.** 2018. Synopsis of the snakes of the Philippines: a synthesis of data from biodiversity repositories, field studies, and the literature. *Proceedings of the California Academy of Sciences, Series 4* 64:399–568.
- Lindell, L. E.** 1994. The evolution of vertebral number and body size in snakes. *Functional Ecology* 8:708–719.
- Minh, B. Q., M. A. T. Nguyen, and A. von Haeseler.** 2013. Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* 30:1188–1195.
- Murphy, J. C., Mumpuni, and K. L. Sanders.** 2011. First molecular evidence for the phylogenetic placement of the enigmatic snake genus *Brachyorrhos* (Serpentes: Caenophidia). *Molecular Phylogenetics and Evolution* 61:953–957.
- Murphy, J. C., and H. K. Voris.** 2013. An unusual, fangless short-tailed snake (Squamata, Serpentes, Homalopsidae) from Sumatra, Indonesia. *Asian Herpetological Research* 4: 140–146.
- Nguyen, L., H. A. Schmidt, A. von Haeseler, and B. Q. Minh.** 2014. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32:268–274.
- Oaks, J. R., C. D. Siler, and R. M. Brown.** 2019. The comparative biogeography of Philippine geckos challenges predictions from a paradigm of climate-driven vicariant diversification across an island archipelago. *Evolution* 73: 1151–1167.
- Oaks, J. R., J. Sukumaran, J. A. Esselstyn, C. W. Linkem, C. D. Siler, M. T. Holder, and R. M. Brown.** 2013. Evidence for Pleistocene-driven diversification? A caution for interpreting ABC inferences of simultaneous historical events. *Evolution* 67:991–1010.
- Olori, J. C., and C. J. Bell.** 2012. Comparative skull morphology of uropeltid snakes (Alethinophidia: Uropeltidae) with special reference to disarticulated elements and variation. *PLoS ONE* 7:e32450.
- Pagès, H., P. Aboyoun, R. Gentleman, and S. DebRoy.** 2019. Biostrings: efficient manipulation of biological strings. R package version 2.50.2.
- Palci, A., and M. W. Caldwell.** 2013. Primary homologies of the circumorbital bones of snakes. *Journal of Morphology* 274:973–986.
- Palci, A., M. N. Hutchinson, M. W. Caldwell, and M. S. Y. Lee.** 2017. The morphology of the inner ear of squamate

- reptiles and its bearing on the origin of snakes. *Royal Society Open Science* 4:170685.
- Paradis, E., and K. Schliep.** 2018. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35:526–528.
- Pili, A. N., and Y. L. C. del Prado.** 2018. Alcalá's Triangle-spotted Snake *Cyclocorus lineatus alcalai* on Sibuyan Island, Romblon Province, Philippines. *Southeast Asia Vertebrate Records* 2018:16–17.
- R Core Team.** 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Sabaj, M. H.** 2020. Codes for natural history collections in ichthyology and herpetology. *Copeia* 108:593–669.
- Sanguila, M. B., K. A. Cobb, C. D. Siler, A. C. Diesmos, A. C. Alcalá, and R. M. Brown.** 2016. The amphibians and reptiles of Mindanao Island, southern Philippines, II: the herpetofauna of northeast Mindanao and adjacent islands. *Zookeys* 624:1–132.
- Savitzky, A. H.** 1983. Coadapted character complexes among snakes: fossoriality, piscivory, and durophagy. *American Zoologist* 23:397–409.
- Sherratt, E., K. L. Sanders, A. Watson, M. N. Hutchinson, M. S. Y. Lee, and A. Palci.** 2019. Heterochronic shifts mediate ecomorphological convergence in skull shape of microcephalic sea snakes. *Integrative and Comparative Biology* 59:616–624.
- Siler, C. D., A. C. Diesmos, A. C. Alcalá, and R. M. Brown.** 2011a. Phylogeny of Philippine slender skinks (Scincidae: *Brachymeles*) reveals underestimated species diversity, complex biogeographical relationships, and cryptic patterns of lineage diversification. *Molecular Phylogenetics and Evolution* 59:53–65.
- Siler, C. D., A. M. Fuiten, R. M. Jones, A. C. Alcalá, and R. M. Brown.** 2011b. Phylogeny-based species delimitation in Philippine slender skinks (Reptilia: Squamata: Scincidae) II: taxonomic revision of *Brachymeles samarensis* and description of five new species. *Herpetological Monographs* 25: 76–112.
- Siler, C. D., J. R. Oaks, J. A. Esselstyn, A. C. Diesmos, and R. M. Brown.** 2010. Phylogeny and biogeography of Philippine bent-toed geckos (Gekkonidae: *Cyrtodactylus*) contradict a prevailing model of Pleistocene diversification. *Molecular Phylogenetics and Evolution* 55:699–710.
- Taylor, E. H.** 1922a. The Snakes of the Philippine Islands. Bureau of Science, Manila, Philippines.
- Taylor, E. H.** 1922b. Additions to the herpetological fauna of the Philippine Islands, II. *Philippine Journal of Science* 21: 257–302.
- Taylor, E. H.** 1963. New and rare oriental serpents. *Copeia* 1963:429–433.
- Thompson, J. C.** 1913. Notes on serpents in the family Colubridae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 65:213–218.
- Trifinopoulos, J., L. Nguyen, A. von Haeseler, and B. Q. Minh.** 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44:W232–W235.
- Uetz, P., P. Freed, and J. Hošek (Eds.).** 2020. The Reptile Database. <http://www.reptile-database.org> (accessed 9 April 2020).
- Untergasser, A., I. Cutcutache, T. Koressaar, J. Ye, B. C. Faircloth, M. Remm, and S. G. Rozen.** 2012. Primer3—new capabilities and interfaces. *Nucleic Acids Research* 40: e115.
- Wake, M. H.** 1986. The morphology of *Idiocranium russelli* (Amphibia: Gymnophiona), with comments on miniaturization through heterochrony. *Journal of Morphology* 189: 1–16.
- Watanabe, A., A. Fabre, R. N. Felice, J. A. Maisano, J. Müller, A. Herrel, and A. Goswami.** 2019. Ecomorphological diversification in squamates from conserved pattern of cranial integration. *Proceedings of the National Academy of Sciences of the United States of America* 116:14688–14697.
- Weinell, J. L., and R. M. Brown.** 2018. Discovery of an old, archipelago-wide, endemic radiation of Philippine snakes. *Molecular Phylogenetics and Evolution* 119:144–150.
- Weinell, J. L., E. Hooper, A. E. Leviton, and R. M. Brown.** 2019. Illustrated Key to the Snakes of the Philippines. *Proceedings of the California Academy of Sciences, Series 4* 66:1–49.
- Welton, L. J., C. D. Siler, L. L. Grismer, A. C. Diesmos, J. W. Sites, and R. M. Brown.** 2016. Archipelago-wide survey of Philippine forest dragons (Agamidae: *Gonocephalus*): multi-locus phylogeny uncovers unprecedented levels of genetic diversity in a biodiversity hotspot. *Biological Journal of the Linnean Society* 120:410–426.
- Welton, L. J., C. D. Siler, C. W. Linkem, A. C. Diesmos, and R. M. Brown.** 2010. Philippine bent-toed geckos of the *Cyrtodactylus agusanensis* complex: multilocus phylogeny, morphological diversity, and description of three new species. *Herpetological Monographs* 24:55–85.
- Yi, H., and M. A. Norell.** 2015. The burrowing origin of modern snakes. *Science Advances* 1:e1500743.
- Zaher, H., R. W. Murphy, J. C. Arredondo, R. Graboski, P. R. Machado-Filho, K. Mahlow, G. G. Montingelli, A. B. Quadros, N. L. Orlov, M. Wilkinson, Y.-P. Zhang, and F. G. Grazziotin.** 2019. Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes). *PLoS ONE* 14:e0216148.

APPENDIX 1

Key to the species of Cyclocoridae; modified from Weinell et al. (2019).

- 1a. Snout broad; anterior chin shields smaller than or similar in size to posterior chin shields; subcaudal scales unpaired..... 2
- 1b. Snout narrow; anterior chin shields much larger than posterior chin shields; subcaudal scales paired or unpaired..... 3
- 2a. Maxilla not strongly angled; no maxillary diastema, although anterior and posterior maxillary teeth are much larger than intervening teeth; posterior maxillary tooth grooved; five infralabial scales in contact with chin shields, and fourth infralabial scale broadly in contact with the anterior and posterior chin shields for about an equal length.... 5
- 2b. Maxilla strongly angled; large diastema between anterior and posterior maxillary teeth; posterior maxillary teeth not grooved; one of the following is also true: (1) five infralabial scales in contact with chin shields, and fourth infralabial scale either not

- in contact with or barely in contact with posterior chin shield, or (2) four infralabial scales in contact with chin shields, and third infralabial scale either not in contact with or barely in contact with posterior chin shield..... 6
- 3a. Five supralabial scales; subcaudal scales unpaired.....
..... ***Levitonius mirus*, new species**
- 3b. Six or more supralabial scales; subcaudal scales paired..... 4
- 4a. Parietal scales in contact with supralabial scales.....
..... ***Myersophis alpestris***
- 4b. Parietal scales not in contact with supralabial scales... 9
- 5a. Posterior border of parietal scales unnotched; dark midventral stripe present; dark midlabial stripe present..... ***Hologerrhum dermali***
- 5b. Posterior border of parietal scales notched; dark midventral stripe absent; dark midlabial stripe absent..... ***Hologerrhum philippinum***
- 6a. Ventral body scales > 137; hemipenes narrow, elongate with minute spines ornamenting walls; usually eight supralabial scales, three bordering eye; usually two anterior temporal scales; prominent white spots present along lateral edge of ventral body scales; many dark, usually triangular, blotches on ventral body scales..... 7
- 6b. Ventral body scales < 136; hemipenes robust, inner walls uniformly spinose, spines of moderate size; supralabial scales 7–8, two or three bordering eye; anterior temporal scale usually one; white spots along lateral edge of ventral body scales, if present, obscure; few or no dark triangular blotches on ventral body scales..... 8
- 7a. Tail length/total length 0.295–0.371 (males), 0.196–0.262 (females); subcaudal scales 52–59 (males), 42–48 (females); white spots along lateral edge of ventral body scales prominent.....
..... ***Cyclocorus lineatus lineatus***
- 7b. Tail length/total length 0.235–0.296 (males), 0.152–0.223 (females); subcaudal scales 42–53 (males), 33–44 (females); white spots along lateral edge of ventral body scales very small.....
..... ***Cyclocorus lineatus alcalai***
- 8a. Usually seven supralabial scales, two bordering eye.....
..... ***Cyclocorus nuchalis nuchalis***
- 8b. Usually eight supralabial scales, three bordering eye.....
..... ***Cyclocorus nuchalis taylori***
- 9a. Loreal scale separated from or in contact with second supralabial scale; if loreal scale in contact with second supralabial scale, their length of contact is less than half the length of the contact between loreal and postnasal scales; usually eight supralabial scales (rarely seven), with 5th and 6th (rarely 4th and 5th) supralabial scales bordering eye; dorsal surfaces of head, body, and tail brown or reddish-brown in color; juveniles have distinct white nuchal collar, but lack light crossbands on other parts of the body... ***Oxyrhabdium modestum***
- 9b. Length of contact between loreal scale and second supralabial scale similar to length of contact between loreal scale and postnasal scale; seven supralabial scales, with 4th and 5th supralabial scales bordering eye; dorsal surfaces of head, body, and tail dark gray or olive in color; juveniles have distinct white nuchal collar plus light crossbands on other parts of body and tail; pale crossbands may be faintly visible in adults..... 10
- 10a. Adult dorsal color pattern uniform (lacking pale crossbands); number of ventral body scales + subcaudal scales 192–230.....
..... ***Oxyrhabdium leporinum leporinum***
- 10b. Adults and juveniles with narrow white dorsal body crossbands and white nuchal collar; number of ventral body scales + subcaudal scales 221–235.....
..... ***Oxyrhabdium leporinum visayanum***