Taxonomic Reappraisal of the Northeast Mindanao Stream Frog, S*anguirana albotuberculata* (Inger 1954), Validation of *Rana mearnsi* Stejneger 1905, and Description of a New Species from the Central Philippines

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ABSTRACT: With a published multilocus phylogenetic analysis as our guide, we use new data from the external phenotype and genetically defined distributions of evolutionary lineages to resolve unclear species boundaries associated with the southwest Mindanao stream frog, *Sanguirana everetti* (Boulenger 1882), and its junior synonym, *Rana mearnsi* Stejneger 1905. We also reconsider the taxonomic status and nomenclatural history of the northeast Mindanao stream frog, *S. albotuberculata* (Inger 1954), in light of phylogenetic relationships, genetically confirmed geographic distributions, morphology, relevant type localities, and examination of type specimens. All evidence clearly indicates that the names *R. mearnsi* and *S. albotuberculata* refer to the same geographically circumscribed, phenotypically distinct lineage, and we recognize the oldest available name (*S. mearnsi*) for this species.

We also define the central Philippine lineage (from Negros, Masbate, and Panay islands) as an evolutionarily distinct new species. Long confused with *S. everetti*, the new taxon possesses a suite of diagnostic character state differences of external morphology, and color pattern. The species is isolated within the Philippines' biogeographically distinct West Visayan faunal region and its identification is substantiated further by its phylogenetic position. The new multilocus estimate of phylogeny and our multivariate analysis of morphological variation demonstrate that the new species is closely related, and phenotypically most similar, to northern Philippine *Sanguirana luzonensis*, to the exclusion of *S. everetti*, the southern species with which it previously was confused. Morphological characters distinguishing the new species include body size, the absence of infracloacal tubercles, the presence of smooth dorsal skin without dorsolateral folds or dermal asperities, its degree of sexual size dimorphism, uniquely stratified flank coloration, bright white subarticular tubercles, bold pectoral patches, and dark transverse bars on the limbs.

The identification of this distinctive new species further emphasizes the predictable nature of island bank-structured endemism in the Philippine archipelago and demonstrates that the country’s vertebrate diversity remains underestimated, and in need of continued study and faunal inventories, necessarily including collection of voucher specimens. Our observations suggest that the new species is relatively rare, patchily distributed, and infrequently encountered. With so little natural habitat remaining in the central Philippines, this species constitutes an immediate conservation priority that qualifies for formal recognition as a threatened species. Management of this urgent species-specific conservation problem will require field-based empirical data on the species’ distribution, local abundance, natural history, reproductive biology, and larval ecology—most of which currently is unknown.

Key words: Anuran Biodiversity; Biogeography; Cascade Frogs; Endemicity; Ranidae; *Sanguirana mearnsi*; Slender Stream Frogs.

PHILIPPINE amphibian diversity currently consists of 112 species, with most (~85%) of these taxa endemic to the archipelago (Brown 2007, 2009; Diesmos and Brown 2012; Diesmos et al. 2014, 2015). Rates of species discovery in the archipelago show no signs of slowing (Brown et al. 2008, 2013; Brown and Stuart 2012; Diesmos et al. 2014, 2015; Brown 2015) with nearly 30% of the country’s amphibian fauna being discovered and described in the last two decades (Brown 2007; Diesmos and Brown 2011; Diesmos et al. 2014, 2015). Unfortunately, more than a third of the archipelago’s species have been found to qualify for formal threatened status at some level (Diesmos and Brown 2011; Diesmos et al. 2014; IUCN 2016).

Endemic ranoid frogs are particularly diverse, with at least 11 species of *Limnonectes* and two species of *Occidozyga* (Dicroglossidae; Taylor 1920, 1922; Evans et al. 2004; Siler et al. 2009; Setiadi et al. 2011), 32 or more *Platymantis* (Ceratobatrachidae; Siler et al. 2010; Brown et al. 2015a,b), two species of *Staurois* (Arifin et al. 2011), and 13 native species of ranids (Brown 2007; Diesmos et al. 2015). Excluding introduced species such as *Hoplobatrachus rugulosus*, *Hylarana erythraea*, and *Lithobates catesbeianus* (Diesmos et al. 2006, 2015; Brown 2007), Philippine ranids are divided into three genera: *Pulchrana* with five species (Brown and Guttman 2002; Brown and Siler 2013; Brown 2015), *Amnirana,* consisting of one non-endemic native species (Inger 1954, 1999; Brown and Alcala 1970; Oliver et al. 2015; Diesmos et al. 2015), and *Sanguirana,* containing seven species formerly referred to the *Rana everetti* Complex (Brown et al. 2000a; Brown 2007; Fuiten et al. 2011; Brown et al. 2016). Philippine *Pulchrana* and *Sanguirana* are found on most major islands of the archipelago and are distributed in accordance with biogeographic regions known as Pleistocene Aggregate Island Complexes (PAICs; Brown and Diesmos 2002, 2009; Brown et al. 2013a), with most PAICs possessing at least one widespread species (Inger 1999; Brown et al. 2000a, 2016; Brown and Siler 2013) and the largest islands (Luzon and Mindanao) supporting 2–4 species, with the respective species distributions structured geographically and/or along elevational gradients (Taylor 1922; Brown 2015; Brown et al. 2000a, 2016; Fuiten et al. 2011).

Boulenger (1882) described *Rana everetti* from an unspecified type locality of "Zamboanga" (an elongate peninsula of western Mindanao Island, southern Philippines; Fig. 1A) and more than two decades later, Stejneger (1905) named *Rana mearnsi* from the mountains of eastern Mindanao. Taylor (1920) recognized both of these taxa and named a third Mindanao stream frog, *Rana dubita* from Bunawan, east-central Mindanao. Particularly important for the current study, in the same work he also referred some of his own specimens from an allopatric population on southern Negros Island (Fig. 1A) to *Rana mearnsi.*

When Inger (1954) later synonymized *Rana mearnsi* and *R. dubita* with *R. everetti*, he characterized the Negros Island population as conspecific with the Mindanao population. He conceived of *R. everetti* as a polytypic taxon, containing three subspecies: *R. e. everetti* Boulenger 1882*, R. e. luzonensis* Boulenger 1896, and *R. e. albotuberculata* Inger 1954). The West Visayan populations (Negros, Masbate, and Panay islands) have resided in synonymy with *Sanguirana everetti* ever since (Brown and Alcala 1970; Sison et al. 1995; Ferner et al. 2000; Brown et al. 2000a,b, 2016). This arrangement has persisted, but without explicit scrutiny of its underlying assumptions and despite the fact that prevailing biogeographic frameworks (Brown and Alcala 1970; Brown and Diesmos 2009; Brown et al. 2013a) such a distribution is highly anomalous because it spans widely allopatric, yet restricted geographic regions on multiple PAICs (Brown and Guttman 2002; Brown and Diesmos 2009; Brown and Siler 2013).

Meanwhile, recent taxonomic works have recognized all of Inger's former subspecies as full species (Brown et al. 2000a; Brown 2007; Diesmos et al. 2015), resurrected Taylor's (1922) *Rana igorota* (Brown et al. 2000a), and described two additional species, *S. tipanan* (Brown et al. 2000a) and *S. aurantipunctata* (Fuiten et al. 2011). Most recently, following higher-level phylogenetic analyses (Wiens et al. 2009), Fuiten et al. (2011) expanded and augmented the definition of the genus *Sanguirana* (Dubois 1992; Brown et al. 2000a) to include the Palawan Wood Frog *S. sanguinea* (Boettger 1893). This Palawan PAIC endemic had previously been considered a Papuan-derived Philippine faunal element (Inger 1954; Dubois 1992); the morphological and biogeographic distinctiveness of *S. sanguinea* most likely led to this view never being challenged by anuran taxonomists (Inger 1954; Fuiten et al. 2011). Recent phylogenetic analyses (Brown et al. 2016) demonstrate that *S. sanguinea* is actually the first-diverging lineage in a 'Palawan-Ark'-facilitated biogeographic diversification scenario (Blackburn et al. 2010; Siler et al. 2012), suggesting that *Sanguirana* first diversified on the isolated Palawan Micro-continental Block (Zamoros et al. 2008; Yumul et al. 2009a; Aurelio et al. 2013), before undergoing range expansion via overseas dispersal after colonization of multiple oceanic Philippine landmasses (Blackburn et al. 2010; Siler et al. 2012; Brown et al. 2016).

The genus *Sanguirana* now consists of species with largely allopatric distributions, including: *S. albotuberculata* from Leyte, Samar, and eastern Mindanao islands (Sanguila et al. 2015); *S. aurantipunctata* from a few sites in the mountains of central Luzon Island (Fuiten et al. 2011); *S. everetti* from southwestern Mindanao Island (Inger 1954); *S.* n. sp. ("*S.* cf. *everetti*) from Negros, Masbate, and Panay islands (Sison et al. 1995; Ferner et al. 2000; Gaulke 2007); *S. igorota* from the Cordillera Mountain Range of Luzon Island (Taylor 1920); *S. luzonensis* from throughout most islands of the Luzon PAIC (Brown et al. 2000a, 2016); *S. sanguinea* from the Palawan PAIC landmasses (Boulenger 1894; Inger 1954; Brown 2007); and *S. tipanan* from the Sierra Madre Mountain Range, of Luzon Island (Brown et al. 2000a; Fuiten et al. 2011; Fig. 1).

Molecular phylogenetic analyses strongly support the monophyly of the group, and confirm the inclusion of *S. sanguinea* as part of this genus (Bossuyt et al. 2006; Stuart 2007; Wiens et al. 2009; Holder et al. 2010). However, a recent multilocus phylogenetic study demonstrated that the West Visayan populations form a highly divergent, well supported clade unrelated to *Sanguirana everetti*, precluding their continued identification as that taxon, and necessitating this study (Brown et al. 2016).

In this paper we reconsider the taxonomic status of the lineage from the northeast Mindanao faunal region, *S. albotuberculata* (Inger 1954), in light of genetically verified species distributions (Brown et al. 2016), relevant type localities, phenotypic variation, and examination of the name-bearing type specimens of these taxa. We find the substitution of *S. mearnsi* (Stejneger 1905) for *S. albotuberculata* (Inger 1954) advisable at this time and we place the latter in synonymy with the former. We also revisit the issue of the biogeographically anomalous West Visayan (Negros, Masbate, and Panay islands) populations of "*Sanguirana everetti,*" and find character-based morphometric, biogeographic, and genetic evidence for the recognition of a new central Philippine endemic species.

MATERIALS AND METHODS

Morphological Character Differences

Specimens of all species of the genus *Sanguirana* were examined (Appendix; museum institutional codes/acronyms follow Sabaj 2016) and data from types were incorporated into definitions and diagnoses presented here. Specimens were examined for the presence/absence of diagnostic morphological character states including color pattern, body proportions, nuptial pad shape, digital characters, dermal asperities, infracloacal tubercles, dermal flanges along limbs, and raised dorsolateral ridges (Taylor 1920; Inger 1954; Brown et al. 2000a; Fuiten et al., 2011.)

Sex was determined by body size (for mature females), the presence/absence of conspicuous secondary sexual characteristics (nuptial pads in males), and/or by gonadal inspection in the case of specimens of intermediate sizes.

Vocalizations

Male advertisement calls and female response vocalizations were recorded with an analog tape recorder (Sony WM DC6 Professional Walkman) with a directional microphone (Sennheise ME80 condenser microphone, equipped with K3U power module). Calls were recorded at distances of 1–3 m, after which ambient and cloacal temperatures were collected. Calls were digitized and analyzed with Raven Pro 1.5 (Bioacoustics Research Group, Cornell Lab of Ornithology, 2012) software set on default spectrogram parameters (256 samples and 50% overlap). We examined oscillograms (waveforms), audiospectrograms (sonograms) and results of the Fast Fourier Transformation (FFT; power spectrum) for a series of spectral and temporal call characteristics following Brown and Guttman (2002) and Brown and Gonzales (2007). Calls are archived at the Cornell Laboratory of Ornithology Macaulay Library (ML) under ML digital media Catalog numbers 224181 and 224348.

Analyses of Continuously Varying Phenotypic Variation

To examine *Sanguirana* populations for lineage-based structure in continuously varying morphometric characters, we supplemented published morphological and mensural data for the genus *Sanguirana* (Brown et al. 2000a; Fuiten et al. 2011), with new data from all species, and exhaustive sampling of *Sanguirana albotuberculata* from northeast Mindanao, Leyte, and Samar islands and *S.* cf. *everetti* from Negros, Masbate, and Panay, islands (Appendix). We included all named *Sanguirana* from the oceanic Philippine islands, the West Visayan population of "*S. everetti*" (the new species), and excluded only *S. sanguinea* from Palawan Island, a species shown to be highly morphologically distinct from congeners (Inger 1954; Brown et al. 2000a; Fuiten et al. 2011). We treated *S. luzonensis* as two putative Operational Taxonomic Units (OTUs) on the basis of observed variation in phylogenetic analysis resulting from mitochondrial (mtDNA) and nuclear (nDNA) DNA datasets (Brown et al. 2016). In our previous study (Brown et al. 2016), we observed moderately-supported incongruence between mtDNA and nDNA datasets, suggesting that *S. igorota* and *S. tipanan* may be nested within *S. luzonensis,* with some northern Luzon Island populations of *S. luzonensis* sister to a ((*S. igorota*, *S. tipanan*), southern *S. luzonensis*) clade. Thus, given that we did not find strong support for the monophyly of all *S. luzonensis* populations, and the possibility that some northern *S. luzonensis* populations could be a distinct evolutionary lineage (but see Brown et al. 2016, for discussion of other possibilities), we designated the northern and southern Luzon populations as two OTUs for our analysis of continuously varying morphometric variation.

We collected data for the following 19 mensural characters following the character definitions of Brown et al. (2000a) and Fuiten et al. (2011): snout–vent length (SVL), head, and snout lengths; head width, interorbital and internarial distances; eye and tympanic annulus diameters; lengths of forearm, femur, tibia, tarsus, foot and hand, Finger-I, Finger-III, and Toe-IV; Finger-III and Toe-IV terminal disk widths; and nuptial pad length. All measurements (taken by AP and RMB only, to reduce inter-measurer bias; Hayek et al. 2001; Lee 1982, 1990) were measured to the nearest 0.1 mm (with digital calipers and stereomicroscope when necessary) from sexually mature adult males; data were excluded to minimize the impact of allometric ontogenetic variation (juveniles) and due to insufficient sample sizes among all groups (females).

Prior to analyses, measurements were corrected for differences in ontogenetic composition (Thorpe 1983a) using the following allometric equation: $X_{adj} = X - \beta(SVL - SVL_{mean})$, where X_{adj} is the adjusted value of the morphometric variable and X is the original value; SVL is the snout-vent length; SVL_{mean} is the overall mean snout–vent length; β is the within-OTU (operational taxonomic unit) coefficient of the linear regression of each original character value (X) against SVL (following Thorpe 1975, 1983b; Turan 1999; Chan et al. 2013). Based on the values of β, a subset of 14 informative morphometric characters were selected for inclusion in subsequent analyses. These characters include SVL, head and snout lengths, head width, tympanic annulus diameter, forearm, femur, tibia, tarsus, foot, and hand width, Toe IV, Finger III disc widths, and nuptial pad length. Because separately conducted Shapiro-wilks tests indicated violations of the assumptions of normality for SVL, head width, and lengths of snout, tibia, tarsus, hand, nuptial pad length and Toe IV disc width (Ps > 0.05) and Levene's tests of homogeneity of variance indicated most were heteroscedastic, we log-transformed all data before performing subsequent multivariate analyses and Analyses of Variance (ANOVAs) with *post hoc* Tukey tests (or Tukey-Kramer tests in cases of unequal sample sizes) to identify individual character differences among means of our seven designated OTUs/species.

A principal component analysis (PCA) was performed to find the best low-dimensional representation of morphological variation in the data and to further determine whether continuous morphological variation could form the basis of statistically detectable group structure. Principal components with eigenvalues of 1.0 or higher were retained in accordance to Kaiser's criterion (Kaiser 1960). To further characterize clustering and distance in morphospace, a discriminant analysis of principal components (DAPC) was performed for all congeners to find the linear combinations of morphological variables that have the largest between-group variance and the smallest within-group variance. The DAPC relies on data transformation using PCA as a prior step to discriminant analysis (DA), ensuring that variables included in the DA are uncorrelated and number fewer than the sample size (Jombart et al. 2010). All analyses were implemented and visualized in the statistical software environment R v3.1.2 (R Core Team 2015). The DAPC analysis was performed using the R package "adegenet 2.0.0" (Jombart 2008).

Phylogenetic Evidence

We refer to the recently-published study of Brown et al. (2016), which included sampling from 161 individuals from throughout the Philippine archipelago (47 localities), and specimens of all currently recognized species of the genus *Sanguirana* (Fig. 1B). That study included an analysis of 6098 nucleotides positions, from two mitochondrial gene regions and six nuclear loci, and standard phylogenetic analyses using likelihood (ML) and Bayesian (BA) methods. Details of PCR temperature regimes, manufacturer laboratory protocols, inference of nucleotide substitution models, partitioning strategy, and details of phylogenetic analyses are provided in Brown et al. (2016). For simplicity, because ML and BA analyses produced identical topological estimates, we summarize here just the Bayesian estimate of phylogeny and posterior probabilities of nodal support. All sequences are deposited in GenBank (Brown et al. 2016: Supplemental Appendix).

Species Concept

We embrace the General Lineage Concept of species (de Queiroz 1998, 1999) as the logical extension of the Evolutionary Species Concept (Simpson 1961; Wiley 1978), which has been articulated in a manner (de Queiroz 2005, 2007) that is particularly consistent with our definition of this new species. A species is the most inclusive lineage segment (ancestor–descendant series of metapopulations) identified as distinct from other such lineages, within which there is evidence of reproductive cohesion, for which we can infer a unique evolutionary history, and predict an independent future evolutionary trajectory or "fate" (Wiley 1978; Frost and Hillis 1990; Brown and Diesmos 2002). We recognize as distinct evolutionary lineages those ancestor–descendent population segments that are (1) sympatric or parapatric (occur on the same landmass), but with discrete, diagnostic, phenotypic and/or ecological character state differences, and genetic evidence of lineage cohesion (inferred absence of reticulation or gene flow with other sympatric congeners) and, thus, lineages for which the hypothesis of conspecificity can be rejected; or those that are (2) allopatric or geographically isolated (i.e., as insular or PAIC endemic lineages and, thus, demonstrably unique evolutionary entities) and morphologically, ecologically, and/or genetically distinct.

For the purpose of recognizing the non-controversial evolutionary lineages of the Mindanao PAIC (Brown et al. 2000, 2016), for example, criterion (1) is applicable: the northeast Mindanao, Leyte, and Samar islands' (Fig. 1) lineage now recognized as *Sanguirana albotuberculata* was originally recognized (described as *Rana mearnsi* [Stejneger 1905]; see below), was later thoroughly redescribed (Inger 1954) with an accompanying analysis of intraspecific mensural and meristic data, was diagnosed as part of a polytypic taxon (Inger 1954) and, later, redefined as an evolutionary species (Brown et al. 2000a), distinct from the parapatric southwest Mindanao Island *Sanguirana everetti* (see Brown et al. [2000a, 2016] for evolutionary species definition, illustration of diagnostic characters, phylogeny and biogeographical inference). Likewise, for the purpose of the new species recognized here, criterion (2) is clearly applicable and the recognition of the new species is not surprising because it represents a distinct evolutionary lineage on a separate geological Pleistocene island bank platform and is non-controversial in that most widespread Philippine vertebrate groups possess distinct species on separate PAICs (Brown and Diesmos 2002, 2009; Brown et al. 2000a, 2013a, 2016).

RESULTS

Definition of the Genus *Sanguirana* and Assignment of Taxa

We follow Fuiten et al.'s (2011) definition of the genus *Sanguirana* and place taxa in this genus based on phylogenetic evidence (Brown et al 2016) and possession of diagnostic character states. Members of the genus can be distinguished from all other Philippine ranids (Inger 1954; Diesmos et al. 2015) by the following combination of shared characters: (1) thin, elongate body; (2) extremely expanded terminal digital disks with circummarginal grooves; (3) elongate nuptial pad, covering nearly entire medial portion of Finger II, present (most species) or absent (*S. sanguinea*); (4) absence of vocal sacs; (5) posterior abdomen coarsely glandular; and (6) absence of humeral glands (Boulenger 1882; Inger 1954, 1966; Taylor 1920; Brown et al. 2000a; Fuiten et al. 2011).

Taxonomic Reappraisal of *Sanguirana albotuberculata* (Inger 1954), and *Rana mearnsi* Stejneger 1905

In considering the status of West Visayan faunal region species, we clarify the boundary between populations now referred to *Sanguirana everetti* (a taxon now restricted to western Mindanao Island; Fig. 1A; Brown et al. 2016:fig. 1) versus its sister species *S. albotuberculata* (Inger 1954; Brown et al. 2000a) of Leyte, Samar, and eastern Mindanao islands (Diesmos et al. 2015) and the unnamed evolutionary lineage of the West Visayan islands. Confusion has resulted from Taylor's (1920) referral of the Negros population to *Rana mearnsi* Stejneger 1905, combined with Inger's placement of *Rana mearnsi* in synonymy with *R. everetti everetti* Boulenger 1882. Additionally, in the same work, Inger (1954) named the northeast Mindanao faunal region lineage as a new subspecies, *Rana everetti albotuberculata*. We assume that the combination of these actions has resulted in an historical delay in what might otherwise have been a natural reconsideration of priority with regards to available names for the eastern Mindanao, Leyte, and Samar evolutionary lineage.

As a result of Brown et al.'s (2016) phylogenetic study, we have no doubt that *Sanguirana mearnsi* Stejneger 1905 has priority over, and is thus the valid name that must be substituted for (a *nomen substitutum*) the northeast Mindanao PAIC species referred to currently as *S. albotuberculata* (Inger 1954; Brown et al. 2000a; Diesmos et al. 2015). We base this name substitution on the chronological order of relevant publications and because several lines of evidence indicate the names *Rana mearnsi* Stejneger 1905 and *R. everetti albotuberculata* Inger 1954 refer to the same evolutionary lineage.

First, the distribution of the species from the northeast Mindanao PAIC is now very well documented (Fig. 1A; Brown et al. 2016:fig. 1; Sanguila et al. 2016), with genetically confirmed identities of fresh samples from northern and central Samar Island, at numerous sites through Leyte Island, and from sites along the northeast coastal mountains of eastern Mindanao, to the southeast corner of the island (Brown et al. 2016:fig. 1). Second, the type locality of *Rana mearnsi* Stejneger 1905 (Baganga River, Eastern Mindanao; > 300 m above sea level; Stejneger 1905; Cochran 1961) falls without any uncertainty within this geographical span of genetically confirmed localities (Fig. 1A). Third, the distributions of *S. everetti* (southwest Mindanao) and "*S. albotuberculata*" (= *S. mearnsi*) are now well circumscribed, confirmed with documented genetic sampling, and demonstrably do not overlap (Fig. 1A). Fourth, the *Rana mearnsi* Stejneger 1905 holotype (USNM 35258) is indistinguishable morphologically from similarly sized "*S. albotuberculata*." Finally, we note that Stejneger's (1905) original description mentions character states used by Inger (1954) to diagnose *R. e. albotuberculata* from *R. e. everetti* (distinct, fleshy glandular dorsolateral folds, prominent "pustules" [termed "asperities" in Inger [1954]; see Brown et al. 2000a:fig 5B; Fig. 2A] on the head, trunk, and eyelids). Admittedly, the poor state of preservation of the *Rana mearnsi* holotype (USNM 35258; preserved in blackberry brandy, brittle, and broken into multiple pieces; as originally reported by Stejneger [1905]) now prevents evaluation of some previously emphasized character states (Taylor 1920; Inger 1954; Brown et al. 2000a). These include the distribution of pustules/asperities on lateral surfaces of the head, the shape of the nuptial pad, morphometric variation, and live color or dorsum, thick dorsolateral folds, and infracloacal tubercles (Inger 1954; Brown et al. 2000a). However, all other evidence points to a single hypothesis.

In summary, despite the absence of genetic material from the exact type locality, multiple lines of evidence discussed above, plus examination of the relevant name-bearing types, convinces us that *Rana mearnsi* Stejneger 1905 has priority over *Rana everetti albotuberculata* Inger 1954, and that *Sanguirana mearnsi* (Stejneger 1905) is the first available, valid name to be applied correctly to populations of the stream frog (Fig. 2) from the northeast Mindanao PAIC

(Leyte, Samar, eastern Mindanao, and most likely Bohol islands). In addition to *Rana everetti albotuberculata* Inger 1954, *Rana dubita* Taylor 1920 (Type locality: Bunawan, eastern Mindanao) is also hereby placed in synonymy with *Sanguirana mearnsi* (Stejneger 1905).

Taylor's (1920) assignment of the name *Rana mearnsi* to the West Visayan population (Negros Island) clearly was in error, as noted correctly by Inger (1954). However, despite the fact that he identified Taylor's *lapsus*, Inger (1954) did not formally act on the distinctiveness of the new species from Negros, Masbate, and Panay islands. Given the limited appreciation of among-faunal region variation at that time (most Mindanao and Negros records were referred to "*Rana everetti everetti*," (Taylor 1922; Inger 1954) it is understandable that Inger (1954) conservatively discounted the validity of *R. mearnsi*, placed it in synonymy with *R. e. everetti*, and described the (same) species as *R. e. albotuberculata*.

Furthermore, remarking on the paucity of available specimens, Inger (1954:310) stated: "The Negros specimens cannot be placed in any of the defined subspecies with any reasonable degree of assurance." Acknowledging Inger's (1954) powers of observation and that his conservative approach set the stage for this study, we define the unassigned population as a new species, below.

Continuously Varying Morphological Variation

Due to the similarity between the quantitative and qualitative results for separately analyzed male and female specimens, we report the details of the results for analyses of males only. Although it took ten principal components to account for >95% of the total variance, the first four principal components each had eigenvalues of more than 1.0 and together accounted for 75% of the total variance (Table 1). The first principal component (PC1) loaded heavily on the lengths of femur, tibia, tarsus, and feet, indicating that differences in lower hindlimb morphology were responsible for most of the variance (29.5%). The second principle component (PC2; 19.5%) loaded heavily on characters pertaining to head morphology (head length, snout length, tympanic annulus diameter), whereas PC3 and PC4 (26%) had significant loadings for the characters SVL, head width, forearm length, and nuptial pad lengths. Ordination of the first two components showed taxon based group structure evident in partial separation between *S. everetti* versus *S. igorata*, *S. tipanan,* and *S. mearnsi* along the PC1 axis. The PC 2 axis exhibited separation between both *S. mearnsi* and *S. luzonensis* South from both *S. everetti* and *S. igorota* (Fig. 3A); additionally, *S. tipanan* is distinct from *S. igorota* along this axis. The new species clustered broadly in morphospace with *S. mearnsi*, *S. luzonensis* North, and *S. tipanan* (Fig. 3A) along both axes and, to a lesser extent with *S. everetti* and *S. luzonensis* South. The DAPC analysis discriminated between groups, as expected, and supported *S. mearnsi*, *S. everetti*, *S. igorata*, and as distinct clusters, whereas the new species, and *S. luzonensis* North overlapped broadly, and the new species further overlapped minimally with *S. tipanan* and *S. luzonensis* South (Fig. 3B).

Results of ANOVAs were highly significant (*P*s >0.0001) for all 14 characters, and Tukey tests (or Tukey-Kramer tests) detected statistically significant differences among means of West Visayan "*S. everetti*" and others species in at least four (northern *S. luzonensis*), but as many as nine (*S. tipanan*) individual characters per pairwise comparison (Table 5).

Phylogenetic Relationships

The available multilocus estimate of phylogeny (Fig. 1B; Brown et al. 2016) has demonstrated the phylogenetic distinctiveness of the West Visayan islands (Negros, Masbate, and Panay) population, which is not closely related to *S. everetti* (the species with which it has long been confused). Instead this newly discovered lineage is the sister lineage to a well-supported clade consisting of *S. igorota*, *S. tipanan*, and two clades referred to *S. luzonensis* (Fig. 1B; Brown et al. 2016). This strongly supported estimate of genealogical affinities bolsters the recognition of the new species as distinct from all OTUs considered here, and leaves us with no doubt that that the West Visayan islands "*S. everetti*" populations constitute a valid species, new to science. For reference, mitochondrial uncorrected genetic distances between the new species and all congeners range from 6.4–12.1 (Table 2), which are equivalent to or exceed those typically observed between morphologically and acoustically well-differentiated anuran lineages (e.g., *Pulchrana moellendorffi* vs. *P. mangyanum* [Brown and Siler, 2013]; *Sanguirana igorota* vs. *S. luzonensis* [Brown et al. 2016]).

Justification for the Recognition of a New Lineage-based Species

The new species clearly is distinct in multivariate space from *S. everetti*, *S. igorata*, *S. mearnsi* and southern populations of *S. luzonensis*. With respect to these species/OTUs, continuous variation of mensural body proportions demonstrated discernable group structure (which lends support to the recognition of the new taxon, emphasizing its distinctiveness from most congeners). Separation was not observed between the new species and northern *S. luzonensis* populations, or between the new species and *S. tipanan* (Fig. 3B). These allopatric northern Luzon populations are, however, readily diagnosed from the new species on the basis of fixed color characters (see Diagnosis and Table 3).

The results of our previous phylogenetic analysis (demonstrating the non-monophyly of populations currently referred to *S. everetti*, and demonstrating the distinctiveness of the West Visayan lineage from Luzon populations), requires the recognition of the new taxon. The fact that the monophyletic West Visayan PAIC *Sanguirana* overlaps broadly in morphospace with some Luzon taxa (northern populations of *S. luzonensis* and *S. tipanan*) does not deter us from recognizing it as a new species. This is because it is (1) the monophyletic, strongly-supported sister clade to a large clade of three or four differentiated Luzon taxa (and not closely related to *S. everetti*, the species with which it has long been confused), and (2) it is isolated biogeographically on the geologically separate West Visayan PAIC, which has never been connected to the Luzon PAIC. Thus, even without diagnostic continuously varying morphological traits that distinguish it from all congeneric populations, we are comfortable recognizing this allopatric, genetically distinct evolutionary lineage as a taxon in which speciation has not been accompanied by complete differentiation in continuously varying morphological characters. However, in addition to the above, we have identified fixed diagnostic coloration characters (Table 3) that, together with phylogenetic and biogeographic evidence, support the recognition of the West Visayan PAIC (Negros, Masbate, and Panay islands) populations of "*Sanguirana everetti*" as a new species, to be known as

Sanguirana ***acai*** sp. nov.

(Figs 4–7)

Rana mearnsi Stejnegeri 1905, Taylor (1920:251), in part.

Rana everetti Boulenger 1882, Sison et al. (1995:21).

Rana cf *everetti* Ferner et al. (2000:12).

Rana everetti everetti Inger (1954:310–311), in part; Brown et al. (2000a:85), in part.

Hylarana cf *everetti* Gaulke (2011:87).

Sanguirana everetti Fuiten et al. (2011:99); Frost (2016).

Holotype.—Adult male (PNM 9800, formerly KU 326381; Field Number RMB 3249), collected by RMB and V. Yngente at 1745 hr on 14 April 2001, in the Philippines, Negros Island, Negros Oriental Province, Municipality of Valencia, Barangay Bongbong, below "Camp Lookout," in a forested stream ("Maite Creek") at 500 m elevation above sea level on Mt. Talinis, Cuernos de Negros Mountain Range (9.2667° N, 123.2062° E; Datum = WGS-84).

Paratypes (Paratopotypes).—Three adult males (TNHC 62794–96), adult male and female (KU 326382, 326383), all with same collection data as holotype; two adult males (USNM 228387 and CM 116128), same locality, collected by C. A. Ross, 15 March 1981, and 10 August 1987, respectively.

Other Paratypes.—Adult female (CAS-SU 16398), collected by W. C. Brown, A. C. Alcala, and D. Empeso, 15 August 1954, Negros Island, Negros Oriental Province, Municipality of Valencia, 4–5 km west of Valencia town, east side Cuernos de Negros Mountain Range, Maite River Gorge; adult female (CAS 131883), collected by Q. Alcala, 16 August 1963, same locality; five adult males (CAS 18144–48) collected by D. Empeso, 28 April 1957, Municipality of Dauin, 15 km north of Dauin Town, southwest side of Cuernos de Negros Mountain Range; three adult males, and an adult female (TNHC 62797, 62798, KU 326382, and 326383), and two juveniles of undetermined sex (KU 326384, 326885), collected by RMB and V. Yngente, 14 April 2001, Municipality of Valencia, Sitio Nasuji, Cuernos de Negros Mountain Range, Mt. Talinis, 1150 m, PNOC/EDC watershed area; two adult males

(TNHC 62798, 62799), collected by RMB and V. Yngente, 2 December 2001, one adult male (USNM 228440) collected by C. A. Ross, 21 March 1980, and four adult females and two immature males (CAS 137498–503), collected by L. C. Alcala and party, 19–23 September 1972, Municipality of Sibulan, Barangay Janya-janya, Sitio Balinsasayo, Cuernos de Negros Mountain Range, Mt. Talinis 850–900 m above sea level, Lake Balinsasayo; three adult males (CAS 138144, 147326, 147327), collected by Q. Alcala and party, 19–20 January 1964, Municipality of Palaypay, Barangay Pamplona; two immature males (CAS 147328, 147329), and two adult males (CAS 147330, 147331), collected by A. C. Alcala and party, 21 December 1960, Pamplona town, east bank of Pinanlaya-an River; adult female (CAS-SU 19541), collected by A. C. Alcala and party, 27 December 1958, Municipality of Siaton, Bantolinao, 4 km NW of Bondo Barrio; adult male (CAS 139275), collected by L. C. Alcala and party, 11 April 1962, Negros Occidental Province, Municipality of Biak na bato, 6 km. N.W. Biak na Bato town, above Sition Tinago: adult and immature male (CAS 185565, 185566, collected by L. C. Alcala and party, 11 April 1962, Negros Occidental Province, Municipality of Tuyom, Bagtik River; three adult males and two adult females (CAS–SU 18134–38), collected by A. C. Alcala and Q. Alcala, 12–21 April 1957, Municipality of Tuyom, 17 km SW of Tuyom town, Bagtik River; adult female (PNM 9801, formerly KU 323855), collected by CDS, M. Yngente, V. Yngente, and J. Fernandez, 16 July 2009, Municipality of Silay City, Barangay Patag, Mt. Bungol; two adult males and a juvenile of undetermined sex (PNM 9802, 9803 [formerly KU 323860, 323862], and KU 323918); six adult males and one adult female (KU 323861, 323864, 323866–70), same locality and collectors, 21 July 2009; three adult males (KU 323873–75), an adult male, and two juvenile of undetermined sex (PNM 9804–06 [formerly KU 323863, 323865, 323871]), same collectors, 24 July 2009, same locality; three adult males (PNM 9807–

09, formerly KU 323872, 323876, and 323886), two adult males and two adult females (KU 323856–59), and four adult males (KU 323877–80), same collectors, 25 July 2009, same locality; two adult females and three adult males (KU 323881–85), and two adult males, and a juvenile of undetermined sex (KU 323887, 323888, 323918), collectors, 26 July 2009, same locality; two adult males (PNM 1372, 1373), collected by R. V. Sison, August 1991, Panay Island, Aklan Province, Municipality of Libacao Nacolon, Barangay Rosal, Sitio Belen; twenty two males (PNM 3800–03, 3806–15, 3817–24) collected by R. V. Sison, 27 February 1994, Antique Province, Municipality of San Remigio, Barangay Aningalan, Sitio Iganyao: two adult females and two adult males (KU 306863–66), collected by CDS, 13–15 March 2006, same locality; adult female (PNM 3913) collected by R. V. Sison, 12 March 1994, Tipuluan Mountain Range; immature female (PNM 8527), collected G. Operiano, 15 May 2004, Municipality of Sebaste, Barangay Alegre; adult male (PNM 8550), collected by N. Paulino, 18 April 2004, Municipality of Pandan, Sito Nanling.

Other referred specimens.—Immature male (CAS 124213), collected by L. C. Alcala and party, 6 May 1969, Calagna-an Island, Iloilo Province, Municipality of Carles, Barangay Barangcalan: three adult males (CAS 144267, CAS 144269, and USNM 305499), collected by L. C. Alcala and party, 13–14 June 1976, Masbate Island, Masbate Province, Municipality of Mobo, “Mapuyo Barrio, Pulangkahoy:” two juvenile specimens of undetermined sex (FMNH 61530, 61531), collected by D. S. Rabor, 25 May 1949, on Negros Island.

Diagnosis.—*Sanguirana acai* differs from all other members of this Philippine endemic genus by the (1) presence of dark pigmentation covering the majority of lateral head surfaces (vs. absence or presence but limited to a canthal stripe); (2) absence of dark color pattern on dorsum and dorsolateral body surfaces (vs. presence); (3) presence of an abrupt dark-above, light-below color stratification (abrupt transition) on the flanks, the position of which is marked with a dark brown line or row of dark spots (vs. absence of abrupt stratification, transition gradual); (4) presence of transverse dark bars on hind limbs but indistinct on forearms (vs. absence or presence on both); (5) presence of uniquely dark plantar surfaces of hand and foot, with bright white subarticular and supernumerary tubercles (vs. more uniformly pigmented ventral hand and foot surfaces); and (6) presence of boldly patterned, contrasting dark humeral patches (vs. absence or indistinct).

Comparisons.—The critical comparisons for the diagnosis of the new species are to the distantly allopatric and unrelated *Sanguirana everetti*, the taxon with which it has long been confused taxonomically, and *S. luzonensis*, the species to which it is most closely related (Brown et al. 2016:fig 1B), geographically most proximate, and phenotypically most similar. From *S. everetti* the new species differs by its much smaller, non-overlapping body size (Tables 3, 4), and by the absence of greatly enlarged infracloacal tubercles (vs. presence in >90% of specimens); from *S. everetti* and *S. luzonensis* by the presence of abruptly stratified flank coloration (vs. absence), presence of distinct white subarticular tubercles (Fig. 5A,B) on dark brown palmar and plantar surfaces of the hand and foot in males (vs. tubercle color similar to palmar and plantar surfaces of hands and feet), and presence of bold humeral patches (vs. diffuse, indistinct or absent; Fig. 4B); from *S. tipanan*, *S. igorota*, and *S. mearnsi* by the absence of dermal asperities on dorsal and lateral body surfaces (vs. presence; Brown et al. 2000a:fig. 4), the presence of yellow, tan or light gray dorsal ground coloration (vs. iridescent green, with a brown reticulum in *S. tipanan* [Brown et al. 2000:fig. 3C,D], vibrant dark green with large dark brown osceli or purplish spots in *S. igorota* [Brown et al. 2012b:fig. 31,31], or metallic bright green with bright yellow dorsolateral folds in *S. mearnsi* [Diesmos et al. 2015:fig. 39F]); from *S. mearnsi* by the absence of greatly enlarged infracloacal tubercles, absence of raised, fleshy dorsolateral folds (vs. presence; Diesmos et al. 2015:fig. 39H), and presence of transverse tibial bars (vs. absence; Diesmos et al. 2015:fig. 39F,H); from *S. aurantipunctata* by having a pointed snout (vs. rounded; Diesmos et al. 2015:fig. 39G), glandular ventral texture limited in distribution to the groin (vs. spanning entire ventrum), yellow, green, tan or light gray dorsal ground coloration (vs. bright green-yellow with black flecks [males] or bright orange spots (females and some males; Fuiten et al. 2011:fig. 2), and purple flank coloration (vs. abruptly stratified flank coloration), and by the presence of dark tibial bars (vs. absent) and dark lateral head coloration (vs. bright green), the absence of enlarged infracloacal tubercles (vs. presence), and the absence of thickened postaxial dermal flanges on posterior surfaces of the hind limbs (vs. presence); and from *S. sanguinea* by its larger, non-overlapping body size (Tables 3, 4), by having a less pronounced sexual size dimorphism (female/male SVL 1.2–1.4 [*S. acai*] vs. 1.9–2.1 [*S. sanguinea*]), having glandular ventral texture around the groin (vs. smooth surfaces), and by the presence of elongate nuptial pads (vs. absence).

Description of holotype.—Adult male in excellent state of preservation (Fig. 4A, B). Snout pointed, but terminally rounded in dorsal profile and extending well beyond lower jaw in lateral view; snout/head length = 0.45; head width narrower than body width, slightly wider than long; Head width/head length = 0.76; head length/SVL = 0.41; canthus rostralis sharply angular, straight in dorsal aspect; loreal region slightly concave; nares slightly protuberant laterally, anterodorsal in position, visible from ventral aspect; interorbital/internarial distance = 0.87; interorbital distance/eye diameter = 1.2; labial region thin, barely visible in dorsal aspect; interorbital region flat, wider than eye diameter; rostrum flat; eyes moderate in size, oriented anterolaterally beyond jaw when viewed in ventral aspect, protuberant on top of head;

tympanum distinct, located immediately behind eye; tympanum smaller than eye; tympanic annulus/eye diameter = 0.86; supratympanic ridge slightly evident, continuous with barely evident dorsolateral ridges; postrictal tubercles irregular, continuous, elongate, arching ventrally, composed of enlarged fleshy tubercles.

Dentigerous processes oriented transversely. Vomerine teeth in row of four atop dentigerous process of each vomer; dentigerous processes just posteromedial to choanae, separate for a distance equal to width of one choana; choanae moderate in size, suboval, widely separated, nearly obscured by maxilla when viewed from ventral aspect; premaxillary and maxillary teeth present; vocal slits absent; tongue elongate (length twice that of width), free for two-thirds its length, posterior margin deeply notched.

Skin of dorsum smooth (Fig. 4A), asperities absent; posterior two-thirds of venter glandular; skin of cloacal region coarsely glandular, especially adjacent to groin; cloacal region lacking prominently enlarged infracloacal tubercles; cloacal opening round, with transverse supracloacal cutaneous flap.

Upper arm slender; humeral glands absent; forearms robust (Fig. 4A, B); forearm/hand length = 0.70; forearm length/SVL = 0.24; fingers in increasing order of length II<III<V<IV (II much shorter than III); Fin2L/Fin4L = 0.47; interdigital webbing absent; lateral fringes present on all digits of hand, most prominent on distal portions of Fingers-III–V; terminal phalanges widely dilated distally, 3–5X width of penultimate phalanges; disks with circummarginal grooves; ventral pads on Fingers-III–V pointed, protruding beyond distal edge of dorsal surface, visible from dorsal aspect; penultimate phalanges with rounded supraarticular cutaneous flap.

Subarticular tubercles of hand large, raised, rounded, protuberant (Fig. 5A); digit (Roman numerals) and tubercle number (Arabic numbers): II (1), III (1), IV (2), V (2); supernumerary tubercles present basally on each finger, moderate in size, slightly raised, elongated on Fingers IV and V, with medial constriction; thenar (inner palmar metacarpal) tubercle elongate, 0.4X length of Finger-II, separate from medial and outer palmar tubercles; thenar tubercle 1.3X length of large, subcircular, flat medial palmar tubercle and 2.1X length of narrow, elongate outer metacarpal tubercle (Fig 4A); entire medial edge of thenar tubercle covered by translucent, velvety nuptial pad; nuptial pad continuing distally to just beyond articulation of penultimate and ultimate phalanges; nuptial pad wrapping around preaxial side of Finger-II entirely and nearly in contact with subarticular tubercle on its anterior edge; nuptial pad length/Finger I length = 0.98.

Hind limbs slender; tibia length/SVL = 0.66; forearm length/SVL = 0.58; forearm /tibia length = 0.87; tarsus/ forearm length = 0.65; tarsus /foot length = 0.64; foot / tibia length = 0.88; heels overlap when thigh segment of hind limbs held at right angles to body; tibiotarsal articulation of adpressed limb reaching beyond rostrum; toes long, in increasing order of length I<II<III≤V<IV (III ≅ V); Toe4L/FL = 0.79; toe disks smaller than those of fingers; Toe IV /Finger III disc width = 0.56; interdigital webbing of foot nearly complete (Fig 4B), homogeneous, acrenulate; modal webbing formula of toes (Savage and Heyer 1969, 1997): I0—0II0—½III0—1^{+}IV1^{+}—0V; webbing diminishing distally to form wide fringes along lateral edges of distal phalanges on portions free of web; tarsal fold distinct, continuous with postaxial dermal flange on edge of Toe-V; subarticular tubercles of foot large, round or occasionally sub-elliptical, nearly pointed; digit (Roman numerals) and tubercle number

(Arabic numbers): I (1), II (1), III (2), IV (3), V (2); inner metatarsal tubercle oval, 3X longer than minute, round, outer metatarsal tubercle; supernumerary tubercles absent from pes.

Measurements of holotype (mm).—SVL 52.1; head length 21.3; head width 16.1; snout length 9.6; interorbital distance 5.9; internarial distance 6.8; eye diameter 5.4; tympanic annulus diameter 5; head width 16.1; forearm length 12.4; femur length 30.2; tibia length 34.6; tarsus length 19.6; foot length 30.5; hand length 17.6; Toe IV length 24.2; Finger I length 6.1; Finger III length 12.8; Toe IV disc width 1.9; Finger III disc width 3.4; nuptial pad length 6.6.

Coloration of holotype in life.—(Based on field notes and photographs of RMB; see similarly-patterned paratopotype; Fig. 6A) Ground color of dorsal surfaces homogenous light green; limbs slightly yellowish green with evenly distributed tiny, dark, grayish-purple spots and flecks; trunk with pale yellow pigment on faint dorsolateral “folds” (=faintly raised dermal ridges; Fig 5A); dark transverse bars on hind limbs (numbering four on femur, four on tibial segment of limb); dorsal head color similar to body; pigment along canthus rostralis, lateral head surface, pre- and post-ocular regions, and tympanum solid dark brown; labial region bright pale yellow, lightening to nearly white below eye, starkly contrasting with dark brown lateral surfaces of head; postrictal tubercles yellow.

Dorsolateral surfaces of body light green above, with sharp transition lateral stratification or transition to pale yellow ventrolaterally; position of dark-above, light-below flank stratification marked by fine dark greenish-brown line (Fig. 6A); lateral inguinal region heavily blotched with dark gray markings on pale yellow background; tibio-tarsal articulation bright white with fine gray markings; dorsal surfaces of hand and foot fade from lighter cream to white on Finger-I to yellowish green on Finger-II, then to dark gray on Fingers III and IV; nuptial pad velvety gray; dorsal humerus yellow between dark green transverse bands, lightening to white by articulation with tiba; dorsal tibial segment nearly white between dark green transverse bands; dorsal surface of foot dark green, interdigital webbing dark gray with faint darker patches of pigment.

Ventral surfaces lighter than dorsal surfaces; throat homogeneous pale yellow; sternal region white with boldly contrasting dark brown humeral patches; venter yellow anteriorly, fading to cream with white glandular surfaces posteriorly.

Ventral surfaces of forearms white with starkly contrasting dark brown ventrolateral coloration, darker distally at wrist; palmar surface of hand dark brown, with grayish purple palmar and carpal tubercles and nuptial pad; ventral surfaces of fingers homogenous dark brown, with bright white subarticular and supernumerary tubercles; ventral surfaces of outer terminal finger discs light gray, ventral surfaces of Fingers I and II discs pale yellow; ventral surfaces of femur, tibia, and shank yellow with boldly contrasting dark brown patches on posterior surfaces; tarsus purple; plantar surface of foot purple with grayish-purple subarticular tubercles; plantar surfaces of foot dark brown, with bright yellow to cream subarticular tubercles, ventral toe discs white proximally, dark gray distally; interdigital webbing of foot dark brown, boldly patterned with distinct white patches (Fig. 4B).

Coloration of holotype in preservative.—In preservative, the holotype's color pattern has been retained, but ventral colors have shifted to white or pale cream (yellow lost), dark brown coloration somewhat lightened. Other than loss or bright yellows and green (e.g., dorsal green coloration, accent colors of the postrictal tubercles, and dorsolateral ridges), difference between live and preserved coloration is minimal (Fig. 4A, B).

Color variation.—Dorsal ground surfaces of body varying shades of brown, from light brown (Negros Island male KU 323885, 323887; female KU 323858; Panay Island male KU

306863) to dark brown (Negros Island males KU 323868, 323873, 323883, 326382; Panay Island female KU 306864) immaculate or homogenous (most specimens) or with distinct darker spots (Negros Island females KU 306649, 323882), or indistinct darker blotches (Panay Island male KU 306863; Negros Island males KU 306437, 323675, 323866, 323869, 323880, 323885, 323887). Masbate Island specimens (CAS 144267, 144269) are patterned more boldly and exhibit stronger contrast between light and dark pigmentation than do Negros and Panay specimens.

Most specimens have some transvers dark bars on tibial and radio-ulnar segments of fore- and hind limbs, respectively. Five specimens lack dark bars on limbs altogether (Negros Island males KU 306438, 323864, 323866, 323874; Panay Island male KU 306863); specimens with dark dorsal coloration have darkest transverse limb bars (Negros Island males KU 323868, 323870, 323873, 323880, 323883, 326382; Panay Island male KU 306865). Most remaining specimens have faint transverse limb bars on all limbs, but some specimens exhibit faint tibial bars and lack forearm bars (Negros Island females KU 323858, 323859, 323881, 326383; Negros Island males KU 323861, 323877, 323878–79; Panay Island female KU 306864).

Ventral body surfaces range from light, immaculate cream with dark pigment absent throughout (Negros Island males KU 306437, 306438, 323859, 323864, 323869, 323875, 323884–85, 323887) to cream with distinct dark spots scattered across all ventral surfaces, and concentrated on throat and pectoral region (Negros Island males KU 323873, 323877, 323883, female KU 323881). The remaining specimens have scattered light brown and indistinct speckling throughout ventral surfaces (Fig. 4B), some with darker congregation of dark pigment on throat (Panay Island males KU 306863, 306865–66; female KU 306864).

Lateral surfaces of heads grayish blue, lacking canthal stripes (most individuals) or with very faint canthal stripe (KU 325898, 325905, 325912, 325916–17). Adult males lacking transverse limb bars (most) or with thin, faint light gray bars (five or six) across forelimbs (KU 325913, 325916–17, 325923, 325926, 325944, PNM 9735); hind limbs lacking transverse bars (most) or with five or six thin, light gray bars (KU 325913, 325926). Flank coloration more clearly partitioned in females than in males, with sharper demarcation between dorsal grayish blue and ventral grayish pink.

Palmar surfaces of hand range from dark gray with yellowish subarticular tubercles (Panay Island female KU 306864 and males KU 306863, 306865–66; Negros males KU 306437, 323866, 323868, 323873, 323878, 323880, 323883, 326382), to dark brown with bold white tubercles (Figs. 3A, 4A; males KU 323861, 323875, 323879, 323887) to very light gray to yellowish cream with little contrast between surface of hand and subarticular tubercles (Fig 4A, B; Negros Island females KU 323857–59). Remaining specimens (majority) of specimens have light gray palmar surface of the hand with distinguishable, brighter yellowish cream subarticular tubercles. Plantar surface of the foot ranges from relatively homogeneous dark gray-brown with yellowish cream subarticular tubercles (Panay Island female: KU 306864 and males KU 306863, 306865–66) or dark gray tubercles (Negros Island females: KU 323858, 323867, 323881–82 and males KU 306437, 323866, 323868, 323870, 323873, 323877–79) to homogeneous light gray with slightly lighter subarticular tubercles (Negros Island females KU 306649, 323856–57, 323859, 326383; males KU 306438, 323861, 323864, 323869, 323874–75, 323885, 323887).

Infracloacal rugosity slightly variable in size and shape, with the following exceptions: some possess minute tuberculation (KU 325896, 325903, 325912, 325919), whereas others have enlarged and irregularly shaped glandular patches (KU 325923, 325928, PNM 9733, 9736).

Morphometric variation.—Summaries of variation in mensural characters in the type series are presented in Table 4.

Distribution.—The new species is known from Negros, Masbate, and Panay islands in the central Philippines (Fig. 1A). Other small islands of the West Visayan PAIC may also harbor populations of *Sanguirana acai*, if appropriate habitat can be located (e.g., Bantayan, Guimaras, Poro, San Francisco,), but we are reasonably certain that the new species does not occur on Siquijor (several surveys in the last 10 years have failed to detect its presence) and that it does not occur—or no longer occurs—on the heavily deforested and well-studied island of Cebu (Brown and Alcala 1970, 1986). A population referred to *S.* "*everetti*" has been reported on Bohol (Brown and Alcala 1970) but as of yet no genetic tissue samples have been obtained and so its position in phylogeny (Brown et al. 2016) cannot be ascertained. We would expect, based on PAIC-structured Philippine biogeography (Brown and Diesmos 2002, 2009), that the Bohol population should be conspecific with the species documented on Leyte, Samar, and eastern Mindanao islands (*S. mearnsi*), but this expectation remains untested. *Sanguirana acai* has been documented from 375 m above sea level to 1350 m on the large mountains of southern Negros, northern Negros, northwest Panay, and the western coastal mountains of Panay (Taylor 1922; Inger 1954; Alcala, 1962; Brown and Alcala, 1970; Ferner et al. 2000; Gaulke 2011).

Natural History.—Frogs of the genus *Sanguirana* are stream breeders with indirect aquatic larval development and poorly characterized larval biology (Taylor 1920, 1922; Inger 1954; Alcala 1962; Brown and Alcala 1982a,b; Brown et al. 2000a; Gaulke 2011). Individuals of *Sanguirana acai* were found at night along forested mountain streams, or in disturbed, regenerating, or second growth forest, provided that it was adjacent to primary forest. The new species perches on rocky stream banks, on midstream boulders, and on rocks along lakeshores, but is most frequently encountered perched on branches and leaves of streamside vegetation (Inger 1954; Ferner et al. 2000; Gaulke 2008, 2011). Brown and Alcala (1955, 1961) described a variety of semi-arboreal substrates for this species, including branches a few meters high in trees and away from water, but emphasized that ovulating females were primarily located near water (lake shores and pools of highly oxygenated streams). Eggs are not laid together in masses, but are scattered and adhere to rocks, branches, pebbles, and other submerged debris (Alcala 1962). Gravid females carry between 800–1000 eggs (Alcala 1962; Brown and Alcala 1982b). Alcala (1962) provided a full technical description of *S. acai* tadpoles including notes on growth rates, morphological characteristics, diet, and behavior. Gaulke (2011) described the live coloration of *S. acai* tadpoles (bronze-green, with white scattered granules; larvae have a maximum body length of nearly 70 mm) and metamorphs (similar to that of adult). The new species appears to have a relatively broad season of reproductive activity; newly laid eggs and/or gravid females have been collected from February to December, although amplexus has only been observed in April and May. Newly emerged metamorphs have been collected in May, June, July and November (Alcala 1962; Gaulke 2011).

Species of *Sanguirana* lack vocal sacs (Inger 1954) but vocalizations have been reported in breeding aggregations of *S. luzonensis* (Brown et al. 2000b) and recently documented in *S. mearnsi* (RMB, personal observations). To the best of our knowledge, vocalizations of *S. acai* have not been reported previously in the literature. Our recordings of the new species include at least two distinct call types (see below).

Sympatric species of anurans, that have been recorded from at least parts of the new species' range (Brown and Alcala 1955, 1961, 1964, 1970, 1982a; Gaulke 2011; Diesmos et al. 2015), include *Kaloula pulchra* (introduced; Diesmos et al. 2015), *K. picta* (widespread, endemic) *K. conjuncta negrosensis* (West Visayan PAIC endemic), *K.* cf. *kalingensis* (West Visayan PAIC endemic and potentially undescribed species; Blackburn et al. 2012), *Platymantis dorsalis* (widespread, endemic), *P. corrugatus* (widespread, endemic), *P. negrosensis* (West Visayan PAIC endemic), *P. hazelae* (West Visayan PAIC endemic), *P. paengi* (northwest Panay endemic), *P. spelaeus* (southern Negros endemic), *Limnonectes visayanus* (West Visayan PAIC and Romblon Island Group endemic), *L. leytensis* (widespread endemic), *Philautus surdus* (widespread endemic), *Kurixalus appendiculatus*, *R. pardalis* (widespread non-endemic natives; Brown and Alcala 1982a, 1994), and the three introduced species *Hoplobatrachus rugulosus*, *Rhinella marina*, and *Hylarana erythraea* (Diesmos et al. 2006, 2015).

Vocalizations.—The advertisement call of *Sanguirana acai* has been recorded on two occasions. The first segment (9 April 2001; ML 224181) was recorded at "Camp Lookout," 500 m elevation (ambient temperature 22.9° C; cloacal temperature 24°C), Barangay Bongbong, Municipality of Valencia (the type locality). The second segment (2 December 2001; ML 224348) was recorded at Lake Balinsasayo, 865 m elevation (ambient temperature 20.1°), Barangay Janya-janya, Municipality of Sibulan. Both sites are on the slopes of Mt. Talinis in the Cuernos de Negros Mountain Range. In the first instance, an adult male (TNHC 62794; not vocalizing when first observed) captured at 8:00 pm and held in an inflated plastic bag inside a tent, began calling at 3:00 am the next morning, apparently stimulated by the sound of light rain striking the tent (= Type 1, a dull, amplitude modulated "rattle" call). Over a six-minute period, TNHC 62794 called eight times and eventually ceased as the shower abated. Twelve subsequent calls were elicited artificially by RMB by simulating the approximate frequency of the rain by wrinkling paper and shaking the walls of the tent. The second unvouchered recording was captured from a dugout canoe, upon approaching the lakeshore of Lake Balinsasayo (20:00 hr). In this instance, two or three males were observed in close proximity to a few larger females, and surrounded by an estimated > 15 additional males perched in nearby shrub-layer vegetation; two distinct call types we captured. In this segment, presumed advertisement calls (“rattles”) from two alternating males, are interspersed with numerous high frequency, brief, tonal, frequency modulated vocalizations (Type 2, chirping “peeps” and “squeaks”) from other males perched in close proximity (RMB, *personal observation*).

The stereotyped presumed “advertisement call” vocalization of *S. acai* is a moderately rapid, dull, amplitude modulated pulsed train, sounding to the human ear like a hollow wooden rattle, initially shaken quickly, then more slowly with a gradual decline in pulse repetition rate (Fig. 8). Over the course of the ~0.5–2.5 s call, call amplitude climbs with successive pulses to maximum (Fig. 8C) as they simultaneously decline in pulse repetition rate (i.e., increase to maximum inter-pulse interval). Calling rate ([total number of calls – 1]/time from beginning of first call to beginning of last) in the unvouchered specimen at Lake Balinsasayo was 0.133 calls/s (in the presence of calling conspecifics) and TNHC 62794 called at 0.028 calls/s in response to rain, and then 0.038 in response to an artificial stimulus. Mean calling duration ranged from 0.89 ± 0.31 SD (0.57–1.79; *n*=8) in the vouchered specimen to 1.03 ± 0.48 SD (0.33–2.29; *n*=20) s in TNHC 62794. Individual calls contained 8–16 ($\bar{x}$=8.2 ± 3.7) distinct pulses (Fig. 8D) in the unvouchered specimen and 4–25 ($\bar{x}$=10.5 ± 5.4) pulses in TNHC 62794.

Pulse repetition rate ([total number of pulses – 1]/time from beginning of first pulse to beginning of last) ranged from 0.06 to 0.09 ($\bar{x}$=0.07 ± 0.02 SD) pulses/s in the unvouchered specimen and 0.061 to 0.122 ($\bar{x}$=0.096 ± 0.017 SD) pulses/s in TNHC 62794. Within-call declines in pulse repetition rate is reflected in increasing interpulse intervals, which were brief at the start of each call (0.04–0.10; $\bar{x}$ = 0.07 ± 0.02 SD in the unvouchered recording; 0.03–0.12; $\bar{x}$ = 0.08 ± 0.02 SD in TNHC 62794), increased by a within-call average of 140% at midcall (0.07–0.12; $\bar{x}$ = 0.10 ± 0.02 SD in the unvouchered recording; 0.07–0.14; $\bar{x}$ = 0.12 ± 0.02 SD in TNHC 62794), and increased further to an average of 290% of the initial interpulse interval at the call's terminus (0.09–0.19; $\bar{x}$ = 0.16 ± 0.03 SD in the unvouchered recording; 0.13–0.21; $\bar{x}$ = 0.27 ± 0.03 SD in TNHC 62794; Fig. 8C). Spectral properties of the advertisement call are structured and apparently invariant across multiple calls from a single individual (Fig. 8A, B), but frequency differences are apparent between the two recorded individuals. Throughout the call energy is apparent at multiple, distinct frequency components (Fig. 8B), with the fundamental frequency (lowest) either the dominant (possessing the highest energy of any of the call's frequency components; Fig. 8B), or apparently subequal to the fourth frequency band in some calls. The call of TNHC 62794 had between three (Fig. 8A, B) to seven detectable frequency components in some calls, with highest energy in the fundamental, dominant frequency (relative power, in dB, included in parentheses) of 0.9 kHz (78–79), 1.8 (73–74), 2.3 (72–73), 2.9 (76–78), 3.6 (64–65), 4.2 (59–62), and 5.0 (54–56) kHz. The unvouchered Lake Balinsasayo male's call had three to six distinct frequency components, peaking at 0.9, 1.7, 2.6, 3.4, 4.1, and 5.9 kHz, respectively. Towards the end (the last 3–5 pulses) of 4/20 calls recorded for TNHC 62794, the majority of the call's energy shifted up into the fourth frequency component, with energy levels that rose above the fundamental (80–82 dB).

The second call type (chirping “peeps” and “squeaks”) initially were thought to represent female “response” calls until it was discovered that the originated from the large group of nearby males. In this single instance RMB observed alternating calling males on rocks, each facing nearby females (~10–15 cm). In the background, interspersed between and overlapping rattle calls we recorded a rapid sequence of chirps. Type 2 chirping calls overlapped temporally (multiple males vocalizing at the same time, temporally overlapping one another and Type 1 calls), unlike the nature of the assumed Type 1 male advertisement call, in which males calling in close proximity alternate and do not overlap temporally. These tonal chirping vocalizations (Fig. 9) took the form of brief (0.05–0.07) frequency arcs, rising from 0.6–0.7 to 1.5–1.7 kHz (*n*=14), with subsequent declines back to 0.6–0.7 kHz, constant frequency tones (2.6–3.2 kHz; *n*=9) with durations of 0.09–1.1 s, followed by a steep frequency sweep (terminating at 0.9–1.0 kHz), or simple frequency sweeps from 2.9–3.1 to 1.0–1.1 kHz over an interval of 0.04–0.06 s (*n*=19). The concordance between observed Type 2 vocalizations in *S. acai* and similar calls reported for *S. luzonensis* (Brown et al. 2000b) suggest that calls reported previously for *S. luzonensis* were Type 2 vocalizations (also observed in large aggregations of males); to date, Type 1 calls have not been observed or reported in *S. luzonensis.* In contrast, both Type 1 (rattles) and Type 2 (chirps) have been reported in *S. mearnsi* (Sanguila et al. 2016), although in that study it was also assumed these represented male advertisement calls and female response vocalizations. Additional field work on Samar and Leyte (2016) confirms our revised interpretation, namely that males of *Sanguirana acai* and *S. mearnsi* both produce multiple classes of vocalizations, which we term

Type 1 and Type 2. Additionally, to date, only documented (vouchered) Type 2 calls (chirps) have been confirmed in males of *S. luzonensis.* The advertisement calls of all other *Sanguirana* species remain unknown.

Finally, the true social context and ultimate function of *Sanguirana* call variation remains poorly understood. Type 1 rattle calls have been recorded in *S. acai* and *S. mearnsi* in solitary males (suggesting advertisement, mate attraction), but also in instances of a one or few males, vocalizing in close vicinity to females (suggesting courtship), and at times when nearby, large aggregations of males were producing only Type 2 calls (suggesting chorusing behavior, possibly longer-distance mate attraction, or even agonistic interactions). The interpretation of multiple call types with functions distinct functions has been reported in other anuran communication studies (Narins and Capranica 1978; Rand and Ryan 1981) and is supported by one recent observation of apparent female phonotactic approach, over a five meter stretch of stream, in the direction of a solitary, Type 2-calling male *S. luzonensis* (J. Binaday and RMB, personal observations, January 2017, Sorsogon Province, Luzon).

Etymology.—We are pleased to name this new species for our mentor, collaborator, and friend Dr. Angel C. Alcala, of the Silliman University (Dumaguete City, Negros Island), in recognition of his numerous contributions to Philippine herpetology. Angel Alcala (known by friends and colleagues by a nickname, derived from his initials; ACA, pronounced “Ah-Kah”) is one of the Philippines’ premier biodiversity and conservation scientists, whose lifelong dedication to conservation of the country’s forests and coral reefs stands as an inspiration to generations of Filipinos. Alcala’s earlier fieldwork (conducted in collaboration with the late Walter C. Brown; Alcala 2004) resulted in the world’s most significant collection (> 30,000 specimens) of Philippine herpetological diversity (deposited at CAS), which form the foundation of what is known globally of the taxonomy, distribution, and conservation status of the country's endemic amphibians and reptiles (Brown and Alcala 1961, 1964, 1970, 1982a,b, 1986; Alcala et al. 2004, 2012; Diesmos and Brown 2011; Diesmos et al. 2014, 2015). The specific epithet is a patronym and a masculine noun in the genitive case. Suggested common name, Alcala's West Visayan Stream Frog.

DISCUSSION

The recognition of the *Sanguirana mearnsi* as the valid name for the Northeast Mindanao Stream Frog (Inger 1954; Brown and Alcala 1970; Sanguila et al. 2016) and the recognition of the West Visayan PAIC populations as a new species (Brown et al., 2000a; Fuiten et al. 2011; Gaulke et al. 2011) represent taxonomic solutions that are long overdue (Brown 2007; Diesmos and Brown 2011; Diesmos et al. 2014, 2015). It is not surprising that either the northeast Mindanao PAIC lineage (*S. mearnsi*) nor the West Visayan lineage (*S. acai*) should be found to be distinct from the nominal *S. everetti* of southwest Mindanao Island (Fig. 1; Brown et al. 2016). With respect to the former, the sister species pair *S. mearnsi* and *S. everetti* are parapatric, separated by deep genetic divergence, are phenotypically distinct, and show no evidence of reticulation or gene flow (Inger 1954; Brown et al. 2000a, 2016). With respect to the latter, *S. acai* and *S. everetti* are distantly allopatric on separate PAICs, phenotypically distinct (Fig. 3), and are distantly related (Brown et al. 2016). In contrast, as might be expected, *S. acai*, actually is phenotypically most similar (Fig. 3) to its closest relative, *S. luzonensis.* Previous studies have suggested that the problematic and disjunct distribution of *S. everetti* warranted scrutiny (Inger 1954; Ferner et al. 2000; Fuiten et al. 2011;

Gaulke 2011) and we find it surprising that this unresolved biogeographic anomaly (Brown and Alcala 1970; Brown and Diesmos 2009; Brown et al. 2013a) has not been addressed until now.

The eight recognized species of the genus *Sanguirana* form a well supported clade (Bossuyt et al. 2006; Stuart 2008; Wiens et al. 2009; Holder et al. 2010; Brown et al. 2016), with most taxa distinguished from congeners by diagnostic morphological character differences, morphometric and body size variation, degree of sexual size dimorphism, allopatry on isolated (separated by deep marine channels) island groups, and considerable genetic divergence (Table 2; Brown et al. 2000a, 2016; Fuiten et al. 2011). As currently understood, no other congeners occur in the West Visayan PAIC, and therefore, none occur in sympatry with the biogeographically isolated *S. acai*.

With the resolution of this taxonomic problem, all available evidence (morphological diagnosability, genetic distinctiveness, position in phylogeny, biogeography) points to a logical PAIC-structured understanding of species diversity in the genus *Sanguirana* of the central and southern Philippines (Brown et al. 2000a,b, 2013a, 2016; Brown and Diesmos 2002, 2009)—with a few lingering minor exceptions. One remaining unanswered question is the taxonomic identification of the central Bohol population of "*S. everetti.*" Given that Leyte, Samar, and northeastern Mindanao populations of *Sanguirana* have all been identified convincingly as *S. mearnsi* (Brown et al. 2000a, 2016), Bohol amphibians are most often allied with the Mindanao PAIC (e.g., Brown and Alcala 1970; Brown and Siler 2013; Gonzales et al. 2014), and that true *S. everetti* populations (Taylor 1920; type locality = "Zamboanga" [western Mindanao]) are known now only from southwestern Mindanao (Inger 1954; Brown et al. 2000a, 2016), the allopatric Bohol population of *S. everetti* should be reexamined. We would not be surprised if this population was identified as *S. mearnsi*, but it remains possible that it may represent an additional, undescribed species.

Three unresolved questions still complicate our understanding of evolutionary relationships and *Sanguirana* species diversity in the northern Philippines (Luzon PAIC). First, *S. luzonensis*, as currently recognized, is widespread across multiple islands within the Luzon PAIC, spanning numerous marine channels (Fig. 1) and known fault zones (Yumul et al. 2003, 2009b), all of which have been shown to be biogeographic barriers that define species distributions in unrelated, codistributed groups (Brown and Diesmos 2002, 2009; Brown and Guttman 2002; Welton et al. 2010; Brown and Siler 2013; Brown et al. 2013a; Gonzales et al. 2014). To date, systematists have not critically evaluated patterns of intraspecific variation in *S. luzonensis*, nor considered whether all of the populations referred to *S. luzonensis* in this region are in fact a single evolutionary lineage (species). One recent study (Brown et al. 2016) has taken a first step towards this goal, finding extensive geographically structured genetic variation in this species. However, because so much of Luzon remains unsurveyed, and no formal species delimitation analyses were conducted, the population-level diversity within *S. luzonensis* remains poorly understood (Fig. 1; Brown et al. 2016).

Second, whether *S. tipanan* (Sierra Madre of Luzon; Brown et al. 2000a,b) is a distinct species relative to *S. igorota* (Central Cordillera of Luzon; Brown et al. 2016) remains an open question. The phenotypic distinctiveness of these two taxa is clear at their most northern extent of their ranges where they are separated by the wide, arid, environmental barrier represented by the Cagayan Valley (Taylor 1922; Brown at al. 2000a). However, much like Brown and Siler's (2013) recent findings from the *Pulchrana signata* Complex (see Brown and Guttman 2002:fig 3), variable and intermediate phenotypes have been documented in the southern extent of their ranges, where the distributions of these two species abut in the Caraballo Mountains of central Luzon (Fuiten et al. 2011; Brown et al. 2012b, 2013b). A recent phylogenetic analysis suggested that *S. igorota* may be paraphyletic with respect to *S. tipanan*, an arrangement that would require the placement of the latter species in synonymy with the former, if verified with additional geographic and gene sampling (Brown et al. 2016).

Finally, with small islands and isolated geological components of large islands increasingly appreciated for their tendency to support endemic species (Welton et al. 2010; Sanguila et al. 2011, 2016; Brown et al. 2013a, 2015a), it would not be surprising if additional species of *Sanguirana* were discovered in the near future. Islands like Bantayan, Basilan, Biliran, Bohol, Burias, Pacijan, Ponson, Poro, Ticao, and the remaining islands of the Sulu Archipelago all deserve amphibian biodiversity survey efforts if trained naturalists can be provided access to the last remaining habitats on these isolated landmasses. Likewise, the recent unexpected discovery of a highly distinct evolutionary lineage of *Sanguirana* in isolated mountains of central Luzon (*S. aurantipunctata*; Fuiten et al. 2011) emphasizes the degree to which this endemic and understudied Philippine genus is prone to differentiation in montane habitats; all high elevation peaks of Luzon and Mindanao deserve particular attention by field biologists (Brown 2015).

Conservation efforts aimed at central Philippine amphibians are plagued by near complete removal of forests in the West Visayan islands of Cebu, Guimaras, Negros, Masbate, and Panay (Brown and Alcala 1961, 1964, 1986; Alcala et al. 2004; Gaulke 2011; Supsup et al. 2016), with wholesale conversion of marginal habitats to agriculture (Brown and Alcala 1986), and the archipelago wide infection of amphibian populations by chytrid fungus (Swei et al. 2011; Diesmos et al. 2012; Brown et al. 2012a). We find that the new species, with its forested habitat severely fragmented and its patchy, but well documented, distribution tied to clean water sources running within, or at the margins of, intact vegetation cover (Ferner et al. 2000; Gaulke 2011; *personal observations*) qualifies for classification at a formal, elevated level of conservation threat under IUCN criteria: "Vulnerable" (VU, IUCN 2010: A2ac; B2ab[iii]; D2). Thus, the new species should be considered an immediate conservation concern (Diesmos et al. 2011, 2014).

Given the absence of new data on the status or distribution of *Sanguirana everetti* on central and southern Mindanao Island (Diesmos and Brown 2011; Diesmos et al. 2014, 2015), the conservation status of true *S. everetti* remains "Data Deficient" (IUCN 2016). Studies of the remaining populations of *S. everetti* (southwestern Mindanao Island) and *S. acai* (West Visayan PAIC) are pressing challenges for future field surveys and conservation research (Brown et al. 2012a). Both *S. tipanan* and *S. igorota* are classified by IUCN (2016) at elevated conservation threat levels, although new survey data suggest both species are more widely distributed than previously thought, and appear tolerant to some level of disturbance (Siler et al. 2011; Brown et al. 2000a, 2000b, 2012b, 2013b), suggesting that their status needs to be reconsidered and revised (Diesmos et al. 2014). The unexpected discovery of so many new amphibian species on larger islands (Fuiten et al. 2011; Siler et al. 2011; Brown 2015; Brown et al. 2015b) emphasizes the need for an accelerated pace of faunal inventories and field-based assessment of species boundaries, informed with basic natural history data. These and other unexpected discoveries of evolutionarily distinctive species of endemic Philippine amphibians (e.g., Sanguila et al. 2011; Blackburn et al. 2010, 2013; Brown and Siler 2013; Brown 2015; Brown et al. 2015a) remind us that the only way to solve persistent taxonomic and conservation status questions of this kind is to encourage and support faunal survey activities—

necessarily including the collection of properly preserved voucher specimens (Rocha et al. 2014), advertisement calls, and genetic samples—in both the unexplored, and previously surveyed (yet still poorly understood), islands of the Philippines (Brown et al. 2013a, 2016).

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APPENDIX

Specimens Examined

All specimens are from the Philippines.

Sanguirana acai.—See holotype and paratypes sections.

Sanguirana aurantipunctata.—LUZON ISLAND, NUEVA VIZCAYA PROVINCE, *Municipality of Quezon*, Barangay Maddiangat, Sitio Parola (16°26’16.8’’ N, 121°13’30.0’’ E; WGS-84): PNM 9727 (holotype), PNM 9728–45, KU 325894–932, 325934–45, 329950–51, 308655, 308665, 308667, 308687, 308705, 308706, 308712, 308775, 308776 (Paratopotypes); AURORA PROVINCE, *Municipality of San Luis*, Barangay Real, Sitio Minoli: KU 322548, 322549 (paratypes); *Municipality of Dingalan*, Mt. Mingan: MVD 066, 068, 069, and 074, DSB 3728 and 3745 (six uncataloged specimens, deposited at PNM)

Sanguirana everetti.—MINDANAO, LANAO DEL SUR PROVINCE, *Lake Lanao,* Camp Keithley: CAS-SU 2141; ZAMBOANGA: CAS 61872; SOUTH COTOBATO PROVINCE, “*near Saub*,” MCZ 14083–84; *Municipality of Tupi*, Barangay Kablon, Masbang creek: PNM 469; *Municipality of Tiboli*, Barangay Salacafe, Lake Parker: PNM 3002–07, 3009–12., 3018–19, 3059, 3073; *Municipality of Tampakan*, Barangay Tablu, Sitio Datal Mangisi: KU 327523, 327527, 327529; Sitio Tukuymal: KU 327525, 327526, 327528.

Sanguirana igorota.—LUZON ISLAND: KALINGA–APAYAO PROVINCE, KALINGA SUBPROVINCE, *Municipality of Balbalan*, Barangay Balbalan: CAS 61484 (EHT F789; holotype of *Rana igorota*); CAS 61483, 61485–89, MCZ 14096–98 (paratypes of *Rana igorota*); NUEVA VIZCAYA PROVINCE, *Municipality of Quezon*, Barangay Maddiangat, Mt. Palali: KU 308688, 308707–11, 325843–93; Benguet Province, *Municipality of Kabayan*, Barangay Apunan: PNM

158, 162; Ifugao Province, *Municipality of Banaue*, Barangay Bayninan, PNM 741, 742; Ilocos Province, *Municipality of Adams,* Barangay Adams, Mt. Pao: KU 329824-89.

Sanguirana luzonensis.—LUZON ISLAND, Aurora Province, *Municipality of Carmen*, Aurora National Park: PNM 5742–5765; CMNH 5605–11; 5612–30; *Municipality of Maria Aurora*, Aurora Memorial National Park “tower site”, KU 322566–67; Barangay Villa Aurora, Sitio Dimani, Aurora Memorial National Park: KU 322568–87; Barangay Villa Aurora, Aurora Memorial National Park, Mt. Dayap, area known locally as “Siete:” KU 322588–90; *Municipality of Baler,* Barangay Zabali, Aurora State College of Technology (ASCOT): KU 322591–619; *Municipality of San Luis*, Barangay Real, Sitio Minoli: KU 322620–28, 322520–39, 322540–47; Barangay Lipimental: KU 322550–65, 322503–19; Mountain Province, *Municipality of Bontoc*: MCZ 10556; Laguna Province, *Municipality of Los Baños*, Mt. Makiling: MCZ 23178–79, 14142–45; Zambales Province: *Municipality of Masinloc*, Barangay Coto: CMNH 4171–72, 4279–85; PNM 2371, 2378–84, 2496–98; trail between Famy (Laguna Prov.) and Infanta (Tayabas Prov.): CAS 61819 (holotype of *R. tafti*); Banguet Province, *Municipality of Baguio*, Baguio City: CM 3271, 3273–78, 3280–81, 3283, MCZ 10482–84 (topotypes of *R. guerreroi*); Quezon Province, *Municipality of Polillo*, Barangay Pinaglubayan: KU 302380, 307649–51; Barangay Salipsip, Sition Kapilijan: KU 307652–60; Quezon Province: 303561–63; Catanduanes, *Municipality of San Miguel,* Sulong: KU 308067, 308090–98; *Municipality of Gigmoto*, Barangay San Pedro: KU 308121, 308139, 308158–69; Camarines del Sur Province: *Municipality of Tabaco*, Barangay Comon: KU 306495–98, 306503–06; Camarines del Norte Province, *Municipality of Labo,* Barangay Tulay na Lupa: KU 306499–502, 306507–306509; Isabela Province, *Municipality of Cabagan*, Barangay Garita, Mitra Ranch: KU

307636; NUEVA VIZCAYA PROVINCE, *Municipality of Quezon*, Barangay Maddiangat, Mt. Palali: KU 308655, 308665, 308667, 308687, 308705–06, 308712, 308774–76, 308835–36, 325501–40; CAMARINES NORTE PROVINCE: *Municipality of Labo*, Barangay Tulay Na Lupa: KU 313647-313681; POLILLO ISLAND: POLILLO PROVINCE, *Burdeos*: CAS 62448 (holotype of *R. merrilli*).

Sanguirana mearnsi.—MINDANAO ISLAND: DAVAO ORIENTAL PROVINCE, *Municipality of Baganga*, "Baganga River, east coast mountain range, 300–1,500 m above sea level:" USNM 35258 (holotype of *Rana mearnsi*); AGUSAN DEL NORTE PROVINCE: *Tagibo and Daydayan rivers*: S. side of Mt. Hilong-hilong: CAS 13922–25, 137533–34; Municipality of Remedios T. Romualdez, Eye Falls, intersection of Dayhopan and Agan Rivers, Mt. Hilong-hilong: KU 332972–007; Municipality of Cabadbaran, Barangay Tag-Ibo, Dalaydayan River: USNM 305594–97; MISAMIS ORIENTAL PROVINCE, *Municipality of Gingoog City*, Barangay Lumotan, Sitio San Isidro, Mt. Balatukan: KU 319777–82; Barangay Lawan, Sitio Kibuko, Mt. Lumot: KU 333014–67; DAVAO DEL NORTE PROVINCE, *Municipality of New Bataan*, Sitio Liboton, Mt. Puting Bato (Malaya River drainage): CMNH 5603–04; DAVAO CITY PROVINCE, *Municipality of Paquibato*, Barangay Malambuon, Mt. Makaayat: PNM 2880–81; DAVAO DEL SUR PROVINCE, *Mt. Apo*: KU 327521; SAMAR ISLAND: NORTHERN SAMAR PROVINCE: *Municipality of San Isidro*: Barangay Matuquinao: CAS-SU 18160, 18167–69, 18172–73; EASTERN SAMAR PROVINCE: *Municipality of Taft*, Barangay San Rafael: KU 338613–34, 338648–61, 310697–98; WESTERN SAMAR PROVINCE: *Municipality of San Jose de Buan*; Barangay Uno, Mt. Huraw: KU 338021, 338635–45; LEYTE ISLAND: CABALIAN: MCZ A-23190 (holotype of *Rana everetti albotuberculata*), A-23188–89, A-132410–14, A-132416–19 (topotypes *Rana everetti albotuberculata*); BOHOL ISLAND, BOHOL PROVINCE, *Municipality of Cantub*, Sierra Bullones: CAS 137028.

Sanguirana sanguinea.—PALAWAN ISLAND: CMNH 3700–01, 3733, 3737; PALAWAN PROVINCE, *Puerto Princesa City*, Barangay Irawan: KU 308987, 309016, 309019–21, 309023–24, 309026, 309027–31, 309033, 309037, 309094; *Municipality of Rizal*, Mt. Bintangor: KU 311312; *Municipality of Brooke's Point*, Barangay Mainit, Mainit Falls: KU 309570; Barangay Samarinana, Mt. Mantalingajan, area known locally as "Pitang:" KU 309577, 309578, 309587.

Sanguirana tipanan.—LUZON ISLAND, AURORA PROVINCE, *Municipality of San Luis*, Barangay Villa Aurora, Aurora National Park: PNM 5727 (holotype of *Rana tipanan*), CMNH 5579–86, 5588, 5590–99, PNM 5720–26, 5728–36, 5738–41 (paratypes of *Rana tipanan*); *Municipality of Maria Aurora*: Aurora Memorial National Park: KU 322755–66; Barangay Villa Aurora, Aurora Memorial National Park, Mt. Dayap, area known locally as "Siete:" KU 322767–94; *Municipality of San Luis*: Barangay Lipimental: KU 322795–805, 322808–58, 323013; Barangay Real, Sitio Minoli: 322806–07, 323014.

TABLE 1.—Character loadings for principal components analysis of 14 continuously varying morphometric characters, selected (from 19 total) on the basis of each variable's within-species/OTU regression coefficient (regressed against SVL). Heavily loading characters in PCs 1 (lower limb dimensions) and 2 (head shape), contributing disproportionately to group structure (see Fig. 1A), are bolded for emphasis.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
SVL	0.172	-0.088	-0.434	0.058	-0.378	0.3934	-0.320	0.428	-0.324
Head length	0.202	**-0.417**	0.182	0.340	0.186	0.1077	-0.053	0.024	0.113
Snout length	0.231	**-0.423**	0.138	0.084	0.148	0.2394	0.257	0.078	0.270
Tympanic annulus diameter	0.126	**-0.475**	-0.224	0.204	-0.068	-0.0116	-0.119	-0.050	0.160
Head width	0.133	0.160	0.423	0.359	0.201	-0.0735	-0.100	0.451	-0.44
Forearm length	-0.028	**-0.358**	0.392	-0.008	-0.261	-0.2412	-0.032	-0.250	-0.431
Femur length	**0.419**	0.065	0.099	-0.327	0.090	0.0724	-0.100	-0.188	-0.209
Tibia length	**0.416**	-0.118	-0.085	-0.232	-0.017	-0.087	-0.127	-0.374	-0.254
Tarsus length	**0.380**	0.078	-0.066	0.015	0.000	-0.7022	-0.230	0.310	0.317
Foot length	**0.422**	0.172	-0.127	-0.064	-0.084	0.055	0.072	-0.048	0.136

Hand length	**0.311**	0.179	-0.235	0.226	0.172	0.005	0.693	-0.007	-0.251
Nuptial pad length	0.156	0.068	0.406	-0.126	-0.705	0.089	0.319	0.189	0.224
Toe 4 disc width	0.212	0.283	0.345	-0.051	0.229	0.443	-0.334	-0.078	0.240
Finger 3 disc width	0.064	0.299	-0.035	0.685	-0.306	-0.004	-0.167	-0.476	0.078
Eigenvalue	4.089	2.729	2.580	1.145	0.681	0.499	0.466	0.444	0.412
Standard deviation	2.02	1.65	1.61	1.07	0.83	0.71	0.68	0.67	0.64
Proportion	0.292	0.195	0.184	0.082	0.049	0.036	0.039	0.032	0.029
Cumulative	0.292	0.487	0.671	0.753	0.802	0.837	0.870	0.901	0.931

TABLE 2.—Uncorrected percent sequence divergence for mitochondrial data (12S–16S) among species of the genus *Sanguirana*. Intraspecific mitochondrial sequence divergences along the diagonal are bolded for emphasis; note intraspecific divergence within *S. acai* (Negros vs Panay populations).

	S. acai	*S. mearnsi*	*S. aurantipunctata*	*S. everetti*	*S. igorota*	*S. luzonensis*	*S. sanguinea*	*S. tipanan*
S. acai	**0.0–6.3**							
S. mearnsi	6.8–9.9	**0.1–1.8**						
S. aurantipunctata	9.0–10.9	6.7–9.0	**4.5**					
S. everetti	8.0–9.1	4.0–5.9	8.4–9.3	**0.1–0.6**				
S. igorota	6.4–7.8	6.4–8.7	9.0–10.3	7.3–8.2	**0.9**			
S. luzonensis	6.0–7.3	5.3–8.3	8.6–9.7	7.0–7.7	4.1–5.0	**0.6–3.5**		
S. sanguinea	10.8–12.1	10.3–12.1	12.2–13.1	10.6–11.5	11.3–12.0	10.8–11.2	**5.8**	
S. tipanan	6.8–7.8	5.6–8.4	9.1–10.1	7.7–8.3	1.6–1.9	4.1–5.3	11.7–12.0	**0.3**

TABLE 3.—Distribution of selected diagnostic color and dermal characters in *Sanguirana acai,* and all known congeners (+ present, – absent, –/+ variable). General geographic range and male body size (SVL in mm) are included for reference.

	S. acai	*S. everetti*	*S. luzonensis*	*S. aurantipunctata*	*S. tipanan*	*S. igorota*	*S. mearnsi*	*S. sanguinea*
Range	Negros, Masbate, Panay	W. Mindanao	Luzon PAIC	Montane central Luzon	NE Luzon	NW Luzon	E. Mindanao, Samar, Leyte	Palawan PAIC
SVL (male)	45.8–57.6	61.7–79.5	43.4–67.1	47.3–53.7	46.0–53.5	49.6–58.3	58.3–68.6	36.3–42.8
Flank coloration	Sharp dark-light stratification	Dark-light gradient	Dark-light gradient	Green-purple stratification	Green with brown reticulum	Green with brown blotches	Green-yellow gradient	Light to dark brown
Dorsal asperities	–	–	–	–	+, fine	+, fine	+, coarse	–
Dark pectoral patches	+	–	–/+	–	–	–	–	–
Infra-cloacal tubercles	–	+	–	+	+	+	+	–
Dorsal color	Yellow, green, tan, or light gray	Light green	Brown, yellow,	Bright green-yellow with black flecks or	Iridescent green or	Bright green with dark	Dark green with yellow dorsolateral	Tan, reddish-orange, or

			green, tan, or light gray	orange spots	golden, with brown reticulum	spots	tubercles	brown
Tympanum translucent	–	–	–	–	+	–/+	–	–
Tibial bars	+	–/+	+	–	+	+	–	+
Forearm bars	–	+	+	–	+	+	–	+
Large dark dorsal spots	–	–/+	–	–	–/+	–/+	–	–
Dark lateral head color	+	Canthal stripe	Canthal stripe	–	Canthal stripe	Canthal stripe	Canthal stripe	Canthal stripe
Snout	Rounded	Rounded	Pointed	Rounded	Rounded	Squarish	Rounded	Pointed
Ventrum tuberculate	Limited to groin	Groin	Groin	Throughout	Groin	Groin	Groin	–
Dorsolateral ridges	Thin to indistinct	Indistinct	Indistinct	Indistinct to moderate	Indistinct to moderate	Moderate	Thick, fleshy	Moderate
Subarticular tubercles	Light on dark plantar foot surface	Variable on dark	Variable on dark	Light on light	Light on light	Light on light	Light on light	Light on light
F:M range, $\bar{x}$ ± standard	1.3–1.4	1.2	1.3–1.4	1.3–1.4	1.3–1.5	1.10–1.1	1.1–1.2	1.8–2.1

deviation	1.4 ± 0.02	—	1.3 ± 0.05	1.3 ± 0.01	1.4 ± 0.06	1.1 ± 0.01	1.2 ± 0.01	2.0 ± 0.5

TABLE 4.—Continuously varying morphometric variation in adult males of *Sanguirana acai*, n. sp., and all known congeners. Table entries include sample size (*n*), $\bar{x} \pm 1$ standard deviation, and range (below; in mm).

	S. acai	*everetti*	*luzonensis*	*aurantipunctata*	*tipanan*	*igorota*	*mearnsi*	*sanguinea*
n	28	7	42	34	41	46	26	22
SVL	53.0 ± 3.7 45.8–57.6	70.9 ± 6.1 61.7–79.5	52.8 ± 6.7 43.4–67.1	50.8 ± 1.8 47.3–53.7	49.6 ± 1.9 46.0–53.5	52.9 ± 2.2 49.6–58.3	64.2 ± 3.0 58.3–68.6	30.7± 1.7 36.3–42.8
Head length	20.7 ± 1.2 18.5–22.6	27.2 ± 2.5 22.8–30.3	20.8 ± 2.0 17.8–24.8	18.7 ± 0.4 16.0–19.2	20.4 ± 0.8 18.0–22.1	20.1 ± 0.8 19.1–21.6	24.4 ± 1.2 22.4–26.7	16.2 ± 0.3 15.8–16.8
Snout length	9.4 ± 0.5 8.7–10.4	12.3 ± 1.1 10.3–13.3	9.5 ± 1.1 8.0–11.8	8.4 ± 0.4 7.3–9.0	9.0 ± 0.5 8.1–10.1	8.7 ± 0.4 7.9–9.3	10.8 ± 0.4 10.2–11.6	7.1 ± 0.4 6.5–7.7
Inter-orbital distance	5.2 ± 0.2 5.0–5.5	7.4 ± 0.3 6.9–7.9	5.0 ± 0.7 4.0–6.9	5.9 ± 0.4 5.5–6.9	5.2 ± 0.4 4.6–6.2	4.5 ± 0.4 3.8–5.1	6.9 ± 0.6 5.3–7.8	3.3 ± 0.3 2.9–3.8
Inter-narial distance	5.2 ± 0.2 4.9–5.7	7.0 ± 0.6 5.8–7.7	9.7 ± 0.6 3.9–5.9	5.2 ± 0.2 4.9–6.3	5.6 ± 0.3 5.0–6.2	5.2 ± 0.4 4.7–6.5	6.2 ± 0.6 5.7–7.8	3.7 ± 0.2 3.4–4.0
Eye diameter	6.3 ± 0.5 5.4–7.3	7.2 ± 0.7 6.0–8.5	6.7 ± 0.6 5.5–8.0	5.5 ± 0.5 4.3–6.0	6.9 ± 0.4 6.2–7.8	6.6 ± 0.4 6.1–7.5	6.8 ± 0.4 6.2–7.5	5.1 ± 0.4 4.4–5.8
Tympanic annulus diameter	4.8 ± 0.5 3.9–5.3	7.3 ± 0.9 5.7–8.5	4.7 ± 0.4 4.0–5.6	3.9 ± 0.3 3.4–4.4	4.4 ± 0.3 3.7–5.1	3.8 ± 0.5 3.0–5.4	5.7 ± 0.3 4.9–6.1	3.9 ± 0.3 3.5–4.4
Head width	15.6 ± 1.1 13.9–17.1	22.7 ± 2.1 19.5–25.5	17.0 ± 1.9 14.1–21.3	17.7 ± 0.7 16.4–18.5	16.6 ± 0.7 14.8–17.8	17.5 ± 0.6 16.6–18.9	20.3 ± 1.1 18.2–22.1	12.5 ± 0.6 11.7–13.4

Forearm length	11.9 ± 1.2 9.8–13.3	14.1 ± 1.9 12.4–18.6	10.9 ± 1.4 8.8–14.1	10.9 ± 0.4 10.4–11.5	11.8 ± 0.6 10.4–12.6	11.0 ± 0.6 10.1–11.9	12.8 ± 0.7 11.6–13.7	8.3 ± 0.6 7.6–9.6
Femur length	29.0 ± 1.8 26.6–31.8	39.7 ± 3.3 34.5–44.2	27.8 ± 3.1 22.6–34.0	26.2 ± 0.8 23.0–27.5	26.5 ± 1.1 24.0–29.2	28.5 ± 1.1 26.3–30.3	34.5 ± 1.7 30.9–37.2	22.0 ± 1.1 20.4–23.7
Tibia length	32.4 ± 2.2 29.0–34.9	43.4 ± 3.5 36.8–47.7	30.6 ± 3.4 25.1–37.6	27.6 ± 0.7 26.3–28.6	28.87 ± 1.3 25.6–31.8	30.2 ± 1.0 28.7–31.6	37.0 ± 2.1 32.5–40.4	24.9 ± 1.5 23.1–27.2
Tarsus length	16.7 ± 1.2 15.0–18.2	24.0 ± 1.8 20.7–26.5	17.5 ± 2.0 14.0–21.3	16.0 ± 0.8 13.4–16.9	15.7 ± 0.8 14.0–17.2	17.2 ± 0.7 16.1–18.5	20.6 ± 1.0 18.6–22.7	13.8 ± 0.7 12.9–15.0
Foot length	26.6 ± 1.5 24.3–28.8	40.3 ± 3.6 33.9–46.6	27.7 ± 3.6 22.6–34.9	26.0 ± 1.1 21.5–27.7	24.5 ± 1.4 21.1–26.6	27.7 ± 1.2 25.6–30.2	34.7 ± 1.8 32.0–38.1	22.1 ± 0.8 20.7–23.1
Hand length	17.3 ± 1.0 15.6–18.9	24.8 ± 2.0 21.8–27.8	17.3 ± 2.0 14.1–22.0	19.2 ± 0.7 18.0–20.1	15.8 ± 0.8 14.2–18.4	17.0 ± 0.8 16.0–18.2	23.1 ± 1.4 20.9–25.7	10.9 ± 0.4 10.1–11.5
Toe IV length	25.9 ± 2.9 20.9–26.6	39.4 ± 0.6 38.7–39.9	27.8 ± 2.2 22.9–32.6	22.0 ± 1.5 18.5–25.6	22.3 ± 1.3 19.0–24.3	23.8 ± 1.5 20.8–26.8	27.7 ± 4.0 22.9–32.1	19.9 ± 1.2 18.3–21.4
Finger III length	11.9 ± 0.8 10.4–12.9	19.4 ± 1.8 17.1–20.3	13.2 ± 0.9 11.4–14.7	12.8 ± 0.9 11.0–15.1	11.8 ± 0.8 10.4–13.5	12.0 ± 1.0 10.6–13.5	16.5 ± 1.0 14.2–18.8	7.1 ± 0.3 6.6–7.7
Nuptial pad length	7.0 ± 0.5 6.0–7.9	9.5 ± 1.4 8.0–12.4	7.9 ± 1.1 6.4–10.3	7.4 ± 0.6 5.9–8.2	7.2 ± 0.4 6.3–7.8	8.0 ± 0.5 7.3–8.9	9.3 ± 0.6 8.2–10.1	6.7 ± 0.4 5.9–7.2
Toe IV Disc width	1.6 ± 0.3 0.9–2.1	2.5 ± 0.2 2.1–2.8	1.9 ± 0.3 1.4–2.6	1.8 ± 0.1 1.7–1.9	1.7 ± 0.2 1.3–2.1	2.0 ± 0.2 1.6–2.4	2.2 ± 0.2 1.5–2.5	1.5 ± 0.2 1.2–1.9
Finger III Disc width	2.8 ± 0.5 2.0–3.4	4.0 ± 0.5 3.3–4.6	3.1 ± 0.5 2.0–4.3	3.8 ± 0.2 3.5–4.3	2.8 ± 0.2 2.2–3.2	3.3 ± 0.3 2.7–3.8	4.5 ± 0.3 3.9–5.1	1.2 ± 0.2 1.0–1.5

FIGURE CAPTIONS

FIG. 1—(A) Distributions of the eight species of the Philippine endemic genus *Sanguirana* with vouchered localities indicated with symbols colored when corresponding to genetic samples; white in cases were no genetic data are available; "m" = type locality of *Rana mearnsi* (Baganga River); "a" = type locality of *Rana everetti albotuberculata* (Cabalian); Pleistocene Aggregate Island Complexes (PAICs; Brown and Diesmos, 2009) indicated with incremental gray shading (key). (B) Multilocus Bayesian phylogenetic estimate of evolutionary relationships in the genus *Sanguirana* (from Brown et al. 2016); Black dots at nodes indicate strongly supported clades (Likelihood bootstraps ≥ 70%; posterior probabilities ≥ 0.95); gray node moderately supported, (<70%/>0.90); symbols at branch tips correspond to those plotted on map (A) and question marks at tree tips indicate populations of uncertain taxonomic status. See text and Brown et al. (2016) for additional details.

FIG. 2—Live male (A) and female (B) *Sanguirana mearnsi* (formerly *S. albotuberculata* [Inger 1954; Brown et al. 2000a, 2016]) from the municipalities of (A) Burauen, Leyte Island, Leyte Province (deposited at KU: RMB Field No. 21807; Photo: J. Fernandez) and (B) Gingoog City, Mindanao Island, Misamis Oriental Province (KU 333014; Photo: RMB). Note thickened, dorsolateral dermal folds and rugose texture of skin (the result of densely distributed keratinized asperities) in males (both character states reduced in female) and the distribution of green pigment throughout dorsal surfaces of males (limited to ventrolateral surfaces in females).

FIG. 3—Bivariate ordination of a first two components from a principal components analysis (PCA; A) and subsequent discriminant analysis of principal components (DAPC; B) for 14 continuously varying morphometric variables (males only) selected by each variable's within-species/OTU linear coefficient when regressed against SVL. Character loadings (Table 1) indicate that distal limb dimensions contributed disproportionately to PC 1, whereas dimensions related to

head length contributed heavily to dispersion along PC 2. See text for character definitions; pale polygon encompassing *S. acai* points added to the PCA plot (A) for emphasis; inertia ellipses included in the DAPC plot (B) for emphasis.

FIG. 4—Adult male *Sanguirana acai*, sp. nov., (holotype PNM 9800), and female (paratopotype KU 326383) in dorsal (A) and ventral (B) views. Scale bars = 5mm.

FIG. 5—Details of the palmar surfaces of the hand in *Sanguirana acai*, sp. nov. (A: male holotype PNM 9800; B: female paratopotype KU 326383), and plantar surface of foot (C, D, same specimens). Scale bars = 5mm.

FIG. 6—*Sanguirana acai*, sp. nov., in life (from the Municipality of Valencia, southern Negros Island): (A) adult male holotype (PNM 9800); (B) adult female paratopotype (KU 326383).

FIG. 7—*Sanguirana acai*, sp. nov., in life, photographed in the Municipality of Sebaste, Antique Province, Panay Island (specimen not collected) in the species' typical, stream-side vegetation perch microhabitat.

FIG. 8—Male advertisement call (Type 1, rattle call) of *Sanguirana acai*, sp. nov. (male paratype TNHC 62794; ML 224181), recorded from the type locality, Barangay Bongbong, the Municipality of Valencia, southern Negros Island (9 April 2001; body temperature 24° C). An expanded sonogram (A: frequency in kHz versus time in ms) and waveform (relative amplitude vs. time in ms) of two notes from mid-call, and relative power spectrum (B; from a Fast Fourier Transformation, relative amplitude vs. frequency in kHz) and a full call as depicted in an 1.8 s oscillogram (C: relative amplitude vs. time in s) and corresponding audiospectrogram (D: frequency in kHz vs. time in s) of a typical 18-note call.

FIG. 9—Audiospectrogram of the complex acoustic repertoires of *Sanguirana mearnsi* (A, B; from Municipality of Burauen, northern Leyte Island; KU XXX; ML XXX) and *Sanguirana acai*, (C; from Lake Balinsasayo, Cuernos de Negros Mountain Range, southern Negros Island; voucher not collected, ML 224348). In both species, structured, presumably advertisement "rattle" vocalizations (Type 1 calls) differ from "chirping" frequency arcs and sweeps (Type 2 calls) of unknown function. A third vocalization, "quacks" have only been recorded in *S. mearnsi* (B); in the lower panel calls of orthopterans overlap vocalization of *S. acai* at 2.2 and 4.7 kHz.