

STATUS OF SOME PHILIPPINE FROGS REFERRED TO *RANA EVERETTI* (ANURA: RANIDAE), DESCRIPTION OF A NEW SPECIES, AND RESURRECTION OF *RANA IGOROTA* TAYLOR 1922

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ABSTRACT: We describe a new species of wide-disked ranine frog from Aurora National Park and possibly Mt. Cetaceo, two montane localities within the geologically distinct Sierra Madres coastal mountain range, eastern Luzon Island, Philippines. This endemic differs from Philippine congeners in the *R. everetti* species group by the combination of a relatively small body size, the presence of densely distributed asperities throughout the skin of most males, a translucent tympanum in females and most males, an iridescent green dorsum with black spots or faint reticulum in males and an iridescent green to golden dorsum with distinctive brown reticulum in females. In addition to the new species, we support the designation of *Rana everetti*, *R. luzonensis*, and *R. albotuberculata* as distinct evolutionary species, and we resurrect *R. igorota* from the synonymy of *R. everetti luzonensis*.

Key words: Aurora National Park; *Chalcorana*; Evolutionary species concept; New species; *Rana albotuberculata*; *Rana everetti*; *Rana igorota*; *Rana luzonensis*; *Rana tipanan*; Sierra Madres Mountains; Cordillera Central; Luzon Island; Philippines; Ranidae

THE distantly allopatric species *Rana everetti* Boulenger 1882 and *R. luzonensis* Boulenger 1896 originally were described from the Philippine islands of Mindanao and Luzon, respectively. Features that readily distinguish the *Rana everetti* complex from other southeast Asian *Rana* include the combination of (1) thin, elongate bodies, (2) extremely expanded terminal digital disks with circummarginal grooves, (3) an elongate nuptial pad covering nearly the entire medial portion of the first finger, (4) an absence of vocal sacs, (5) a coarsely glandular posterior portion of the venter, and (6) an absence of humeral glands. Although no phylogenetic analyses have been performed on this group, various workers have considered these Philippine species to be allied with *R. hosii* and *R. chalconota* of the Greater Sunda Shelf (Boulenger, 1882; Dubois, 1992; Inger, 1954, 1966; Taylor, 1922a, 1962; Van Kampen, 1923).

Subsequent to the descriptions of *R. everetti* (from Mindanao Isl.) and *R. luzonensis* (from Luzon Isl.), a variety of names have been applied to Philippine frogs related to (or possibly conspecific with) these species. Additional Mindanao populations have been described as *R. mearnsi* (Stejneger, 1905) and *R. dubita* (Taylor, 1920). In addition to the three Mindanao species, Taylor also recognized Boulenger's *R. luzonensis* and described *R. igorota* (Taylor, 1922a) and *R. guerreroi* (Taylor, 1920) from Luzon and *R. tafti* (Taylor, 1922a) and *R. merrilli* (Taylor, 1922b) from southwestern Luzon and Polillo Island (Fig. 1). The types of *R. guerreroi* were later recognized by Taylor (1922a) to be immature specimens of *R. luzonensis* and placed in the synonymy of this species. *Rana igorota*, *R. tafti*, and *R. merrilli* were maintained as valid species endemic to the Greater Luzon aggregate island complex (Fig. 1).

Consistent with his application of the polytypic species concept, Inger (1954) placed *R. igorota*, *R. tafti*, *R. dubita*, *R.*

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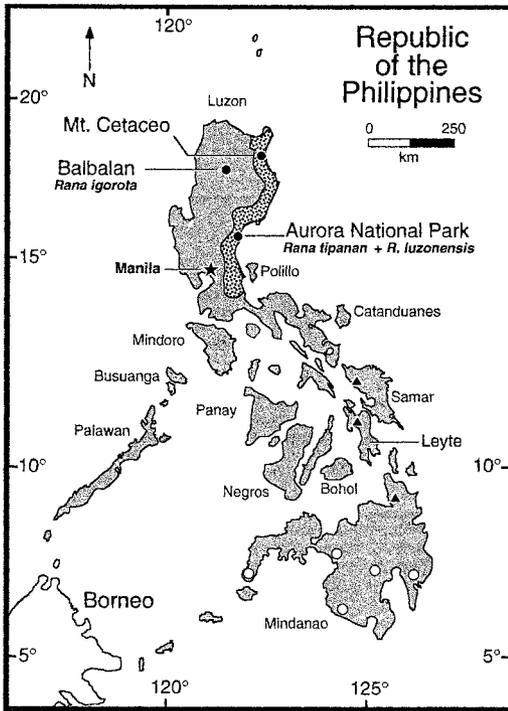


FIG. 1.—Distribution of selected members of the *Rana everetti* complex in the Philippines. The type localities for *Rana tipanan* (Aurora National Park) and *Rana igorota* (Balbalan) are shown; the locality of the photographic record of *Rana tipanan* in the northern Sierra Madres range (Mt. Cetaceo) is also indicated. Collection localities (Appendix I) for *Rana albotuberculata* (shaded triangles) and *Rana everetti* (open circles) are also shown. The approximate distribution of the geological components constituting the Sierra Madres Mountain Range are darkly stippled.

mearnsi, *R. merrilli*, and *R. luzonensis* in the synonymy of *R. everetti*, retaining only *luzonensis* and *everetti* as subspecies. Inger described another subspecies, *R. everetti albotuberculata* from Leyte Island, bringing the number of subspecies of *everetti* to three: *R. e. everetti*, *R. e. luzonensis*, and *R. e. albotuberculata* (Inger, 1954).

We suspect that the available taxonomy (Inger, 1954) underestimates the species diversity of Philippine frogs in the *R. everetti* complex. Inger's (1954) review was primarily based on pre-WWII specimens, many of which were poorly preserved and considerably faded. Inger himself was unable to examine any live specimens, lacked many ecological and behavioral data that

are now available, and usually discounted color variation when making taxonomic decisions. Although the taxonomic decisions of Inger have never been contested in print, notes in Taylor's handwriting found by R. I. Crombie in the section on the *R. everetti* complex in the USNM library copy of Inger's (1954) monograph suggest that Taylor emphatically disagreed with Inger's taxonomic treatment.

A phylogenetic analysis of the *Rana everetti* complex is now underway (Brown and Crombie, unpublished data); accordingly, the taxonomic status of the seven species recognized by Taylor, but synonymized with *R. everetti* by Inger (1954), will not be comprehensively treated here. Our purpose, rather, is to clarify the status of the Luzon island members of the *R. everetti* complex, address the status of the nominal subspecies (*R. e. everetti*), and consider the status of other Philippine subspecies (*R. e. albotuberculata*) that may be confused with some of the the Luzon island species. Our taxonomic decisions are based on newly-collected material as well as specimens available to Taylor and Inger at the time of their earlier work. Furthermore, although we examined specimens from a wide variety of Philippine localities (including most of Taylor's and Inger's types), we hold consideration of the status of many of these populations in abeyance until the phylogenetic study is completed.

Recently, Dubois (1992) listed as full species (in his genus *Chalcorana*) all of Inger's (1954) subspecies without comment or accompanying data; his treatment was followed by Duellman (1993). Although we are opposed to taxonomic changes made without substantiation, Dubois' (1992) taxonomic arrangement stands as a series of untested hypotheses that we will address here.

On 10 May 1992, while participating in the Department of the Environment and Natural Resources-International Council for Bird Preservation (DENR-ICBP) Biodiversity Assessment of the northern Sierra Madres, one of us (A. C. Diesmos) encountered and photographed a striking unidentified species of frog in upper mon-

tane forest (sensu Whitmore, 1984) at 1500 m above sea level on Mt. Cetaceo, Cagayan Valley, Sierra Madres Mountain Range, Luzon Island. The specimen was not collected, but the photograph was distributed among Philippine and American herpetologists by whom it invariably defied identification. The unidentified species was not seen again until recent collaborative survey efforts between the National Museum of the Philippines, the Philippine Department of Environment and Natural Resources, and Cincinnati Museum of Natural History in the central eastern coastal Sierra Madres mountains of Luzon Island (Fig. 1) resulted in the collection of additional specimens. On 14 May 1997, Vicente Yngente captured the first of a series of vivid iridescent green frogs on a rock near a tributary of the Kabatangan River within the boundaries of the Aurora National Park, Aurora Province, southeast Luzon Island. Consideration of the extensive morphological and ecological variation between this new species and the sympatric *R. luzonensis* has provided us with the opportunity to clarify the taxonomies of some of the frogs synonymized with *R. everetti*, reconsider the specific rank of *R. igorota*, and describe the remarkable new Philippine endemic that was first encountered by A. C. Diesmos in 1992.

MATERIALS AND METHODS

We examined fluid-preserved and cleared and stained (alizarin red and alcian blue; Dingerkus and Uhler, 1977) specimens of frogs from the collections at the California Academy of Sciences (CAS), the Harvard University Museum of Comparative Zoology (MCZ), the Field Museum of Natural History (FMNH), the United States National Museum (USNM), the National Museum of the Philippines (PNM), the Carnegie Museum of Natural History (CM), and the Cincinnati Museum of Natural History (CMNH). Specimens (including types of as many species as possible) were examined for diagnostic morphological character states (color pattern, dermal asperities, infra-cloacal tubercles, nuptial pads, digital characters, and body proportions), and the following 25 men-

sural characters (Matsui, 1984) were taken for multivariate analyses: snout-vent length (SVL), head length (HL), snout length (SNL), interorbital distance (IOD), internarial distance (IND), eye diameter (ED), tympanic annulus diameter (TAD), eye-tympanum distance (ETD), head width (HW), upper arm length (UA), forearm length (FA), femur length (FL), tibia length (TBL), tarsus length (TSL), pes length (PL), manus length (ML), fourth toe length (Toe4L), first toe length (Toe1L), first finger length (Fin1L), third finger length (Fin3L), nuptial pad length (NPL), metatarsal tubercle length (MTTL), fourth toe disk width (Toe4DW), first finger disk width (Fin1DW), third finger disk width (Fin3DW), and width of the widest transverse tibial band of right rear limb (TBW). All measurements were taken to the nearest 0.1 mm (with digital calipers and microscope when necessary) from sexually mature adults. Only data scored by R. M. Brown were used in an effort to reduce inter-measurer inconsistencies (Lee, 1990). Terminology for osteological descriptions follows Graybeal and Cannatella (1995).

An evolutionary species is the largest single lineage (ancestor-descendant series of populations) that can be characterized as distinct from other such lineages and within which there is reproductive cohesion (Frost and Hillis, 1990). For the purposes of this paper, we consider as distinct lineages populations that are (1) geographically isolated (as montane or insular endemics) and morphologically distinct and (2) sympatric, reliably diagnosable forms for which the hypothesis of conspecificity confidently can be rejected (Frost and Hillis, 1990; see also Wiens, 1993). Our intent is to clarify the status of some of the Luzon Island species related to *R. luzonensis* within the framework of a lineage-based species concept that emphasizes evolutionary history (Frost and Hillis, 1990). However, due to the presence (in some samples of frogs) of characteristics considered by Inger (1954) to be diagnostic for *R. albotuberculata* (infra-cloacal tubercles and dermal asperities) comparisons with specimens referred to that taxon (described

TABLE 1.—Morphometric variation (in mm) in adult *Rana tipanan*, *R. luzonensis*, *R. igorota*, *R. albotuberculata* and *R. everetti*. Table entries include mean \pm 1 standard deviation (range below) and sample size (n). See text for character abbreviations.

	<i>R. tipanan</i> (Aurora)		<i>R. igorota</i> (holotype)		<i>R. luzonensis</i> (Aurora)		<i>R. albotuberculata</i> (Samar and Leyte)		<i>R. everetti</i> (S. Mindanao)	
	male n = 41	female n = 5	male n = 1	male n = 31	female n = 6	male n = 11	female n = 1	male n = 5	female n = 3	
SVL	49.6 \pm 1.9 46.0-53.5	75.2 \pm 2.4 72.0-78.8	57.3	57.1 \pm 3.6 50.7-64.0	76.0 \pm 4.2 72.6-83.7	60.9 \pm 4.4 55.7-68.6	73.8	78.3 \pm 0.8 77.8-79.4	84.2 \pm 9.4 73.7-91.8	
HL	20.4 \pm 0.8 18.0-22.1	28.0 \pm 0.8 27.3-29.4	21.5	23.4 \pm 1.2 20.1-25.3	28.4 \pm 1.1 27.3-29.7	23.2 \pm 1.6 21.6-25.6	27.2	29.8 \pm 0.5 29.1-30.3	30.5 \pm 1.0 29.7-32.0	
SNL	9.0 \pm 0.5 8.1-10.1	12.8 \pm 0.9 11.9-14.0	8.8	11.0 \pm 0.6 9.3-12.1	13.4 \pm 0.7 12.7-14.3	10.2 \pm 1.0 9.1-11.9	12.1	13.3 \pm 0.6 13.2-13.4	13.8 \pm 1.0 12.6-14.4	
IOD	5.2 \pm 0.4 4.6-6.2	8.4 \pm 1.0 7.7-10.1	5.1	7.2 \pm 0.5 6.5-8.0	9.2 \pm 1.1 7.2-10.3	5.6 \pm 0.5 5.0-6.3	6.2	7.3 \pm 0.1 7.2-7.4	9.8 \pm 1.8 7.8-11.0	
IND	5.6 \pm 0.3 5.0-6.2	7.7 \pm 0.6 6.8-8.4	6.5	5.9 \pm 0.3 5.2-6.8	7.7 \pm 0.7 6.9-8.9	6.3 \pm 0.8 5.4-7.6	7.4	7.6 \pm 0.2 7.5-7.7	8.2 \pm 0.2 8.0-8.4	
ED	6.9 \pm 0.4 6.2-7.8	9.2 \pm 0.5 8.4-9.9	7.2	7.2 \pm 0.5 6.5-8.3	8.8 \pm 0.2 8.5-9.2	7.2 \pm 0.8 6.5-8.1	8.4	7.9 \pm 0.6 7.3-8.5	9.2 \pm 0.9 8.2-9.8	
TAD	4.4 \pm 0.3 3.7-5.1	4.7 \pm 0.3 4.4-5.0	5.4	5.9 \pm 0.4 4.9-6.5	6.1 \pm 0.5 5.5-6.8	6.5 \pm 0.2 6.3-6.9	6.4	8.5 \pm 0.9 7.5-9.4	6.6 \pm 0.5 6.5-6.6	
HW	16.6 \pm 0.7 14.8-17.8	26.4 \pm 0.8 25.5-27.5	17.3	17.7 \pm 0.9 15.9-19.6	24.4 \pm 1.0 23.4-26.1	18.4 \pm 2.2 16.6-21.6	23.0	25.1 \pm 0.4 24.6-25.5	27.9 \pm 2.9 24.5-30.0	
UA	9.5 \pm 0.6 8.1-10.6	13.2 \pm 0.6 12.6-13.9	9.5	10.8 \pm 1.2 8.2-12.8	13.7 \pm 1.4 12.6-15.5	10.9 \pm 1.0 9.8-12.3	13.8	13.8 \pm 0.7 13.0-14.4	16.2 \pm 1.3 14.6-16.9	
FA	11.8 \pm 0.6 10.4-12.6	17.0 \pm 0.9 15.6-17.8	11.5	13.8 \pm 1.2 11.1-15.6	18.1 \pm 0.9 16.6-19.0	13.1 \pm 1.4 11.4-14.6	16.6	17.7 \pm 1.1 16.4-18.6	19.7 \pm 2.3 17.5-22.2	
FL	26.5 \pm 1.1 24.0-29.2	39.6 \pm 1.5 37.5-41.6	28.3	31.7 \pm 2.1 26.9-35.3	42.7 \pm 2.8 39.7-47.8	30.6 \pm 4.6 25.6-36.0	36.2	41.7 \pm 1.7 40.6-43.6	45.4 \pm 5.2 39.5-49.0	
TBL	28.87 \pm 1.3 25.6-31.8	42.6 \pm 1.5 40.9-44.7	31.5	34.9 \pm 2.3 29.3-39.8	47.5 \pm 2.8 44.5-52.5	35.8 \pm 3.8 30.6-39.0	40.8	45.7 \pm 1.7 44.5-47.7	50.1 \pm 4.4 45.2-53.6	
TSL	15.7 \pm 0.8 14.0-17.2	22.7 \pm 0.8 22.0-24.1	16.5	18.7 \pm 1.2 16.7-22.4	25.1 \pm 1.36 23.3-26.7	18.3 \pm 1.9 16.4-20.6	21.9	24.5 \pm 1.3 23.3-25.9	28.4 \pm 4.7 23.5-33.0	
PL	24.5 \pm 1.4 21.1-26.6	36.5 \pm 1.5 34.7-38.0	25.6	30.3 \pm 2.3 25.7-35	39.5 \pm 2.09 34.6-43	29.8 \pm 3.9 25.8-35.3	36.4	41.5 \pm 1.6 39.8-43.1	45.8 \pm 5.6 39.5-50.0	
ML	15.8 \pm 0.8 14.2-18.4	24.9 \pm 1.1 23.5-26.0	16.9	17.9 \pm 1.1 15.3-19.7	24.2 \pm 1.31 22.0-25.5	19.4 \pm 2.7 16.0-22.1	26.0	24.8 \pm 1.3 23.7-26.3	28.5 \pm 3.7 25.7-32.6	
Toe4L	22.3 \pm 1.3 19.0-24.3	33.5 \pm 1.4 31.7-35.0	24.2	27.8 \pm 2.2 22.9-32.6	37.1 \pm 2.6 32.8-40.8	27.7 \pm 4.0 22.9-32.1	34.2	39.4 \pm 0.6 38.7-39.9	41.7 \pm 4.4 36.7-45.3	
Toe1L	5.8 \pm 0.6 4.5-7.4	9.5 \pm 1.0 8.5-10.6	7.1	7.0 \pm 0.8 5.3-8.4	9.5 \pm 0.8 8.4-10.5	6.9 \pm 1.1 5.5-8.3	8.1	9.8 \pm 0.6 9.3-10.5	10.5 \pm 0.6 9.8-11.0	
Fin1L	7.5 \pm 0.6 5.9-8.8	11.2 \pm 1.5 9.6-13.0	7.5	8.9 \pm 0.8 7.2-10.4	11.8 \pm 0.9 10.8-12.8	8.3 \pm 1.9 7.2-9.7	10.5	11.6 \pm 0.9 10.5-12.1	16.6 \pm 0.9 16.0-17.1	
Fin3L	11.8 \pm 0.8 10.4-13.5	18.2 \pm 1.5 16.7-20.2	13.5	13.2 \pm 0.9 11.4-14.7	17.9 \pm 0.8 16.8-18.9	16.5 \pm 1.0 14.2-18.8	21.0	19.4 \pm 1.8 17.1-20.3	24.6 \pm 4.6 19.3-28.0	

TABLE 1.—Continued.

	<i>R. tipanan</i> (Aurora)		<i>R. igorota</i> (holotype)		<i>R. luzonensis</i> (Aurora)		<i>R. albotuberculata</i> (Samar and Leyte)		<i>R. everetti</i> (S. Mindanao)	
	male n = 41	female n = 5	male n = 1	male n = 31	female n = 6	male n = 11	female n = 1	male n = 5	female n = 3	
NPL	7.4 ± 0.5	—	7.3	8.6 ± 0.6	—	7.84 ± 1.4	—	11.7 ± 0.7	—	
Toe4DW	6.12-8.5	3.2 ± 0.2	1.6	7.6-10.2	3.1 ± 0.3	6.5-9.5	2.1	11.0-12.4	3.3 ± 0.6	
Fin1DW	1.7 ± 0.2	3.0-3.5	1.7	2.1-2.5	2.8-3.7	1.7 ± 0.5	2.1	2.6 ± 0.2	2.7-4.0	
Fin3DW	1.3-2.1	2.5 ± 0.3	3.3	1.5 ± 0.2	2.5 ± 0.3	1.2-2.4	2.1	2.3-2.8	3.0 ± 0.2	
MTTL	1.5 ± 0.1	2.3-3.1	2.3	1.3-1.9	2.1-3.0	1.8 ± 0.4	4.5	2.4 ± 0.1	2.9-3.2	
ETD	1.0-1.8	4.8 ± 0.3	3.0	3.0 ± 0.3	4.7 ± 0.7	1.3-2.4	2.5	2.3-2.4	6.5 ± 1.2	
TBW	2.8 ± 0.2	4.6-5.3	3.0	2.5-3.7	4.2-5.9	3.8 ± 0.9	—	4.6 ± 0.1	5.1-7.4	
	2.2-3.2	2.7 ± 0.6	1.9	2.0 ± 0.2	3.0 ± 0.3	2.7-4.8	3.2	2.8 ± 1.0	3.0 ± 0.3	
	1.9 ± 0.1	1.2-3.5	1.9	1.7-2.5	2.7-3.6	2.3 ± 0.3	—	2.0-3.8	2.7-3.3	
	1.5-2.1	3.6 ± 0.2	3.0	1.9 ± 0.3	3.0 ± 0.3	1.9-2.6	—	2.1 ± 0.2	3.3 ± 1.0	
	2.0 ± 0.2	3.3-3.7	3.0	1.0-2.4	6.7 ± 1.0	1.3 ± 0.1	—	1.8-2.2	2.2-4.0	
	1.4-2.5	5.0 ± 0.6	3.0	4.0 ± 0.6	6.0-8.6	1.1-1.4	—	4.1 ± 0.8	7.1 ± 1.3	
	3.0 ± 0.4	4.3-5.9	3.0	3.1-5.4	—	—	—	3.0-5.7	5.9-8.9	
	2.4-3.9	—	—	—	—	—	—	—	—	

from Leyte; now known from Leyte, Samar, and northern Mindanao) were necessary. For simplicity and clarity, comparisons with the distantly allopatric *R. everetti* [greater Mindanao aggregate island complex; considered a full species by Dubois (1992)] are provided below, but we did not include this species or Visayan (Panay, Negros, Cebu Islands; see Alcalá, 1986) populations in the multivariate statistical analyses. These populations (and the status of other Taylor species from Mindanao) will be treated fully in another paper (Brown and Crombie, unpublished data).

Analyses were performed using Statview® (Abacus concepts, 1992), Super-Anova®, and Statistica® (StatSoft, 1994) software. Multivariate analyses were conducted using males only due to a lack of sufficient sample sizes for females. Principal component analyses (PCA) and canonical variates analysis (CVA) were performed on log-transformed data, and all variables except TBW (a color character that is absent in *R. albotuberculata*) were included.

Although we tentatively identified the four groups of interest (*R. luzonensis*, *R. albotuberculata*, *R. sp. nov.*, and *R. igorota*) on the basis of color pattern and discrete character differences, we applied principal component analysis to assess whether continuous morphometric characters could form the basis of qualitatively detectable structure (group separation without a priori taxonomic designation) in the data. We also sought to explore the relative contributions of specific variables to group separation in multivariate space. In the PCA, we successively extracted components until they cumulatively accounted for 90% of the variation.

We performed canonical variates in an attempt to maximize separation between the three a priori groupings (*R. luzonensis*, *R. albotuberculata*, and *R. sp. nov.*), to assess the contributions of various morphological variables to intergroup discrimination, and to assess whether the holotype of *R. igorota* could be classified with confidence with any of our three larger samples. Because the type series of *R. igorota*

contains only a single fully mature adult male (the remaining specimens consist of juveniles of undetermined sex, a single immature female, and two immature males), we performed canonical variates calculations on the basis of *R. luzonensis*, *R. albotuberculata*, and *R. sp. nov.* and then attempted to classify the holotype of *R. igorota* with one of these samples. For the discrimination procedure, we used canonical coefficients standardized by within-group pooled standard deviations for each character (Neff and Marcus, 1980).

RESULTS

Comparisons of Qualitative Characters, Biogeography, and the Recognition of Evolutionary Species

Rana albotuberculata (from Samar, Leyte, and northern Mindanao) and *R. everetti* (sensu Boulenger, 1882; from southern Mindanao) possibly are sympatric on Leyte, Samar, and in the northern Diwata Mountains of Mindanao (Fig. 1) and are readily and consistently diagnosed on the basis of (1) the dense distribution of dorsal asperities on the body and limbs of *R. albotuberculata* (versus absent in *R. everetti*), (2) the absence of transverse tibial bars in *R. albotuberculata* (versus present in *R. everetti*), (3) the absence of large dorsal spots in any *R. albotuberculata* (versus present in some *R. everetti*) (4) the much more prominent, thickened and fleshy dorsolateral ridges of *R. albotuberculata* (versus faint or indistinct in *R. everetti*), and (5) the smaller body size in *R. albotuberculata* (Table 1).

We distinguish the distantly allopatric *R. albotuberculata* from both *R. igorota* and *Rana sp. nov.* by (1) the absence (versus presence) of tibial bars, (2) the presence of a dark gray, reddish brown or bluish black dorsum (versus olive green in *R. igorota* and iridescent green to golden in *Rana sp. nov.*), (3) distinct, thick, and fleshy dorsolateral ridges (versus thinner, non-fleshy, occasionally indistinct or reduced to a row of spicules in *Rana sp. nov.*), (4) greatly enlarged, white infraclacal tubercles (versus smaller, and colored as surrounding skin), and (5) much larger,

less densely-distributed dermal asperities (versus smaller asperities more densely congregated). *Rana albotuberculata* differs from *R. luzonensis* by (1) the presence of a dark gray, reddish brown or bluish black dorsum (versus dorsum yellow, brown, light gray, or dark green), (2) the presence (versus absence) of dermal asperities, (3) the absence (versus presence) of transverse tibial bars, (4) the presence (versus absence) of infraclacal tubercles, and (5) much thicker, fleshy dorsolateral folds (versus less distinct or absent).

The geographical separation and ancient marine barriers (Heaney, 1985, 1986) between *R. everetti* and the Luzon species (*R. luzonensis*, *Rana sp. nov.*, and *R. igorota*) would seem to preclude the possibility of these forms being conspecific. We have seen specimens of *R. everetti* from Zamboanga (near the type locality; Boulenger, 1882) and other S. Mindanao localities (Appendix I, Fig. 1) and all agree well with Boulenger's (1882) description and illustrations; none can be mistaken for any of the other species considered in this report. *Rana everetti* differs from all the Luzon species by a much larger body size (Table 1) and differs from both *R. igorota* and *Rana sp. nov.* by the absence of dermal asperities. *Rana everetti* is further diagnosed from *R. igorota* by a rounded (versus squarish) snout shape and is further distinguished from *Rana sp. nov.* by homogeneous dull brown or gray dorsal coloration, with or without large indistinct dark gray spots (Boulenger, 1882: his plate 6; versus iridescent green to golden coloration with black spots or dark brown reticulum). *Rana everetti* can easily be diagnosed from *R. albotuberculata* by (1) the absence (versus presence) of dorsal asperities (2) the presence (versus absence) of transverse tibial bars, (3) the presence of dorsal spots in some specimens (versus absent in all *R. albotuberculata*), (4) thinner, less prominent dorsolateral ridges (versus thickened, fleshy), and (5) the larger body size (Table 1).

Rana luzonensis, although presumably sympatric with *Rana sp. nov.* and *R. igorota* (Taylor, 1920), is markedly distinct from *Rana sp. nov.* on the basis of micro-

habitat and behavior (see remarks in the description of *Rana* sp. nov.), and a slightly larger body size (Table 1). *Rana luzonensis* differs from both *Rana* sp. nov. and *R. igorota* by (1) the absence (versus presence) of infraorbital tubercles, (2) a pointed snout shape (Fig. 4; versus rounded in *Rana* sp. nov. and squarish in *R. igorota*), and (3) the absence (versus presence) of dermal asperities. *Rana luzonensis* exhibits markedly different coloration from *Rana* sp. nov. (Fig. 3) and numerous osteological differences are included in the diagnosis of the new species, below. All of these species are easily diagnosed on the basis of morphological characters, and color and the sympatric species are just as easily diagnosed as the allopatric species; these are clearly distinct evolutionary lineages.

Although we were unable to locate the holotype of Taylor's (1920) *Rana guerreroi* (EHT F881; not found in the holdings of USNM, CAS, FMNH, KU, AMNH, or CM), we follow Taylor (1922a) and Inger (1954) in maintaining *R. guerreroi* in the synonymy of *R. luzonensis*. This decision was based on the original color description of the type material (Taylor, 1920), Taylor's assertion that his type of *R. guerreroi* was an immature specimen of *R. luzonensis* (Taylor, 1922a:259), and examination of 13 of the 19 specimens that formed Taylor's type series in the description of *R. guerreroi* (although they were not specifically designated paratypes). The 13 specimens that we have examined were collected at the type locality on or near the same date as the holotype. The topotypes clearly are not *Rana* sp. nov. or *R. igorota* because they lack dermal asperities, infraorbital tubercles, and the coloration and color pattern characteristics of the new species and *R. igorota* (Taylor, 1920, 1922a). While the topotypes cannot be distinguished from *R. luzonensis* on the basis of character differences, their poor preservation and immaturity at the time of preservation do not allow us to identify them with complete confidence to this species. However, we believe that the most conservative taxonomic decision is to follow Taylor (1922a), who placed *R. guerreroi* in the synonymy of *R. luzonensis*. Taylor (1922a) based this

decision on a reexamination of the type material and a collection of adult specimens later obtained from the type locality.

The absence of dermal asperities on the types of *R. merrilli* (CAS 62448) and *R. tafti* (CAS 61819) and a comparison of Taylor's color descriptions eliminates any possibility that either species is conspecific with *Rana* sp. nov. or *R. igorota*. The poorly preserved type of *R. merrilli* does not allow an accurate assessment of this species' status with respect to *R. luzonensis*. While Taylor's (1922a) description and biogeographical considerations would suggest that it is a distinct lineage, we have no other basis for distinguishing it from *R. luzonensis* at the present time. While the type of *R. tafti* (from Polillo Island) is in good condition, the specimen and Taylor's description are close enough to our concept of *R. luzonensis* that we cannot assess this species' status until more specimens are available for study. Thus, we tentatively consider *R. tafti* a synonym of *R. luzonensis* as well. At present, we will not address the status of these species until adequate sample sizes, ecological data, larvae, or other data become available and permit a reconsideration of their taxonomic rank.

Multivariate Analyses

Standard univariate statistics for the morphometric variables are summarized in Table 1. Although we had to extract seven principal components in order to account for 90% of the variation detected in the PCA, we present only the first three components (accounting for 78.5% of the variance) because components IV–VII each accounted for only a small fraction ($\leq 4\%$) of the total variance and did not possess heavily-loading factor scores. Most of the loadings for PC I are large and positive (except ETD), indicating that PC I primarily is a size variable (Table 2). PC I nearly separates *R. luzonensis* and *Rana* sp. nov., but the presence of some group overlap (Fig. 2A,C) precludes discriminating these species on the basis of this axis alone. The PC II axis loads most heavily and positively on IOD, NPL, Toe4DW, and ETD and negatively on IND, Fin3L, Fin1DW, Fin3DW, and MTTL. This pri-

TABLE 2.—Loadings for the first three principal components extracted from the correlation matrix and canonical coefficients for canonical axes CV I and II (standardized by within-group pooled standard deviations for each variable). All variables were log-transformed. Heavily loading variables with relatively greater discriminating power are in bold for emphasis (see text for discussion).

Variable	PC I	PC II	PC III	CV I	CV II
SVL	0.814	-0.254	0.050	-0.571	-0.270
HL	0.932	0.031	-0.129	0.048	0.050
SL	0.904	0.169	-0.177	-0.194	0.570
IOD	0.753	0.405	-0.223	-0.267	0.638
IND	0.654	-0.357	-0.214	-0.208	-0.243
ED	0.559	0.152	-0.316	0.132	0.195
TD	0.783	-0.123	0.404	-1.190	-0.128
HW	0.897	-0.155	-0.224	0.755	-0.635
UA	0.778	0.171	-0.031	0.353	0.150
FA	0.903	0.254	-0.085	-0.202	0.310
FL	0.950	0.171	-0.048	0.644	-0.614
TBL	0.949	0.013	-0.170	-0.317	0.118
TSL	0.830	0.037	-0.134	-0.042	-0.094
PL	0.945	0.130	-0.178	0.059	0.635
ML	0.901	-0.242	0.038	-0.782	-0.071
Toe4L	0.945	0.079	-0.159	-0.511	0.116
Toe1L	0.866	0.062	-0.041	0.741	0.330
Fin1L	0.836	0.250	-0.123	-0.025	0.404
Fin3L	0.809	-0.483	0.046	0.490	-0.460
NPL	0.781	0.342	-0.105	-0.399	0.470
Toe4DW	0.621	0.387	-0.433	0.233	0.723
Fin1DW	0.513	-0.312	-0.652	0.803	-0.108
Fin3DW	0.679	-0.546	-0.339	-0.988	-1.144
MTTL	0.633	-0.418	0.112	-0.531	0.166
ET	-0.044	0.656	-0.565	0.594	0.524
Eigenvalue	15.7	2.3	1.7	22.2	12.9
% Variance	63.0	8.9	6.7	63.2	36.8

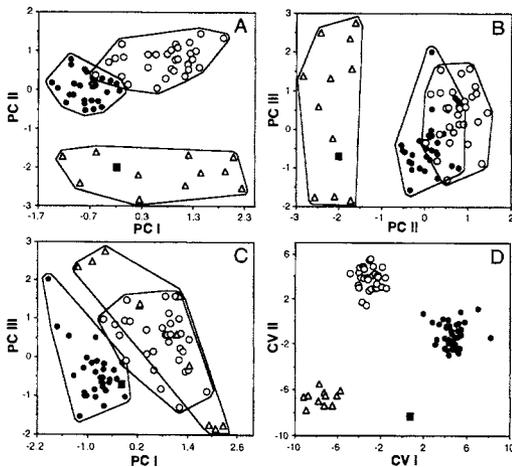


FIG. 2.—Orthogonal bivariate orientation of the first three principal components (A–C) and canonical variate (D) scores for males only. See Table 2 for loadings and text for explanation of characters. Open circles = *Rana luzonensis*; shaded circles = *Rana tivanan*, n. sp., open triangles = *Rana albotuberculata*; shaded square = *Rana igorota* (holotype).

marily shape-based axis forms the basis of multivariate segregation of the holotype of *R. igorota* from both *R. luzonensis* and *Rana* sp. nov. (Fig. 2A,B) and also separates *R. albotuberculata* from *R. luzonensis* and *Rana* sp. nov. Some shape-based differences between *R. luzonensis* and *Rana* sp. nov. are apparent on this axis, but considerable overlap between these species exists (Fig. 2A,B). The low loading of ETD on PC I may reflect the difficulty (and, presumably, imprecision) associated with this measurement; its substantial contribution to PC II indicates that some shape-based variation in PC II is influenced by this variable. The PC III axis loads most heavily and positively on TAD, and negatively on ED, Toe4DW, Fin1DW, Fin3DW, and ETD but does not form the basis of dispersion between any of the groups defined a posteriori (Fig. 2B,C). The apparent negative correlation of individual scores within species between PC

III and PC I may indicate either remnants of size contributions to PC III or possibly allometric growth pattern trajectories (i.e., a change in shape with a corresponding change in size; Voss and Marcus, 1992). In the context of the principal component analysis, *R. luzonensis* and *Rana* sp. nov. are nearly separated from one another on the basis of size and both are separated from *R. albotuberculata* and the holotype of *R. igorota* on the basis of shape. *Rana albotuberculata* and the holotype of *R. igorota* are not readily separated from one another on the basis of a particular axis. The large contributions of IOD, IND, ED, TAD, and ETD to PC's II and III confirms our initial observations that head shape may contribute to differences between these samples (Figs. 4, 5). Digital characters (Fin3L, Fin1DW, Fin3DW, Toe4DW, MTTL, NPL) also contribute to structure in the variation, but these characters were not qualitatively identified by examination of the specimens.

The CVA clearly discriminates between *R. albotuberculata*, *Rana* sp. nov., and *R. luzonensis* on both CV I and CV II. The holotype of *R. igorota* is discriminated from the three remaining groups by CV I and is discriminated from *R. luzonensis* and *Rana* sp. nov. by CV II (Fig. 2D). As reflected by the standardized canonical coefficients, the most influential coefficients for CV I are TAD, Fin3DW, and ML, which load negatively, and Fin1DW, HW, and Toe1L, which load positively. The most influential coefficients for CV II are Fin3DW and HW, which load negatively, and Toe4DW, PL, and IOD, which load positively (Table 2). Again, cephalic dimensions and measurements associated with the manus and pes contribute heavily to dispersion in multivariate space.

The classification analysis correctly placed all specimens of *Rana albotuberculata*, *R. luzonensis*, and *Rana* sp. nov. in accordance with their a priori groupings. The holotype of *R. igorota* is classified most confidently with *Rana* sp. nov., as indicated by the following posterior probabilities: $P = 0.97$ for *Rana* sp. nov., $P = 0.001$ for *R. luzonensis*, and $P = 0.03$ for *R. albotuberculata*. The holotype of *R. igorota*

is similarly distant in multivariate morphospace from the centroids of *R. sp. nov.* and *R. albotuberculata* (Mahalanobis distances of 126.5 and 130.9, respectively). However, the distances separating *R. igorota* from these group centroids are substantially greater than those exhibited by the most distant *Rana* sp. nov. and specimens of *R. albotuberculata* from their respective group centroids (maximum distances of 59.1 and 43.9), suggesting that *R. igorota* is morphometrically distinct and cannot be placed with confidence with any of the three species included in this analysis (Fig. 2D).

The differences in numerous morphological characters, size, ecology, microhabitat (see below), and color patterns, require the recognition of two species in sympatry in the southern Sierra Madres mountains of Luzon. In view of the character differences and discrete multivariate separation between sympatric *Rana luzonensis*, *Rana* sp. nov., allopatric *R. igorota*, and the distantly allopatric *R. albotuberculata*, and *R. everetti*, we recognize each of these taxa as full evolutionary species (Frost and Hillis, 1990; Simpson, 1961; Wiley, 1978). We resurrect *R. igorota* Taylor, 1922 from the synonymy of *R. luzonensis* and provide the formal taxonomic description for the new taxon, below. Although the original description of *R. igorota* (Taylor, 1922a) provides an adequate account of characters that differentiate it from *R. luzonensis* (to which Taylor specifically compared it), Taylor's (1922a) description does not provide sufficient information on the characters that diagnose *R. igorota* from the new species, *R. albotuberculata*, or *R. everetti* (sensu stricto). Therefore, we briefly rediagnose *R. igorota* as well.

Rana tipanan sp. nov.

Suggested common name.—Brown and Alcalá's Sierra Madres frog.

Holotype.—PNM 5727 (Field No. RMB 876; Fig. 4A), an adult male, collected 17 May 1997 between 1900 and 2100 h by V. Yngente, in the Kabatangan river drainage, east side of Mt. Ma-aling-aling, (15° 39' 6" N, 121° 21' 7" E), at 470 m, Aurora Na-

tional Park, 1.2 km S, 1.3 km E of Barangay Villa Aurora, Municipality of San Luis, Aurora Province, Luzon Island, Republic of the Philippines.

Paratopotypes.—CMNH 5587, collected 14 May 1997 at 1500 h at the type locality by V. Yngente; CMNH 5580, PNM 5719, 5725–26, 5729, 5733, 5735, collected 15 May 1997 between 2200 and 2230 h at the type locality by V. Yngente and J. Bulalacao; PNM 5720, 5722, CMNH 5581–82, 5584, 5594, 5598–99, collected 16 May 1997 at 2100 h at the type locality by V. Yngente and J. Bulalacao; CMNH 5579, 5583, 5585–86, 5588, 5590–93, 5595–97, 5600–02, PNM 5721, 5723–24, 5728, 5730–32, 5734, 5736, 5738–41, collected 17 May 1997 between 1900 and 2100 h at the type-locality, by V. Yngente, J. Bulalacao, J. A. McGuire and R. M. Brown.

Etymology.—We derive the specific epithet from the traditional Tagalog “tipanan,” meaning “a covenant of partnership”. The name, a noun in apposition, is chosen to honor Angel Alcala and Walter Brown, whose 45-year collaboration has resulted in more than 70 co-authored publications and an extraordinary contribution to our knowledge of the systematics and biogeography of the amphibians and reptiles of the Philippines.

Diagnosis.—Members of the *Rana everetti* complex can be distinguished from all other Philippine *Rana* by the presence of a coarsely glandular posterior portion of the venter (Inger, 1954); in addition to the combination of the absence of vocal sacs and a nuptial pad extending to the last phalanx of the first digit, the members of the *R. everetti* complex can be distinguished from other Philippine *Rana* by their extensive degree of digital disk expansion (Fig. 6; Inger, 1954). The only currently recognized Philippine *Rana* with digital disks that approach the degree of expansion exhibited by members of the *R. everetti* complex members include the following (characters further distinguishing each from the *R. everetti* complex are in parentheses): members of the *R. signata* complex (i.e., *R. grandocula*, *R. moellenborffi*, *R. similis*; presence of humeral

glands and vocal sacs), *R. erythraea* (first finger longer than second; broad dorsolateral light lines present), *R. nicobariensis* (small body size; presence of vocal sacs), and *R. sanguinea* (distinctly dark loreal and temporal region; first finger longer than second).

Diagnoses of *Rana tipanan* (Fig. 3) from each of the currently-recognized *Rana everetti* complex members are as follows: *R. tipanan* can be distinguished from *Rana igorota* by a smaller maximum body size in males (Table 1), a rounded (versus squarish) snout in dorsal aspect (Figs. 4, 5), an extensive distribution of dermal asperities throughout the body of males (versus asperities limited to sacral, femoral, tibial, postocular, infralabial, sternal, and dorsolateral regions), the presence (in life) of black spots or black reticulum on an iridescent metallic green dorsum in males and a distinct dark brown reticulum on iridescent metallic green to golden yellow dorsum in females (versus bronze spots on an olive green dorsum in both sexes and no reticulum), and a pearly white (versus yellow) throat with gray spots and pearly white to dull cream (versus yellow) venter. *Rana tipanan* apparently also differs from *R. igorota* by wide separation (>2 mm versus contact) between the ventral edge of the tympanum and post-riatal tubercle in females.

Rana tipanan further differs from all other frogs in the *R. everetti* complex by having an entirely translucent tympanum (Fig. 3) in females and most (96%; $n = 35$) males and differs from all members of the *R. everetti* complex except *R. albotuberculata* by the presence (versus absence) of dorsal asperities throughout the body of males. *Rana tipanan* can be distinguished from the allopatric *R. albotuberculata* by its iridescent green dorsal coloration (*R. albotuberculata* has a dark gray, reddish brown, or bluish black dorsum), indistinct dorsolateral ridges (versus thick and fleshy), presence (versus absence) of transverse bars on the hindlimbs, infracloacal tubercles that are small and brown (versus greatly enlarged and white in *R. albotuberculata*), and smaller, more densely distributed dorsal asperities (versus enlarged,

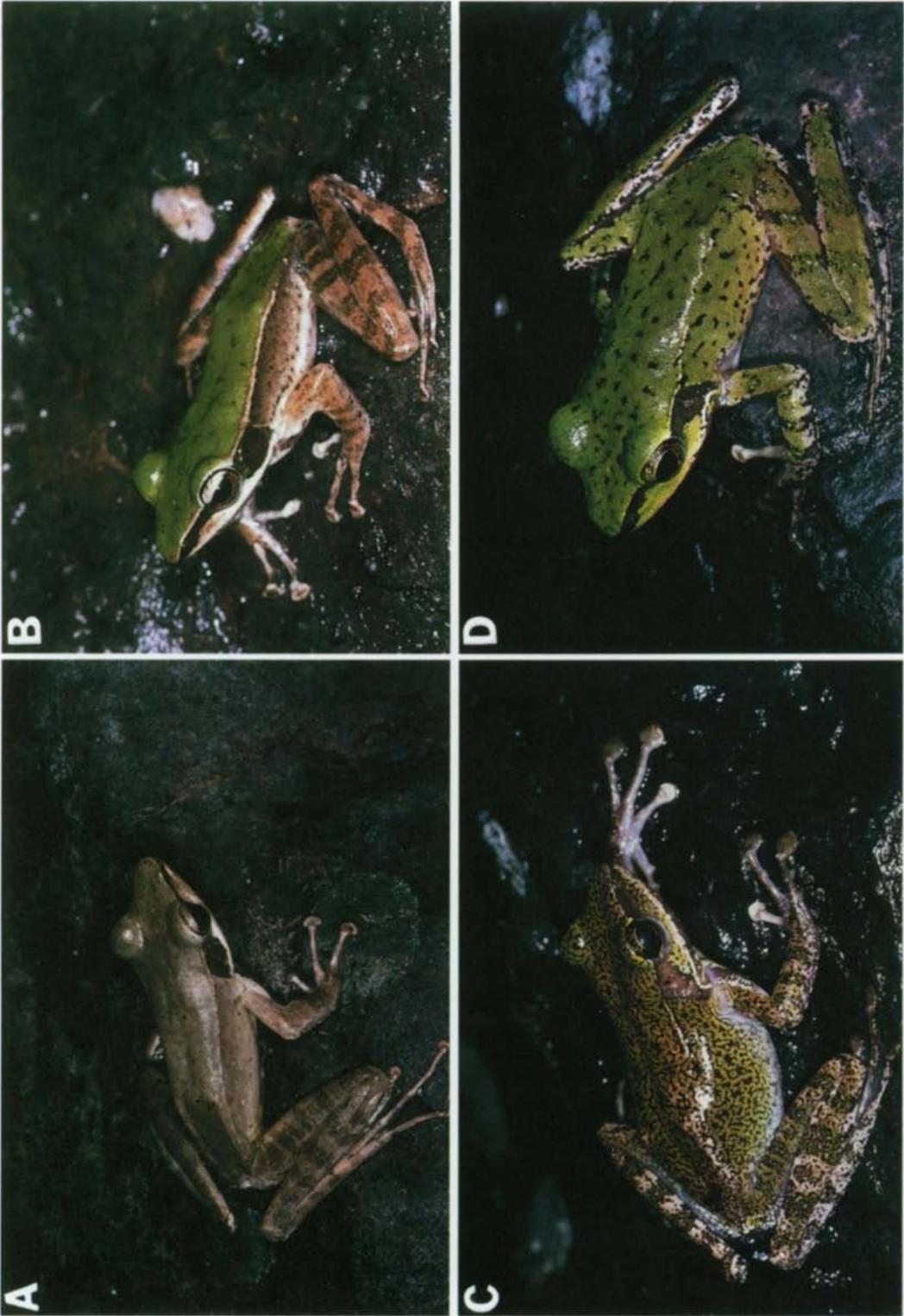


FIG. 3.—Photographs of live specimens from Luzon Island: (A) *Rana luzonensis*, PNM 5757, male, SVL = 49.0 mm (B) *Rana luzonensis*, CMNH 5623, male, SVL = 61.0; (C) *Rana tipanan*, female, CMNH 5582, SVL = 74.5; (D) *Rana tipanan*, male, CMNH 5598, SVL = 52.0. Note columella visible through the translucent tympanum of *Rana tipanan* (C, D).

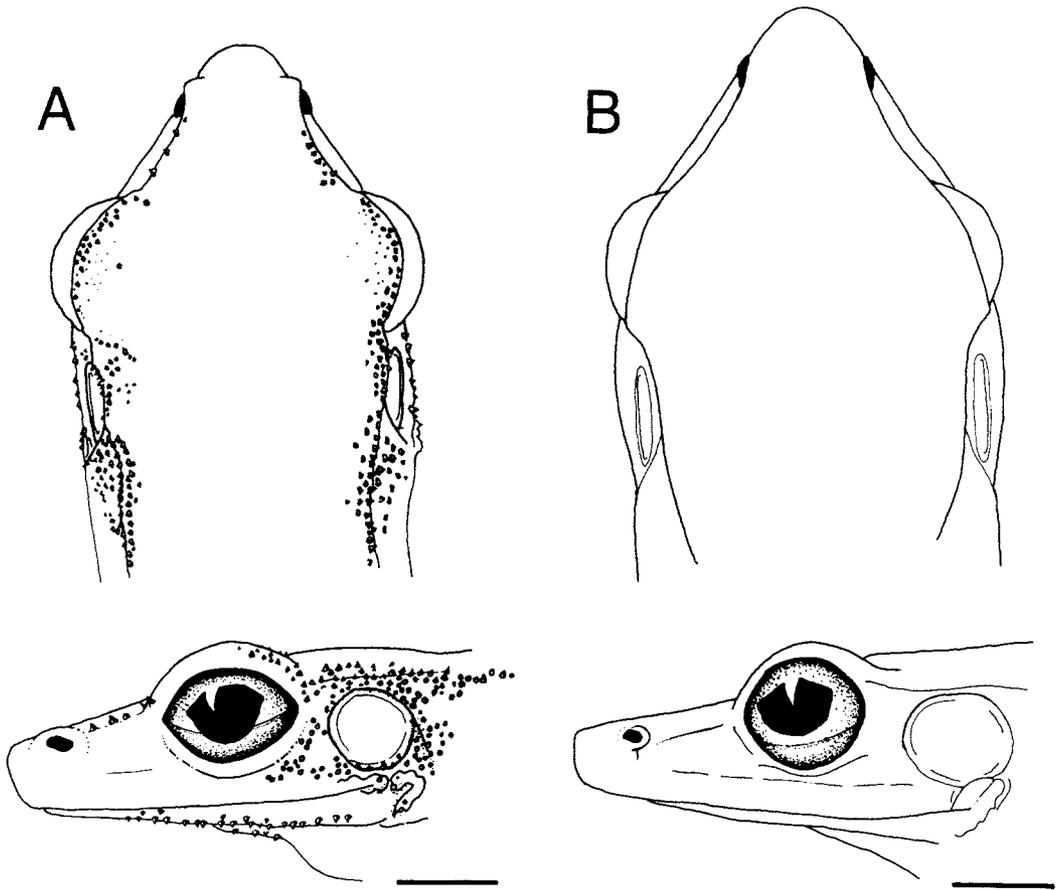


FIG. 4.—Lateral and dorsal views of heads of males of (A) *Rana tipanan* holotype (PNM 5727) and (B) *Rana luzonensis* (PNM 5755). Scale bars = 5 mm.

and not as densely congregated). *Rana tipanan* can be distinguished from the distantly allopatric *R. everetti* by its smaller size (Table 1), and presence (versus absence) of dermal asperities. *Rana tipanan* further differs from *R. everetti* by iridescent green dorsal coloration in males [versus light brown to gray, with or without dark, indistinct large spots; (Boulenger, 1882, his plate 6)] and throat that is bright white with small gray spots (versus dull cream). The new species can be further distinguished from sympatric *Rana luzonensis* by the presence (versus absence) of infra-cloacal tubercles and dermal asperities, and by a smaller body size (Table 1). Additionally, *R. tipanan* differs from *R. luzonensis* by the presence of an iridescent green (in males) to golden yellow (in some

females) dorsum (versus dorsum yellow, brown, gray, or occasional dark green) and by the presence of a distinct brown dorsum in females (absent in *R. luzonensis*). To aid in the identification of live specimens, a summary of the distribution of conspicuous diagnostic characters are presented in Table 3.

The following osteological differences diagnose *R. tipanan* (as exemplified by cleared and double stained specimens of both males and females; CMNH 5579, 5580; PNM 5738) from *R. luzonensis* (CMNH 5611, 2117, 2159). (1) The anterior terminus of the skull of *R. luzonensis* bears a prominent rounded rostral cartilage (Fig. 7A) that is lacking in *Rana tipanan* (Fig. 7B). (2) The alary processes of the premaxillae of *Rana tipanan* are small-

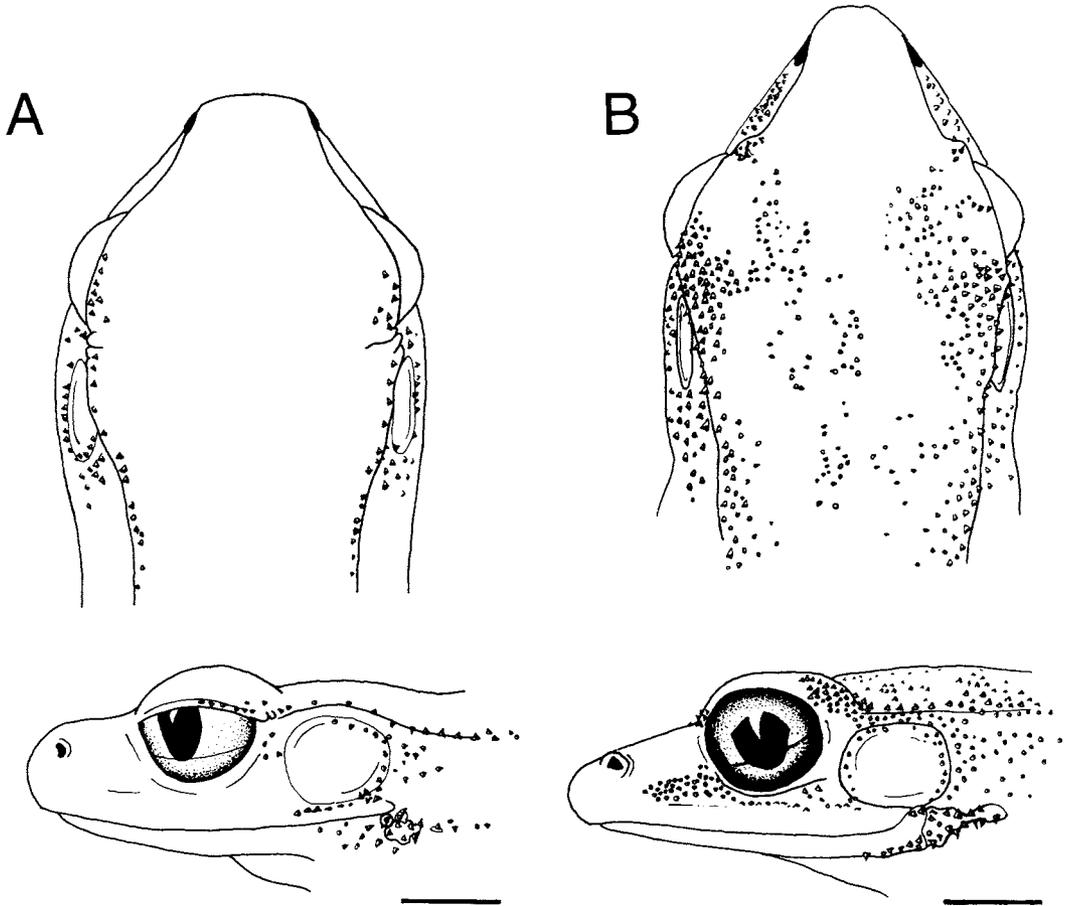


FIG. 5.—Lateral and dorsal views of heads of males of (A) *Rana igorota* holotype (CAS 61484) and (B) *Rana albotuberculata* paratype (MCZ 23189). Scale bars = 5 mm.

TABLE 3.—Distribution of selected diagnostic color and dermal characters in selected members of the *Rana everetti* complex of Philippine frogs. See text for further comparisons and Table 1 for morphometric proportions.

Character	<i>R. tipanan</i>	<i>R. luzonensis</i>	<i>R. everetti</i>	<i>R. igorota</i>	<i>R. albotuberculata</i>
Asperities	+, fine	—	—	+, fine	+, coarse
Infra-cloacal tubercles	+	—	—, +	+	+
Tympanum translucent	+	—	—	—	—
Tibial bars	+	+	+	+	—
Dark dorsal spots	—, +	—	—, +	—, +	—
Dark dorsal reticulum	—, +	—	—	—	—
Snout	rounded	pointed	rounded	squarish	rounded
Dorsolateral ridges	indistinct to moderate	indistinct	indistinct	moderate	thick, fleshy
Dorsal color	iridescent green or golden	brown, yellow, green, or light gray	gray or brown	olive green	dark gray or blueish black

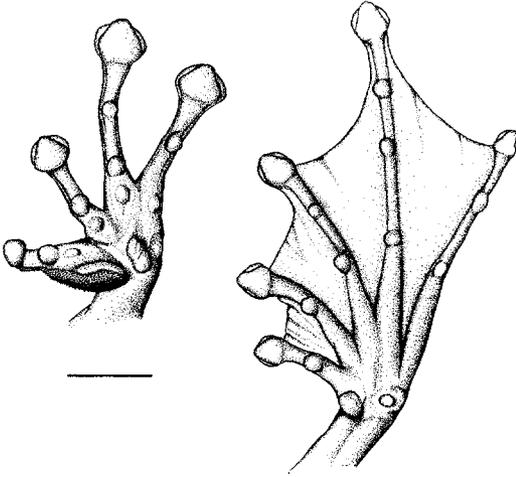


FIG. 6.—Palmar and plantar views of manus and pes of the holotype of *Rana tipanan* (male, PNM 5727). Scale bar = 5 mm.

er than those in *R. luzonensis*, and the medial edges of the alary processes bear a slight medial projection that appears less developed in *Rana tipanan* than in *R. luzonensis*. This results in vertically straight medial edges of the alary processes of *R. luzonensis* when viewed rostrally, whereas those in *Rana tipanan* are oriented at nearly 45° angles from the sagittal axis of the skull. (3) The medial portions of the palatines are broader in *R. luzonensis* (Fig. 7A) than they are in *Rana tipanan* (Fig. 7B), contact or nearly contact the vomers, and are partially obscured by dentigerous process. (4) The dentigerous processes of the vomer of *Rana tipanan* (Fig. 7B) are shorter and slightly thicker than in *R. luzonensis* (Fig. 7A). (5) *Rana tipanan* has 6–8 vomerine teeth; *R. luzonensis* has 9–12. (6) In *Rana tipanan*, the cultriform process of the parasphenoid terminates in an irregular point slightly anterior to the level of the medial ends of the palatines. In *R. luzonensis*, this process terminates slightly posterior to the level of the palatines (Fig. 7A). (7) The alae of the parasphenoid abut the medial rami of the pterygoids in *R. tipanan* (Fig. 7B) but terminate just short of the pterygoids in *R. luzonensis* (Fig. 7A). (8) The posterior process of parasphenoid terminates anterior to the margin of the foramen magnum

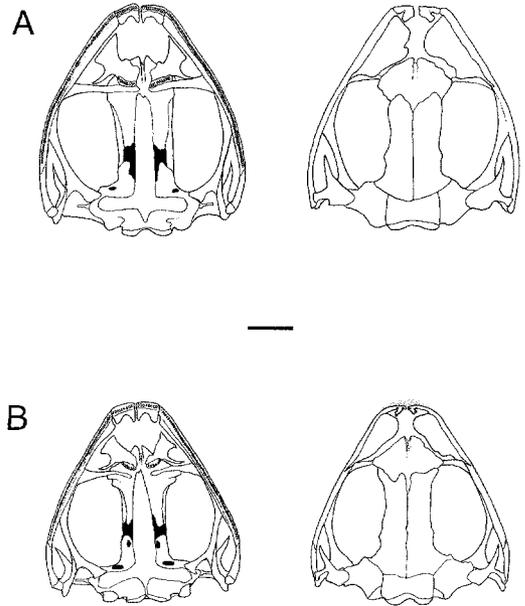


FIG. 7.—Skulls of males of (A) *Rana luzonensis* (CMNH 5611) and (B) paratype of *Rana tipanan* (PNM 5738) in dorsal (right) and ventral (left) view. Gray region indicates cartilage. Scale bars = 4 mm.

in *R. luzonensis*, but contacts the anterior edge of the foramen magnum in *R. tipanan*. (9) The tympanic annulus is relatively larger in *R. luzonensis* (CMNH 5611: 5.5 mm) than in *R. tipanan* (PNM 5738: 4.0 mm) when specimens of similar head lengths (20.4 and 20.3 mm, respectively) are compared; the tympanic annulus obscures considerably more of the zygomatic ramus of the squamosal in *R. luzonensis*. The diameter of the tympanic annulus in

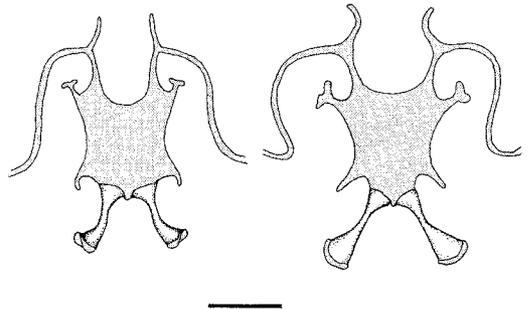


FIG. 8.—Dorsal views of hyoids of males of (left) paratype of *Rana tipanan* (PNM 5738) and (right) *Rana luzonensis* (CMNH 5611). Gray region indicates cartilage. Scale bar = 4 mm.

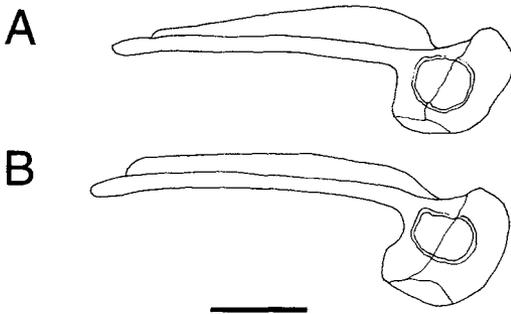


FIG. 9.—Lateral view of left ilia of males of (A) *Rana tipanan* (paratype PNM 5738) and (B) *Rana luzonensis* (CNMH 5611). Left = anterior; scale bar = 4 mm.

R. luzonensis is $\frac{1}{5}$ the distance from the anterior end of the zygomatic ramus to the posterior end of the otic ramus of the squamosal; in *R. tipanan* this ratio is approximately $\frac{1}{5}$. (10) The ceratohyals of the hyoid possess anterior processes that are more medially bowed in *R. luzonensis* than in *R. tipanan* (Fig. 8). (11) The hyoglossal sinus extends posterior to the level of attachment of hypobranchial 1 in *R. tipanan* (Fig. 8A), but anterior to this process in *R. luzonensis* (Fig. 8B). (12) The anterolateral (hypobranchial 1) processes of *R. tipanan* are anteriorly oriented with a very narrow base, whereas those of *R. luzonensis* are more laterally oriented with a thickened base. (13) The posterolateral processes (hypobranchial 2) are oriented posteriorly in *R. tipanan* and more laterally in *R. luzonensis*. (14) The medial edges of the thyrohyals are straight in *R. luzonensis* but are laterally curved in *R. tipanan* (especially in the female, CMNH 5579), resulting in an overall straight appearance of these elements in *R. luzonensis*, whereas those of *R. tipanan* appear laterally bowed (Fig. 8). (15) The transverse processes of presacral II are moderately thick, directed anteriorly, and not expanded distally in *R. tipanan* (possessing small cartilaginous tips) but are moderately expanded in *R. luzonensis* (cartilaginous tips ossified). (16) The transverse processes of presacral IV are slightly expanded at distal ends in *R. luzonensis*, but not expanded in *R. tipanan*. (17) The dorsal ilial crest of *R. luzonensis* is nearly homogeneous in height through-

out most of the length of the ilium whereas that of *R. tipanan* is much lower anteriorly and markedly higher posteriorly (Fig. 9).

Description of holotype.—Snout elongate (Figs. 4, 6), obtusely pointed, terminally rounded and caudoventrally angled, extending well beyond lower jaw in lateral view; SL/HL = 0.45; head slightly wider than body, longer than wide; HW/HL = 0.78; HL/SVL = 0.42; canthus rostralis sharply angular and concave such that upper lip is visible when viewed in dorsal aspect; loreal region deeply concave; nares laterally protuberant, located near anterior and dorsal termini of snout, visible when viewed in ventral aspect; IOD/IND = 1.0; IOD/ED = 0.81; labial region thin and only moderately swollen; interorbital region flat, wider than single eyelid; dorsal rostrum flat to slightly concave; eyes large, oriented anterolaterally beyond jaw when viewed in ventral aspect, protuberant on top of head; pupil horizontally elliptical in life, vertically elliptical in preserved specimens; tympanum distinct, immediately behind eye; columella visible through tympanum; tympanum slightly raised, smaller than eye; TAD/ED = 0.64; supratympanic ridge evident, continuing caudally and ventrally toward angle of jaw, continuous with prominent dorsolateral ridges; ventral edge of tympanum separated by 1 mm gap from post-riotal tubercle; post-riotal tubercle irregular, continuous, elongate, slightly arching ventrally, composed of enlarged spicules (Fig. 4).

Six teeth in obliquely transverse row atop each dentigerous process of vomers, slightly posteromedial to choanae, separate for a distance slightly larger than width of one choana and subequal to distance of process from choana; choanae large (0.9 mm), round, widely separated, partially obscured by maxilla when viewed from below; premaxillary and maxillary teeth present; vocal sacs and slits absent; tongue elongate (length > 2 times width), stretching nearly to glottis, free for more than $\frac{2}{3}$ its length with deep terminal notch.

Underlying skin of dorsum smooth with minute, densely distributed homogeneous asperities; density and size of asperities in-

creased at posttympanic and supratympanic regions, supra-axial region, lateral regions of head, sacral region, femoral and tibial segments of hindlimbs, lower jaw, throat, sternal region, and anterior ½ of venter; asperities largest along dorsolateral ridges, in sacral region, and in transverse bars on hindlimbs (see color section, below); posterior ½ venter coarsely glandular; skin of cloacal region coarsely glandular with six enlarged infraclacal tubercles; cloacal opening round, with transverse supracloacal cutaneous flap.

Upper arm slender; humeral glands absent; forearms robust; UA/FA = 0.85; FA/ML = 0.65; FA/SVL = 0.22; order of fingers from shortest to longest II-I-IV-III (first and second finger nearly equal in length); Fin1L/Fin3L = 0.54; palmar webbing absent (Fig. 6); lateral fringes present on all digits of manus, most prominent on distal portions of second and third fingers; distal ends of fingers widely dilated, 3–5 times width of penultimate phalanges; Fin1DW/Fin3DW = 0.52; disks with circummarginal grooves; ventral pad pointed, protruding beyond distal edge of dorsal surface, visible from above; ultimate and penultimate phalanges with rounded, cup-like suprarticular cutaneous flap.

Subarticular tubercles of manus very large, raised, subcircular, occasionally nearly pointed on ventral surfaces (Fig. 6); digit number indicated by Roman numerals (tubercle count in Arabic numbers): IV (1), III (2), II (1), I (1); supernumerary tubercles present ($n = 1$) on the base of each finger, moderate, round, slightly raised; inner metacarpal tubercle longer and nearly twice as wide as outer, lateral edge in contact with supernumerary tubercular ridge of first finger, medial edge covered by nuptial pad; metacarpal tubercles do not contact; outer metacarpal tubercle nearly divided into larger, more distinct, medial portion and outer, smaller, lateral portion; nuptial pads velvety in texture, continuing distally to just beyond articulation of penultimate and ultimate phalanges; nuptial pad wrapping entirely around preaxial side of the first finger and nearly contacting subarticular tubercle on its anterior edge.

Hindlimbs slender; TBL/SVL = 0.59; FL/SVL = 0.53; FL/TBL = 0.91; TSL/FL = 0.55; TSL/PL = 0.66; PL/TBL = 0.84; heels overlap when femoral segment of hindlimbs held at right angles to body; tibiotarsal articulation of adpressed limb reaching well beyond rostrum; toes long, their order from shortest to longest 1-2-3-5-4 (3 and 5 nearly equal); Toe4L/FL = 0.93; toe disks smaller than those of fingers (absolutely and relative to penultimate phalanx); Toe4DW/Fin3DW = 0.68; interdigital webbing of pes nearly complete, homogeneous, acrenulate; modal webbing formula of toes (Savage and Heyer, 1969, 1997): I 0—1/2 II 0—1 3/4 III 0—2+ IV 1/2—0 V (Fig. 6); webbing diminishes distally to form wide fringes along lateral edges of distal phalanges on portions free of web; tarsal fold very slight, continuous with postaxial fringe on edge of toe V. Subarticular tubercles of pes large, round or occasionally subelliptical, nearly pointed; digit number indicated by Roman numerals (tubercle count by Arabic numbers): V (2) IV (3) III (2), II (1), I (1); inner metatarsal tubercle oval, twice as long as subcircular outer metatarsal tubercle; supernumerary tubercles absent from pes.

Measurements of holotype (in mm).—SVL 50.2; HL 21.0; SNL 9.5; IOD 5.4; IND 5.4; ED 6.7; TAD 4.3; HW 16.4; UA 9.4; FA 11.0; FL 26.8; TBL 29.4; TSL 16.2; PL 24.7; ML 17.0; Toe4L 23.0; Toe1L 6.2; Fin1L 6.7; Fin3L 12.3; NPL 7.3; Toe4DW 2.1; Fin1DW 1.6; Fin3DW 3.1; MTTL 1.9; ETD 1.8.

Color in preservative.—Dorsum very dark, homogeneous gray with thin black reticulate network; reticulum most distinct on head, nearly absent on sacrum, where it is replaced by a series of round black spots, each with white-tipped spicule at center; dorsolateral ridges light gray with white-tipped asperities; dorsal half of cantus black, ventral half with gray and black reticulum; tympanum translucent light brown; labial and subocular regions with gray and black reticulum; faint labial stripe made up of white blotches; post-rectal tubercle bright white; supra-axial tubercle white; flanks dark gray with distinct round black spots.

Dorsal color of forelimbs light gray with 5/5 (left/right) thin, slightly curved transverse gray-brown bars, most with conspicuous white-tipped asperities in a transverse row at center of each bar's longitudinal axis; 6/7 similar femoral bars; 5/7 tibial bars; 2/3 tarsal bars; dorsal surfaces of digits light gray; interdigital webbing light gray with faint darker gray blotches; throat pearly white with irregular, dark silvery gray spots; venter silvery bluish gray with faint irregular gray blotches; ventral portions of forelimbs yellowish green; ventral portions of hindlimbs yellowish white with irregular, very faint but distinct pale gray spots; posterior portions of femoral segments of hindlimbs light gray with large and faint, circular gray spots or marbling of light and dark gray; anterior portions of femoral segments of hindlimbs usually with small faint circular dark spots at margin of barred (dorsal) and immaculate (ventral) patterns; ventral surfaces of manus light gray with lighter (proximal) and darker (distal) tubercles and terminal disks; ventral surfaces of pes homogeneous medium gray; tubercles similarly colored.

Color in life.—(From color notes of R. M. Brown, deposited at CMNH; Fig. 3.) Dorsum bright iridescent metallic green with dark brown reticulum where green pigment is absent; laterally, iridescent greenish gold with small black spots following continuation of dorsal reticulum to midbody; fading to pinkish gray ventrally; snout with lighter reticulum; dorsolateral ridges bright iridescent gold; limbs colored as dorsum but with purplish dark brown transverse bars with distinct rows of white spicules; canthal bar pinkish gray; tympanum translucent, light pink; chin pearly white with gray spots, venter light gray to white with faint gray spots; ventral portions of limbs pinkish gray with light gray spots; anal tubercles bright white; ventral surfaces of pes medium gray with yellowish-gray disks; ventral surfaces of manus light gray with dirty white disks; iris golden yellow.

Variation.—A summary of univariate morphometrics are presented in Table 1. The snout is obtusely pointed (rounded) in males, and is obtusely pointed to barely

TABLE 4.—Variation in ratios of morphometric variables in adult males and females of *Rana tipanan*. See text for character abbreviations and Table 1 for interspecific comparisons of each variable. Table entries include mean \pm 1 standard deviation (range below).

Character	Males (n = 39)	Females (n = 5)
SL/HL	0.44 \pm 0.02 0.40–0.48	0.49 \pm 0.03 0.47–0.53
HW/HL	0.81 \pm 0.02 0.76–0.85	0.94 \pm 0.01 0.93–0.95
HL/SVL	0.41 \pm 0.01 0.37–0.40	0.37 \pm 0.01 0.36–0.38
IOD/IND	0.93 \pm 0.09 0.80–1.08	1.09 \pm 0.08 1.01–1.19
IOD/ED	0.76 \pm 0.07 0.64–0.87	0.92 \pm 0.07 0.84–1.02
TAD/ED	0.51–0.04 0.49–0.54	0.57 \pm 0.02 0.54–0.76
UA/FA	0.81 \pm 0.05 0.71–0.90	0.78 \pm 0.07 0.71–0.89
FA/ML	0.74 \pm 0.04 0.65–0.80	0.68 \pm 0.05 0.62–0.76
FA/SVL	0.24 \pm 0.01 0.22–0.26	0.23 \pm 0.01 0.21–0.24
Fin1L/Fin3L	0.77 \pm 0.08 0.64–0.99	0.61 \pm 0.04 0.57–0.68
Fin1DW/Fin3DW	0.53 \pm 0.04 0.46–0.61	0.54 \pm 0.09 0.46–0.69
TBL/SVL	0.54 \pm 0.02 0.52–0.61	0.57 \pm 0.01 0.55–0.58
FL/SVL	0.54 \pm 0.02 0.49–0.56	0.53 \pm 0.02 0.50–0.54
FL/TBL	0.92 \pm 0.02 0.88–0.98	0.93 \pm 0.02 0.91–0.95
TSL/FL	0.55 \pm 0.01 0.51–0.57	0.57 \pm 0.01 0.56–0.59
TSL/PL	0.64 \pm 0.02 0.61–0.69	0.62 \pm 0.01 0.61–0.64
PL/TBL	0.85 \pm 0.03 0.80–0.90	0.86 \pm 0.01 0.84–0.87
Toe4L/FL	0.84 \pm 0.03 0.77–0.89	0.84 \pm 0.02 0.83–0.87
Toe4DW/Fin3DW	0.63 \pm 0.06 0.50–0.79	0.69 \pm 0.09 0.63–0.76

rounded in female. The ventral edge of the tympanum contacts ($n = 6$) or is separate from ($n = 34$) the post-rectal tubercle in males, and widely separate (≥ 2 mm) in females. The post-rectal tubercle is discontinuous (spicules and underlying row of bulges interrupted in three specimens) or continuous ($n = 41$), elongate, slightly arching ventrally in males, and strongly arched in females. Variation in ratios of morphometric variables in *R. tipanan* is presented in Table 4.

There is considerable variation in the

color and color patterns in *R. tipanan* (Fig. 3). Three dominant color patterns are evident in our sample, including (1) a silvery to golden or green base color with fine brown reticulum throughout the body in all mature females and some mature males in life (fades to gray or silver dorsum with brown reticulum in preservative), (2) iridescent metallic green in life (very dark homogeneous gray in preservative) in some mature males and (3) iridescent metallic green with black irregular or circular spots (Fig. 3D) evenly spaced throughout the dorsum in life (gray to light brown with dark spots in preservative). In life, the reticulate dorsal pattern is strikingly evident in females (Fig. 3C) and covers the entire dorsal body except the tympanum (pigment absent) and the upper half of the canthus. There is a pinkish to purplish brown canthal stripe from the eye to the tip of the snout. The bright iridescent metallic green to nearly golden background of the dorsum is nearly obliterated in patches by the close apposition of darker (reticulate) coloration, giving the appearance of 10–15 dark brown or black round spots on the dorsum of adult females. The reticulum fades posteriorly in some males and is limited to the head and snout in six specimens.

Dorsal color of fore- and hindlimbs is iridescent green to greenish golden in life (tan to gray in preservative) with thin transverse purplish gray and brown bars in life (gray to brown in preservative), most with conspicuous white-tipped spiculae in a transverse row at center of each bar's longitudinal axis. There are 3–5 ($\bar{x} = 3.6 \pm 0.7$ SD; $n = 40$) forearm bars in males, and 3–4 ($\bar{x} = 3.2 \pm 0.45$ SD; $n = 5$) in females. There are 3–7 ($\bar{x} = 4.9 \pm 0.8$ SD; $n = 40$) tibial bars in males and 4–6 ($\bar{x} = 4.9 \pm 0.8$ SD; $n = 5$) in females. There are 4–8 ($\bar{x} = 5.4 \pm 1.02$ SD; $n = 40$) femoral bars in males and 4–6 ($\bar{x} = 4.8 \pm 0.8$ SD; $n = 5$) in females. In life, the dorso-lateral folds in males and females are marked by lighter color (light green, gold or white) of densely congregated spiculae and are bordered laterally by a thin darker stripe in eight of 40 specimens. There is a faint labial stripe (fading rostrally at su-

bocular region) evident in some specimens, strongest where labia are contiguous with post-riatal tubercles (posterior to tympanum). The throat is pearly white (32 specimens) to bluish (six) or greenish white (three), with dark gray to silver irregular spots. The venter is silvery gray to pearly white with faint irregular gray blotches.

Photographs of the (uncollected) specimens from Mt. Cetaceo show a large presumably female specimen with the distinctive reticulate pattern present in females from Aurora province. While the color pattern is sufficiently distinct among Philippine *Rana* to convince us that the two localities contain conspecific populations (there are no other *Rana* in the Philippines with an extensive dorsal reticulum of alternating brown and green to golden), the specimen from Mt. Cetaceo did possess a slightly different color pattern than do the majority of the specimens from Aurora Province: the dorsum and dorsal surfaces of limbs are golden yellow (greenish yellow anteriorly on body). The brown reticulum is extensively expanded such that the usual pattern is seemingly reversed, with thin golden and iridescent green reticulate lines on dark purplish brown. The tympanum is translucent, surrounded by darker skin that resembles the underside of the limbs and ventrolateral portions of body in that it is purplish brown. The tibial and femoral spiculae are bright white.

Remarks.—The collections of *R. tipanan* that form the basis of this report were taken along the Kabatangan River, Aurora National Park (Fig. 1), between 14 and 17 May 1997, the early dry season for this locality. These specimens were collected near a boundary between first growth and regenerating lower montane tropical rainforest (Whitmore, 1984) that had been cleared for timber 45 yr before the date of collection. Specimens were taken from high banks of the Kabatangan River (5–7 m width; 430 m) or its smaller tributaries (3–5 m width; 430–490 m) between 1500 and 2230 h. When captured, specimens were sitting on top of large bank-rocks, estimated to be 3–5 m in diameter, 25 m (horizontally) from the edge of the water

and 3–6 m above the surface of the water. The banks of the Kabatangan River were estimated to range from 10–20°, and those of the smaller tributaries were estimated to be somewhat steeper (20–35°). The microhabitat where most individuals of *R. tipanan* were found contrasts markedly with the vertical and horizontal position of *R. luzonensis* at this site. The new species appears to prefer areas farther away from and relatively higher above the water than does *R. luzonensis*. Most specimens of *R. luzonensis* were collected at or close to (≤ 1 m) the water's edge, usually on small rocks (≤ 0.5 m diameter) or the muddy river bank itself, and they dove into the river or small adjacent pools when disturbed. No individuals of *R. luzonensis* were collected from the steep-banked tributary or very large rocks (3–5 m in diameter) where most of the *R. tipanan* were taken. No *R. tipanan* were observed at the water's edge and none were observed to escape into water but rather retreated into bank vegetation and under large rocks when disturbed. These observations suggest ecological differences between the species.

Pools along the large Kabatangan river were densely populated by tadpoles of *R. luzonensis*; emergent metamorphs were identified as *R. luzonensis*, and multiple adult pairs of *R. luzonensis* were found in amplexus. No amplexus was observed in *R. tipanan*, and we have not identified the tadpoles of this second species despite extensive searching. One female of *R. tipanan* (CMNH 5580) had 394 mature ova with yellow vegetal and black animal hemispheres. Although *R. luzonensis* at this locality calls from within 20 cm of the water's edge (R. Brown, personal observation), no calling males of *R. tipanan* were observed and no unidentified calls were heard that could be associated with *R. tipanan*.

Other anurans observed sympatrically included *Rana similis*, *Limnonectes macrocephalus*, *R. luzonensis*, *Rhacophorus pardalis*, *Kaloula kalingensis*, *Philautus* cf. *surdus*, *Platymantis dorsalis*, *P. corrugatus*, *P. sierramadrensis*, and unidentified species of *Platymantis* in the *hazelae* and *guentheri* species groups (Brown et al.,

1997a,b). The distinctive vocalizations of *Platymantis pygmaeus* were heard (by R. Brown and J. McGuire), but no specimens of this species were collected.

Rana igorota Taylor 1922

Rana igorota. Taylor, 1922a:260.

Rana everetti luzonensis. (part) Inger, 1954:311.

Rana (Chalcorana) luzonensis. Dubois, 1992:328.

Diagnosis.—Adult *Rana igorota* [as exemplified by the male holotype (CAS 61484; Fig. 5), the largest of the male (MCZ 14096) and female (CAS 61487, MCZ 14097) paratypes, and Taylor's original description] differs from *Rana tipanan* by the characters discussed above (*Rana tipanan* diagnosis; Tables 1, 3). As noted by Taylor (1922a:260), when the hindlimb is stretched forward, the tibiotarsal articulation barely reaches the nares in *R. igorota* but extends past the snout in *R. luzonensis*; the latter is true for *R. tipanan* as well.

Rana igorota differs from *R. albotuberculata* by the sparse distribution of much smaller dorsal asperities that are only found in dorsolateral, infralabial, sternal, sacral, posttympanic, femoral and tibial regions (versus thickly distributed throughout dorsum and dorsal portions limbs and posterior $\frac{2}{3}$ of eyelid; Fig. 5), by olive green dorsal coloration (*R. albotuberculata* exhibits a dark brown, black, or bluish dorsum with light, spiculate, dorsolateral ridges), by the presence (versus complete absence) of transverse femoral and tibial bars, by the near immaculate posterior portions of femur (versus distinctly marbled dark gray and white in *R. albotuberculata*), by slightly smaller light brown (versus large, immaculate white) infra-cloacal tubercles, by less prominent (versus thick and prominently raised) dorsolateral ridges, and by a yellow (versus dirty cream) venter.

Rana igorota differs from *R. luzonensis* by the presence (versus absence) of dermal asperities and infra-cloacal tubercles, by an olive green dorsum in life (versus brown, yellowish, gray, or dark green mid-

dorsally only) and by the presence of bronze spots (versus spots absent) on the dorsum or lateral portions of the body. *Rana igorota* differs from *R. everetti* by the presence (versus absence) of dermal asperities, by an olive green dorsum in life (versus dorsum brown to gray), and by a smaller body size (Table 1).

Remarks.—The holotype [a large male with nuptial pads, contrary to Taylor's (1922a) report] is the largest mature specimen in the type series; no further material representative of this species has been collected since its discovery. A recent visit to the type locality (severely degraded) produced no further sightings of this species (Brown and Diesmos, personal observation, July 1998). The largest female paratype (CAS 61483) conspicuously lacks the extensive dorsal reticulum of *R. tipanan*; from this we conclude that both males and females exhibit color differences that distinguish them from the morphologically similar *R. tipanan* (above). Taylor's collections of *R. igorota* were taken along the edge of a small brook, and specimens dived into the water when disturbed (and subsequently were caught among the rocks at the bottom of a pool; Taylor, 1922a:262). These behavioral observations suggest ecological differences between *R. igorota* and *R. tipanan*.

DISCUSSION

It is not surprising that the geologically distinct Sierra Madres massif (Fig. 1) contains populations of an endemic frog in the *Rana everetti* complex. The northern extensions of the Sierra Madres are separated from the Cordillera Central (containing populations of *R. luzonensis* and the endemic *R. igorota*) by the central Cagayan valley that lacks adequate habitat for strictly montane species and undoubtedly represents a barrier to dispersal for many montane forest obligates. Although no suitable habitat currently connects these two mountain ranges, the moderate elevations of Neuva Viscaya and Quirino Provinces (i.e., Caraballo Mountains) suggest that suitable intervening submontane habitat may have once existed between the southern portions of the Sierra Madres

and the southern Cordillera Central before this region was deforested. While we can not wholly dismiss the possibility of gene flow between the southern portions of these two largely isolated geological components of Luzon, evidence supporting isolation of populations of amphibians and reptiles of the Sierra Madres from those in the Cordillera Central includes the recognition of numerous endemics known only from one of these mountain ranges but not the other. Other than *Rana igorota* (Taylor 1922a), Cordillera Central endemics include *Kaloula rigida*, and *Platymantis cornutus* (Taylor, 1922b), *Lipinia pulchella levitoni*, *Brachymeles wrighti*, *Sphenomorphus lawtoni*, and possibly *S. luzonensis* (Brown and Alcala, 1980), whereas other than *R. tipanan*, the Sierra Madres endemics include *Platymantis sierramadrensis* (W. Brown et al., 1999a), *Platymantis pygmaeus* (W. Brown et al., 1999b), *Sphenomorphus tagapayo* (R. Brown et al., 1999), and possibly *Brachymeles bicolor* (R. Brown, personal communication with R. Crombie). While the present status of some of the species as Cordillera Central of Sierra Madres endemics may be confounded by sampling errors or the lack of survey efforts in certain localities, we consider the taxa included above to be a conservative indicator of each mountain range's endemicity for several reasons. First, Taylor (1920, 1922a,b,c,d, 1923, 1925) described or recognized numerous additional species that were later subsumed by application of the polytypic species concept [e.g., Inger (1954), Leviton (1964), Leviton and Brown (1959)] and have not been re-evaluated in the context of a lineage-based species concept. We suspect that many more endemic species will soon be recognized with reconsideration of these and other earlier taxonomic works. Secondly, we expect the degree of endemism in each mountain range to rise with additional sampling in the Cordillera Central and the Sierra Madres. At present, several additional new species from Sierra Madres (apparently endemic) await description (Brown et al., in press b; W. Brown, A.

Alcala, A. Diesmos, and R. Brown, unpublished data).

The presence of frogs currently referable to *R. luzonensis* on the four major geological components of Luzon (Fig. 1; Auffenberg, 1988; Hall, 1996) suggests the possibility that further taxonomic partitioning of this species may be required once adequate collections are available. Many other related and non-related populations of amphibians and reptiles with the same distribution clearly warrant taxonomic recognition (Brown et al., 1995a,b, 1996, 1997a,b). In particular, the status of Taylor's *R. tafti*, *R. merrilli*, and *R. guerrieri* must be addressed with new collections from as close to the now degraded type localities as possible.

The observation that Luzon is composed of four distinct geological subunits (Auffenberg, 1988; Hall, 1996) that were formerly isolated from one another has not escaped the attention of biogeographers seeking to explain faunal diversity and endemism in Luzon (Auffenberg, 1988; Brown and Alcala, 1970, 1994; Brown et al., 1995a, 1997b). The past fragmentation and isolation of the geological elements of Luzon appears to have contributed to the island's overall faunal diversity (Auffenberg, 1988; Brown et al., 1995a,b, 1997a,b; Ruedas et al., 1994). The taxonomic status of frogs of the *Rana everetti* group (currently considered *R. everetti*) on different Philippine Pleistocene aggregate island complexes (sensu Heaney, 1985, 1986) also awaits further consideration.

The identification of numerous osteological differences between *R. luzonensis* and *R. tipanan* substantiate the taxonomic recognition of *R. tipanan* as an evolutionary species occurring in sympatry with *R. luzonensis* and may indicate a considerable level of divergence between these sympatric species. Further studies with larger sample sizes and including the remaining taxa in this group are warranted to assess the potential value of these characters for phylogenetic analysis and to explore their distribution in other closely related taxa.

We have presented data that substantiate Dubois' (1992) elevation of Inger's (1954) subspecies of *R. everetti*. Dubois'

(1992) decisions were presented without accompanying data (see comments by Duellman, 1993) but are borne out by our analysis, as is the specific recognition of *R. tipanan* and *R. igorota*. *Rana everetti*, *R. luzonensis*, and *R. albotuberculata* have been included as distinct species by Dubois in his genus *Chalcorana*, along with *R. crassiovis*, *R. hosii*, *R. macrops*, *R. raniceps*, and *R. chalconota*. Given the resemblance of *R. igorota* and *R. tipanan* to *R. luzonensis*, *R. everetti*, and *R. albotuberculata*, inclusion of *R. tipanan* and *R. igorota* in *Chalcorana* might seem warranted by implication alone. However, we are unable to support the recognition of the taxon *Chalcorana* until its monophyly can be addressed by a phylogenetic analysis.

Very little attention has been paid to the status, taxonomy and biogeography of populations of amphibians of the Sierra Madres, save for very recent surveys by the authors and colleagues. Given the conservation crisis in the Philippines (Abate, 1992; Balete et al., 1992; Heaney, 1993; Heaney and Uzzurum, 1991; Oliver et al., 1993; Uzzurum, 1991), current restrictions placed on Filipino and foreign biologists (La Viña et al., 1997), and the rapid rate of deforestation (Bawa et al., 1990; Collins et al., 1991; Dickinson and Kennedy, 1991; Kummer, 1992; Lewis, 1988; Quinnell and Balmford, 1988), we urge immediate and exhaustive faunal surveys throughout the remaining forests of the Sierra Madres and the Cordillera Central. Such efforts will be required to document adequately the diversity and endemism of these insular massifs and to assess the conservation status of rare and endemic Philippine amphibians.

LAGOM (ABSTRACT IN TAGALOG)

Isinasalarawan ang isáng bagong uriñ ng palaka na kabilang sa pangkát ng mga ranine na tagláy ang malalapad na disks sa duluhan ng mga dalirì ng kamáy at paá. Ang katutubong palakâ, na ito ay mátatagpuan sa Pambansáng Parke ng Aurora at Bundók Cetaceo, dalawáng lugar mataás na kabubatan na saklâw ng bukúd-tanging bulúbundukin ng Sierra Madre sa hilang-silangan ng Luzon, Pilipinas. Ang

kaibhán ng palakáng ito sa mga kahalintulad na palakáng kabilang rin sa pangkat ranine ay ang pagkakaroon nito ng mas maliit na sukat ng katawán, ang pagkakaroon ng mga matutulis na butol sa balát lalo na sa mga palakáng may kasariang lalaki, at ang tympanum nito ay napaglálágusán ng liwanag lalo na sa mga palakáng lalaki. Bukód sa rito, ang mga palakáng lalaki ay maningning na luntiang kulay ang likod ng katawán ng na may batik na itim at may guhit-guhit; maningning na luntian o kaya'y malagintóng kulay na may kayumangging guhit-guhit naman ang likod ng katawán ng mga palakáng babae. Bukod sa pagsasalarawan ng nabanggit na bagong uriín, palaka, ang mga palakáng *Rana everetti*, *R. luzonensis*, *R. albotuberculata* (itinaás sa antás na species), at *R. igorota* (muling ipinanunumbalik mula sa pagkakasapí sa *R. everetti luzonensis*) ay kinikilalang mga ebolusyonaryong uriín.

Acknowledgments.—The Protected Areas and Wildlife Bureau of the Philippines Department of the Environment and Natural Resources (DENR) facilitated collecting permits necessary for a portion of this study. For logistical assistance, we thank A. Alcalá, D. Felicitas, and R. Flores (Silliman University), M. Manuel, R. Sison, and R. and F. Caberoy (PNM), and the provincial DENR authorities of Villa Aurora and Aurora National Park. We thank R. Kennedy for inviting R. Brown and J. McGuire to participate in the Aurora Memorial National Park survey (supported by CMNH benefactors). The dedicated field assistance of V. Yngente and J. Bulalacao is greatly appreciated.

For the loans of specimens or assistance while visiting museum collections, we thank the following individuals and their respective institutions (museum acronyms follow Leviton et al. (1985): W. Brown, R. Drewes, M. Koo, A. Leviton, J. Slowinski, and J. Vindum (CAS), R. Crombie, K. de Queiroz, and G. Zug (USNM), J. Cadle and J. Rosado (MCZ), J. Ferner (CMNH), J. Wiens and S. Rogers (CM) R. Sison and R. Caberoy (PNM), A. Resetar, C. Redhead, H. Voris, and R. Inger (FMNH). A visit to CAS was made possible by generous financial assistance of the C. Stearns Fellowship (awarded to R. Brown) of the California Academy of Sciences. We especially thank C. Spencer and J. Vindum for assistance compiling the publications of W. Brown and A. Alcalá.

Support for R. Brown's field work was provided in part by the Zoology and Botany Departments and the College of Arts and Sciences of Miami University (Oxford, Ohio), the Department of Zoology and Texas Memorial Museum, University of Texas at Austin, the Explorers Club, the Society for the Study of Amphibians and Reptiles, and the American Society of Ichthyologists and Herpetologists. J. McGuire's field work was supported by National Geographic Grant

5606-96 and by the Department of Zoology and Texas Memorial Museum, University of Texas at Austin. Publication of some of our data (taken from specimens collected under the auspices of collaborative PNM and CMNH survey work in Aurora Memorial National Park) constitutes contribution 21 to the results of the PNM/CMNH Philippine Biodiversity Inventory.

We thank J. Redor for assistance with the derivation of deep tagalog species epithet and for his help with the tagalog translation of the abstract; A. Diesmos thanks N. Mallari and the team members of the 1992 DENR-ICBP Sierra Madres Exploration group. Financial support of for the color plate was generously provided by L. and G. Hopple, John Sr., John Jr., Cheryl, and Mary Agnes Phenix, M. and J. Dickinson, Lila, Sam, and Eli Dillon, W. W. Brown, S. Johnson, L. and P. Saunders, H. Cochrane, Z. and C. Gersten, W. and D. Moore, M. and L. Higginbotham, L. Varon, P. Early, C. Redwine, the Richey and Collins families, and the Childrens' Meeting House Montessori school. We are grateful to C. Bell, D. Cannatella, M. Harvey, J. Wiens, J. Yeh, an anonymous reviewer for critical reviews of earlier drafts of this manuscript.

LITERATURE CITED

- ABACUS CONCEPTS. 1992. Statview. Abacus Concepts, Inc. Berkeley, California, U.S.A.
- ABATE, T. 1992. Into the northern Philippines. *BioScience* 42:246–251.
- ALCALA, A. C. 1986. Guide to Philippine Flora and Fauna, Vol. X, Amphibians and Reptiles. Natural Resource Management Center and Ministry of Natural Resources and University of the Philippines, Manila, Philippines.
- AUFFENBERG, W. 1988. Gray's Monitor Lizard. University of Florida Press, Gainesville, Florida, U.S.A.
- BALATE, D. S., H. C. MIRANDA, L. R. HEANEY, AND J. F. RIEGER. 1992. Diversity and conservation of Philippine land vertebrates: an annotated bibliography. *Silliman Journal* 36:129–149.
- BAWA, S. B., R. PRIMACK, AND D. WOODRUFF. 1990. Conservation of biodiversity: a southeast Asian perspective. *Trends in Ecology and Evolution* 5:394–396.
- BOULENGER, G. A. 1882. Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum, 2nd ed. Taylor and Francis, London, U.K.
- . 1896. Descriptions of new batrachians in the British Museum. *Annals and Magazine of Natural History* 6:401–406.
- BROWN, R. M., J. W. FERNER, AND L. A. RUEDAS. 1995b. A new species of lygosomine lizard (Reptilia: Lacertilia: Scincidae; *Sphenomorphus*) from Mt. Isarog, Luzon Island, Philippines. *Proceedings of the Biological Society of Washington* 108:18–28.
- BROWN, R. M., J. W. FERNER, AND R. V. SISON. 1995a. Rediscovery and redescription of *Sphenomorphus beyeri* (Reptilia: Lacertilia: Scincidae) from the Zambales Mountains, Luzon, Philippines. *Proceedings of the Biological Society of Washington* 108:6–17.

- BROWN, R. M., J. W. FERNER, R. V. SISON, P. C. GONZALES, AND R. S. KENNEDY. 1996. Amphibians and reptiles of the Zambales Mountains of Luzon Island, Republic of the Philippines. *Herpetological Natural History* 4:1-22.
- BROWN, R. M., J. A. MCGUIRE, J. W. FERNER, AND A. C. DIEMOS. 1999. A new species of diminutive scincid lizard (Squamata; Lygosominae; *Sphenomorphus*) from Luzon Island, Republic of the Philippines. *Copeia* 1999:362-370.
- BROWN, W. C., AND A. C. ALCALA. 1970. The zoogeography of the of the Philippine Islands, a fringing archipelago. *Proceedings of the California Academy of Sciences* 38:105-130.
- . 1980. *Philippine Lizards of the Family Scincidae*. Silliman University Press, Dumaguete City, Philippines.
- . 1994. Philippine frogs of the family Rhacophoridae. *Proceedings of the California Academy of Sciences* 48:185-220.
- BROWN, W. C., A. C. ALCALA, AND A. C. DIEMOS. 1999b. Two new species of the genus *Platymantis* (Amphibia: Ranidae) from Luzon Island, Philippines. *Proceedings of the California Academy of Sciences* 50:381-388.
- BROWN, W. C., A. C. ALCALA, A. C. DIEMOS, AND E. ALCALA. 1997b. Species of the *guentheri* group of *Platymantis* with descriptions of four new species. *Proceedings of the California Academy of Sciences* 50:1-20.
- BROWN, W. C., A. C. ALCALA, P. S. ONG, AND A. C. DIEMOS. 1999a. A new species of *Platymantis* (Amphibia: Ranidae) from the Sierra Madres Mountains of Luzon Island, Philippines. *Proceedings of the Biological Society of Washington* 112:510-514.
- BROWN, W. C., R. M. BROWN, AND A. C. ALCALA. 1997a. Species of the *hazela* group of *Platymantis* (Amphibia: Ranidae) from the Philippines, with descriptions of two new species. *Proceedings of the California Academy of Sciences* 49:405-421.
- COLLINS, N. M., J. A. SAYER, AND T. C. WHITMORE. 1991. *The Conservation Atlas of Tropical Forests: Asia and The Pacific*. Simon and Schuster, New York, New York, U.S.A.
- DICKINSON, E. C., AND R. S. KENNEDY. 1991. The vegetation of the Philippines and bird habitats. Pp. 15-24. *In* E. C. Dickinson, R. S. Kennedy, and K. C. Parks (Eds.), *The Birds of the Philippines*. Dorset Press, Dorchester, Dorset, U.K.
- DINGERKUS, G., AND L. D. UHLER. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technology* 52:229-232.
- DUBOIS, A. 1992. Notes sur la classification des Ranidae (Amphibiens Anoures). *Bulletin Mensuel Société Linnéenne de Lyons* 61:305-352.
- DUPELLMAN, W. E. 1993. *Amphibian Species: Additions and Corrections*. University of Kansas Press, Lawrence, Kansas, U.S.A.
- FROST D. R., AND D. M. HILLIS. 1990. Species in concept and practice: herpetological applications. *Herpetologica* 46:87-104.
- GRAYBEAL, A., AND D. C. CANNATELLA. 1995. A new taxon of Bufonidae from Peru, with descriptions of two new species and a review of the phylogenetic status of supraspecific bufonid taxa. *Herpetologica* 52:105-131.
- HALL, R. 1996. Reconstructing Cenozoic SE Asia. Pp. 153-184. *In* R. Hall, and D. Blundell (Eds.), *Tectonic Evolution of Southeast Asia*. Geological Society, London, U.K.
- HEANEY, L. R. 1985. Zoogeographic evidence for middle and late Pleistocene land bridges to the Philippine Islands. *Modern Quaternary Research of Southeast Asia* 9:127-144.
- . 1986. Biogeography of small mammals in SE Asia: estimates of rates of colonization, extinction and speciation. *Biological Journal of the Linnean Society* 28:127-165.
- . 1993. Biodiversity patterns and the conservation of mammals in the Philippines. *Asia Life Sciences* 2:261-274.
- HEANEY, L. R., AND R. C. B. UTZURRUM. 1991. A review of the conservation status of Philippine land mammals. *Association of Systematic Biologists of the Philippines Communication* 3:1-13.
- INGER, R. I. 1954. Systematics and zoogeography of Philippine Amphibia. *Fieldiana Zoology (Old Series)* 33:182-531.
- . 1966. The systematics and zoogeography of the Amphibia of Borneo. *Fieldiana Zoology (Old Series)* 52:1-402.
- KUMMER, D. M. 1992. *Deforestation in the postwar Philippines*. Ateneo De Manila University Press, Manila, Philippines.
- LA VIÑA, A. G. M., M. A. CALEDA, M. L. L. BAYLON, P. BENAVIDEZ, AND D. P. CALICA. 1997. *Regulating Access to Biological and Genetic Resources in the Philippines*. Foundation for Philippine Environment and World Resources Institute, Quezon City, Philippines.
- LEE, J. C. 1990. Sources of extraneous variation in the study of meristic characters: the effect of size and inter-observer variability. *Systematic Zoology* 39:31-39.
- LEVITON, A. E. 1964. Contributions to a review of Philippine snakes, V. The snakes of the genus *Trimeresurus*. *Philippine Journal of Science* 93:250-276.
- LEVITON, A. E., AND W. C. BROWN. 1959. A review of the snakes of the genus *Pseudorabdion* with remarks on the status of the genera *Agrophis* and *Typhlogeophis* (Serpentes: Colubridae). *Proceedings of the California Academy of Sciences* 29:475-508.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802-832.
- LEWIS, R. E. 1988. Mt. Apo and other national parks in the Philippines. *Oryx* 22:100-109.
- MATSUI, M. 1984. Morphometric variation analyses and revision of the Japanese toads (genus *Bufo*, Bufonidae). *Contributions of the Biology Laboratory, Kyoto University* 26:209-428.
- NEFF, N. A., AND L. F. MARCUS. 1980. A Survey of

- Multivariate Methods for Systematics. Privately published, New York, New York, U.S.A.
- OLIVER, W. L. R., C. R. COX, P. C. GONZALES, AND L. R. HEANEY. 1993. Cloud rats in the Philippines—preliminary report on distribution and status. *Oryx* 27:41–48.
- QUINNELL, R., AND A. BALMFORD. 1988. A future for Palawan's rainforests? *Oryx* 22:30–35.
- RUEDAS, L. A., J. R. DEMBOSKI, AND R. V. SISON. 1994. Morphological and ecological variation in *Otopteropus cartilagonodus* Kock, 1969 (Mammalia: Chiroptera: Pteropodidae) from Luzon, Philippines. *Proceedings of the Biological Society of Washington* 107:1–16.
- SAVAGE, J. M., AND W. R. HEYER. 1969. Variation and distribution of the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. *Beitrag zur Neotropischen Fauna* 5:111–131.
- . 1997. Digital webbing formulae for anurans: a refinement. *Herpetological Review* 28:131.
- SIMPSON, G. G. 1961. *Principles of Animal Taxonomy*. Columbia University Press, New York, New York, U.S.A.
- STATSOFT. 1994. *Statistica for the Macintosh*. Statsoft Inc., Tulsa, Oklahoma, U.S.A.
- STEJNEGER, L. 1905. Three new frogs and one new gecko from the Philippine Islands. *Proceedings of the United States National Museum* 28:343–348.
- TAYLOR, E. H. 1920. Philippine Amphibia. *Philippine Journal of Science* 16:213–359.
- . 1922a. Additions to the herpetological fauna of the Philippine Islands, II. *Philippine Journal of Science* 21:257–303.
- . 1922b. Additions to the herpetological fauna of the Philippine Islands, I. *Philippine Journal of Science* 21:161–206.
- . 1922c. The Lizards of the Philippines Islands. *Philippine Bureau of Science, Manila, Philippines*.
- . 1922d. The Snakes of the Philippine Islands. *Philippine Bureau of Science, Manila, Philippines*.
- . 1923. Additions to the herpetological fauna of the Philippine Islands, III. *Philippine Journal of Science* 22:515–557.
- . 1925. Additions to the herpetological fauna of the Philippine Islands, IV. *Philippine Journal of Science* 26:97–111.
- . 1962. The amphibian fauna of Thailand. *University of Kansas Science Bulletin* 63:278–599.
- UTZURRUM, R. C. B. 1991. Philippine island biogeographical patterns: practical considerations for resource conservation and management. *Association of Systematic Biologists of the Philippines Communication* 3:19–32.
- VAN KAMPEN, P. N. 1923. *The Amphibia of the Indo-Australian Archipelago*. Brill, Leiden, The Netherlands.
- VOSS, R. S., AND L. F. MARCUS. 1992. Morphological evolution in muroid rodents II. Craniometric factor divergence in seven neotropical genera, with experimental results from *Zygodontomys*. *Evolution* 46:1918–1934.
- WHITMORE, T. C. 1984. *Tropical Rain Forests of the Far East*. Clarendon Press, Oxford, U.K.
- WIENS, J. J. 1993. Systematics of the leptodactylid frog genus *Telmatobius* in the Andes of Peru. *Occasional Papers of the Museum of Natural History, University of Kansas* 162:1–76.
- WILEY, E. O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology* 21:17–26.

Accepted: 14 February 1999
Associate Editor: John Wiens

APPENDIX I.

Specimens Examined

Rana albotuberculata.—Philippines, Mindanao Island, Agusan Del Norte Province, Tagibo and Daydayan rivers, S. side of Mt. Hilong-hilong; CAS 13922–25, 137533–34; Samar Island, Samar, Municipality of San Isidro, Barangay Matuquiniao: CAS-SU I8160, 18167–69, 18172–73; Leyte Island; Cabalian: MCZ 23190 (holotype), 23188–89, 132410–14, 132416–19 (topotypes).

Rana erythraea.—Philippines, Samar Island: TNHC 54945–6.

Rana everetti.—Mindanao, Lanao Del Sur Province, Lake Lanao, Camp Keithley: CAS-SU 2141; Mindanao, Zamboanga CAS 61872; Mindanao, Davao Del Norte Province, Municipality of New Bataan, Sitio Liboton, Mt. Puting Bato (Malaya River drainage): CMNH 5603–04; Mindanao, South Cotobato Province, near Saub: MCZ 14083–84; Mindanao: USNM 305594–97, 35258 (holotype of *Rana mearnsi*); CM 3506–07, 3509–10 (paratypes of *R. mearnsi*); Bohol Island, Bohol Province, Municipality of Cantub, Sierra Bullones: CAS 137028.

Rana grandocula.—Philippines, Mindanao Island, TNHC 56127–33.

Rana igorota.—Luzon Island, Kalinga–Apayao Province, Kalinga Subprovince, Municipality of Balbalan, Barangay Balbalan: CAS 61484 (EHT F789; Holotype); CAS 61483, 61485–89, MCZ 14096–98 (paratypes).

Rana luzonensis.—Luzon Island, Aurora Province, Municipality of Carmen, Aurora National Park: PNM 5742–5765; CMNH 5605–5611; 5612–5630; Luzon Isl., Mountain Prov., Municipality of Bontoc: MCZ 10556; Luzon Isl., Laguna Prov., Municipality of Los Baños, Mt. Makiling: MCZ 23178–79, 14142–45; Luzon Island, Zambales Province, Municipality of Masinloc, Barangay Coto: CMNH 4171–72, 4279–85; PNM 2371, 2378–84, 2496–98.0; Luzon Isl., trail between Famy (Laguna Prov.) and Infanta (Tayabas Prov.): CAS 61819 (holotype of *R. tafti*); Polillo Isl., Polillo Prov., Burdeos: CAS 62448 (holotype of *R. merrilli*); Luzon Isl., Banguet Prov., Municipality of Baguio, Baguio City: CM 3271, 3273–3278, 3280–81, 3283, MCZ 10482–84 (topotypes of *R. guerreroi*).

Rana moellendorffi.—Philippines, Palawan Island: TNHC 56134–42.

Rana nicobariensis.—Malaysia, Sabah (N. Borneo Island): FMNH 76654, 76659.

Rana sanguinea.—Philippines, Palawan Island: CMNH 3700–01, 3733, 3737.

Rana tipanan.—See species account.