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Systematics of the Garden Lizards, *Calotes versicolor* Group (Reptilia, Squamata, Agamidae), in Myanmar: Central Dry Zone Populations

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The Burmese garden lizards represent a complex of several species. DNA sequence and morphological analyses reveal that two species occur sympatrically in the Central Dry Zone of Myanmar. These two new species are described herein. Additionally, the molecular data demonstrate that *Calotes versicolor* represents multiple species and at least two clades: one from India-Myanmar and another from Myanmar-Southeast Asia. The morphological investigation does not currently recognize unique trait(s) for each clade, but it does establish a set of morphometric, scalation, and quantitative coloration traits that permit statistical comparison of intra- and interpopulational variation in the *versicolor* species group.

Calotes versicolor and *Calotes mystaceus* are the most commonly seen diurnal lizards in Myanmar. Both appear to be forest-edge species, hence readily adapted to the fence-row, roadside and garden habitats created by humans. Our collaborative (CAS-NWCD-SI[5]) survey and inventory of the Burmese herpetofauna have enabled us to document the distribution of these lizards and many other amphibians and reptiles, and critically, to obtain tissue samples and adequate voucher series to initiate studies of regional differentiation at both the morphological and molecular levels in a variety of common Burmese frogs and lizards.

Our attention has become increasingly focused on the "common" species. We have discovered from our earliest site-specific surveys that a common species often consisted of two species, often within the same paddy or forest fragment. We further noted that individuals of the same species from distant localities regularly appear subtly different. These differences are sufficiently muted that they can be easily overlooked, and in hurried inventories of sites, it is easier and more expedient to label a specimen with a readily available name. The unfortunate consequence of this practice is an underestimate of a site's true biodiversity and more broadly the biodiversity of the region or country being surveyed and inventoried.

The Chatthin Wildlife Sanctuary (23°35′N, 95°44′E) was the first site surveyed (Zug et al. 1998) in our country-wide inventory of the Myanmar herpetofauna. It lies at the northern end of the Central Dry Zone and is largely a secondary or recovering indaing forest surrounded by paddies.

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The garden lizard is only modestly abundant at this site and did not attract any special attention until J. Schulte began a regional analysis of molecular differentiation of *Calotes versicolor* populations and discovered that two "*versicolor"* species occur at Chatthin. His continuing analysis has identified other "*versicolor*" species, on which we will report subsequently. Here our focus is on a preliminary definition of the "*versicolor*" group and the description of two Chatthin species. The latter has called our attention to the uncertainty of which population represents true *Calotes versicolor*, i.e., *Agama versicolor* Daudin, 1802. We examine that question briefly owing to its importance in diagnosing the new species. That question will be addressed more critically subsequently in a broader regional study.

Taxonomic History of *Calotes versicolor*

Calotes versicolor was described by Daudin in 1802, then a half-dozen more times by 19th century biologists. All these descriptions apply to Indian populations and, where the type-locality is designated, to populations on the east coast of India (Pondicherry, Chenai [Madras], and Kolkata [Calcutta]). Remarkably, this wide ranging and abundant lizard of gardens and fence-rows has not had populations recognized as distinct species in other parts of Asia. This phenomenon derives from the seeming uniformity of "*versicolor*" populations and, as noted above, the ease of labeling them with the "*versicolor*" epithet. This uniformity is more apparent than real, because even without close examination, we recognized that the *C. versicolor* from different areas in Myanmar were subtly different. We certainly are not the first to notice such differences. Auffenberg and Rehman (1993, 1995) recognized two distinct morphologies in Pakistan and described one of them as a new subspecies (*farooqi*). Kästle (in Schleich and Kästle 2002) noted that the Nepal *C. versicolor* consist of several varieties, and he seems to have been the first to label these strictly *C. versicolor*-morphs as the *C. versicolor* complex. This narrower usage differs from that of Malcolm Smith's *versicolor* group, and we believe that this recognition of a distinct *versicolor* group/complex is a useful phenetic hypothesis prior to a full scale phylogenetic analysis.

Using Malcolm Smith's "Fauna of British India" (1935) as a historical marker, *Calotes* consisted then of four species groups: *cristatellus*; *microlepis*; *versicolor*; *liocephalus*; and unassigned, *C. kingdonwardi* and two dwarf species (*C. ellioti*, *C. rouxii*). Subsequently, no one appears to have examined the relationship within or among these groups until the 1980s. At that time, Moody, in his unpublished dissertation (1980), examined morphological variation in the Agamidae and provided the first phylogenetic analysis of intrafamilial relationships. To ensure a comprehensive study of the family with a full representation of all agamid clades (= genera and subgenera), Moody examined more than 95% of the types of the then described species. This examination resulted in his decision to recognize 53 clades in contrast to the 34 genera listed in Wermuth's 1967 agamid checklist. Moody's nomenclatural groupings were defined only by their species composition (1980: Appendix A). Owing to the thoroughness and scope of this dissertation, Moody's nomenclature was broadly accepted even though he never published formal descriptions of the new and resurrected taxonomic groups. Smith's *cristatellus* group was assigned to the genus *Bronchocela* Kaup, 1827 (see Hallermann's [2005] taxonomic review of the genus). The *liocephalus* and *versicolor* groups remained in *Calotes* Cuvier, 1817. The *microlepis* group became *Pseudocalotes* Fitzinger, 1843 (see Hallermann and Böhme [2000] for generic diagnosis, species content, and nomenclatural history), and Smith's recognition of C. *kakhiensis* as an aberrant member of *Calotes* was "corrected" by placement in the genus *Salea* Gray, 1845. Ota and Hikida (1991) described *Calotes nigrigularis* from Mt. Kinabalu, Sabah. Subsequently, Manthey and Grossmann (1997) erected the genus *Complicitus* for this peculiar lizard, and in 2000, Manthey and Denzer proposed a new genus, *Hypsicalotes* for *C. kinabaluensis*. The validity of these monotypic taxon has not yet been tested.

Smith (1935:183) recognized that his *versicolor* group was "not very homogeneous" because the included taxa shared only a few features. Subsequent studies of *Calotes, sensu* Moody, have examined neither the species composition nor the interspecific relationships within this taxon or the intraspecific ones among *versicolor* populations. We have initiated a morphological review of the species of *Calotes* with the intent of determining phylogenetic relationships based on shared-derived morphological features. That review is still in its earliest stages; nonetheless, we propose that the *versicolor* group (phenetic now) consists of *Calotes* species sharing the following traits: 1) pre-axillary scales uniform-sized, i.e., absence of a crescent-shaped patch of granular scales (pigmented or unpigmented) in front of the shoulder; 2) trunk scales somewhat smaller than or equal to size of ventral scales; 3) dorsal crest scales in a continuous row to (at least) above the shoulders; 4) supratympanic area with a pair of spine patches or patches fused as a single longitudinal series; and 5) multiple (2–4) distinctly linear rows of elongate loreal and subocular scales above the supralabial scales. Each of these traits occurs in other species of *Calotes* but only in combination in the *versicolor* group.

Materials and Methods

The present study focuses on the two *versicolor* morphotypes of Myanmar's Central Dry Zone. DNA sequence data (Fig. 3) demonstrate their genetic distinctiveness from one another and other *versicolor* group populations in Myanmar and elsewhere. This discovery resulted from J. Schulte's on-going investigations of relationships among agamid "genera." The initial discovery of striking genetic differences among a few Burmese "*versicolor*" populations led to an increase sampling of populations throughout Myanmar. All these tissue samples derive from the Myanmar Herpetological Survey. The origin of these samples and those from other areas of southern Asia are detailed in Appendix, section C. Methodology for the extraction of DNA and its subsequent analysis are in Appendix, section A.

The DNA data were examined phylogenetically using PAUP* beta version 4.0b10 (Swofford 2002) and implementation of a heuristic search with TBR branch swapping and 1000 random taxon additions using maximum parsimony (MP). Bootstrap resampling (Felsenstein 1985) assessed the support for individual nodes using 1000 bootstrap replicates with TBR and 100 random taxon additions per replicate. Decay indices (= "branch support" of Bremer 1994) were calculated for all internal branches using TreeRot.v2c (Sorenson 1999) and heuristic searches as conducted above for each node present in the overall MP tree(s).

Data examination also included maximum-likelihood (ML) analyses. Simultaneous optimization of ML parameters and phylogenetic hypotheses for this data set were computationally impractical. Iterative searches were conducted for these mtDNA data using a successive approximations approach (Swofford et al. 1996; Sullivan et al. 2005). To reduce computation time, the program ModelTest v3.7 (Posada and Crandall 1998) was used to find the best fitting model of sequence evolution for a tree reconstructed using neighbor joining (NJ), as it has been determined that the starting tree does not significantly influence the estimated model discovered by ModelTest (Posada and Crandall 2001). These parameters were fixed in the initial searches. Heuristic search conditions were: 1) Starting trees were obtained via NJ; 2) TBR branch-swapping; 3) reconnection limit set to eight. Tree(s) obtained from this search protocol were used to estimate new parameter values under an identical model. These new parameter values were fixed in a second search with the same conditions as the initial run. This process was repeated until the same tree and parameter values were found in two successive searches. Bootstrap resampling was applied using ML with 100 replicates and heuristic searches as above except that successive approximations were not conducted for each replicate. In our evaluation of branch support strength, we consider a bootstrap value of 95% and

above as strongly supported (Felsenstein and Kishino 1993), 95–70% as moderately supported, and below 70% as poorly supported.

For morphological comparisons, we assembled a small set of *Calotes versicolor* samples from throughout Myanmar to examine the variation within and between select Myanmar populations and two external samples (Pondicherry, India [the putative type-locality of *Agama versicolor* [Daudin] and eastern Thailand) for a perspective on the intra-Myanmar variation. The composition of these samples is presented in the Appendix C.

Our preliminary examination of morphological differences between the genetically distinct units at Chatthin identified several scalation and coloration differences. From this initial comparison and examination of the *Calotes* literature, we developed a set of 25 mensural, 12 meristic (scalation), and 10 coloration traits; definitions of these traits are presented in Appendix section B. Each trait has a unique abbreviation and those are used throughout the following text. Each specimen was dissected to examine the gonads to determine sex and maturity. Data were gathered by HB and GZ, who, periodically and independently, would record data from the same subsample of specimens to ensure that they were measuring and counting identically. The same protocol was followed by JV and GZ for CAS specimens. SYSTAT version 10.2 was used for all statistical analyses.

A map showing principal localities in Myanmar for the major samples of specimens examined in this study will be found in the Appendix (Fig. 11).

Observations on Molecular Sequence Differentiation among Populations of Myanmar *Calotes* "*versicolor*"

The twenty-one new mitochondrial DNA sequences range in size from 1702–1728 base pairs and were aligned with 33 additional draconine sequences from Macey et al. (2000) and Schulte et al. (2002, 2004) for a total of 1915 aligned positions. All sequences are inferred to be authentic mitochondrial DNA rather than nuclear encoded copies based on the criteria discussed in Schulte et al. (2004). Site homology was inferred to be ambiguous at 408 nucleotide positions. In the phylogenetic analysis of 1507 unambiguously aligned sites in 54 DNA sequences, 888 were phylogenetically informative (parsimony criterion) and 1028 were variable.

Analysis of DNA sequence data containing 1507 aligned positions produced one overall most parsimonious phylogenetic hypothesis with a length of 6452 steps. Overall phylogenetic relationships among draconine genera are similar to those reported in Macey et al. (2000) and Schulte et al. (2004) (Fig. 1). Differences among intergeneric relationships are restricted to those branches that are weakly supported by bootstrap values and decay indices. All *Calotes* species were recovered as monophyletic with strong support (bootstrap 100%, decay index 39). Two sequences of the recently described species *C. chincollium* (Vindum et al. 2003) were recovered as the sister group to a sample identified tentatively as *C. emma* from Rakhine State in Myanmar (bootstrap 100%, decay index 34) with these three samples forming a strongly supported monophyletic group to a sample of *C. emma* from Vietnam (bootstrap 100%, decay index 44).

The clade containing sequences of *C. calotes, C. htunwini, C. irawadi,* and *C.* "*versicolor*" is strongly supported (bootstrap 98%, decay index 11). The four DNA sequences representing *Calotes htunwini* form a strongly supported monophyletic group (bootstrap 100%, decay index 39) that is the sister group to all remaining species in this clade. All samples of *C.* "*versicolor*" and *C. irawadi* form a monophyletic group with strong support (bootstrap 100%, decay index 52) exclusive of *C. calotes.* The four DNA sequences of *C. irawadi* are monophyletic (bootstrap 100%, decay index 19) but are nested within sequences of *C.* "*versicolor*" with weak support (bootstrap 58%, decay index 3). DNA sequences of *C.* "*versicolor*", except the sample from Rakhine State, are moderate-

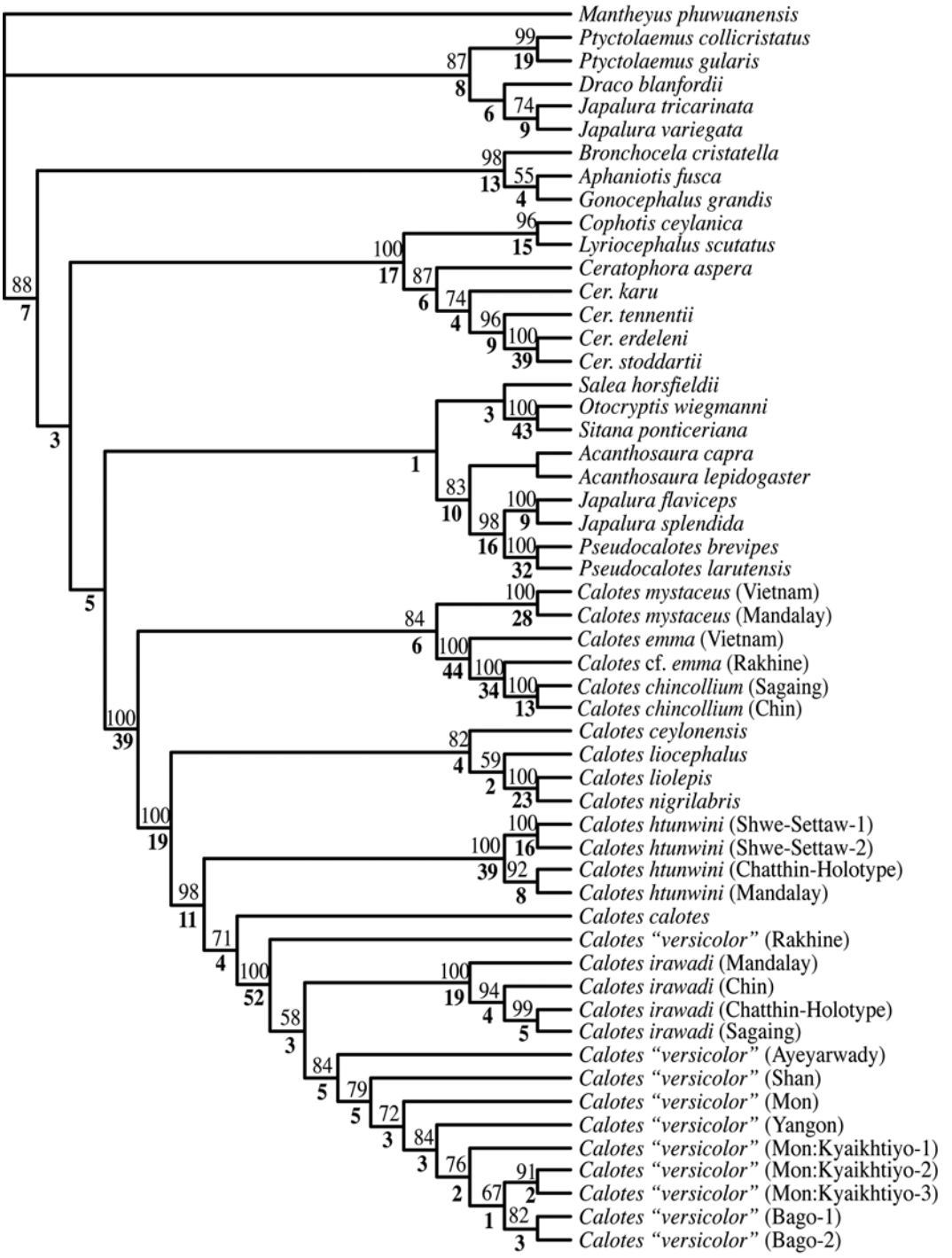

FIGURE 1. Phylogenetic relationships among agamid lizards based on maximum parsimony analysis of DNA sequence data (length = 6452 steps). Bootstrap values are presented above branches and decay indices are shown in bold below branches on the cladogram.

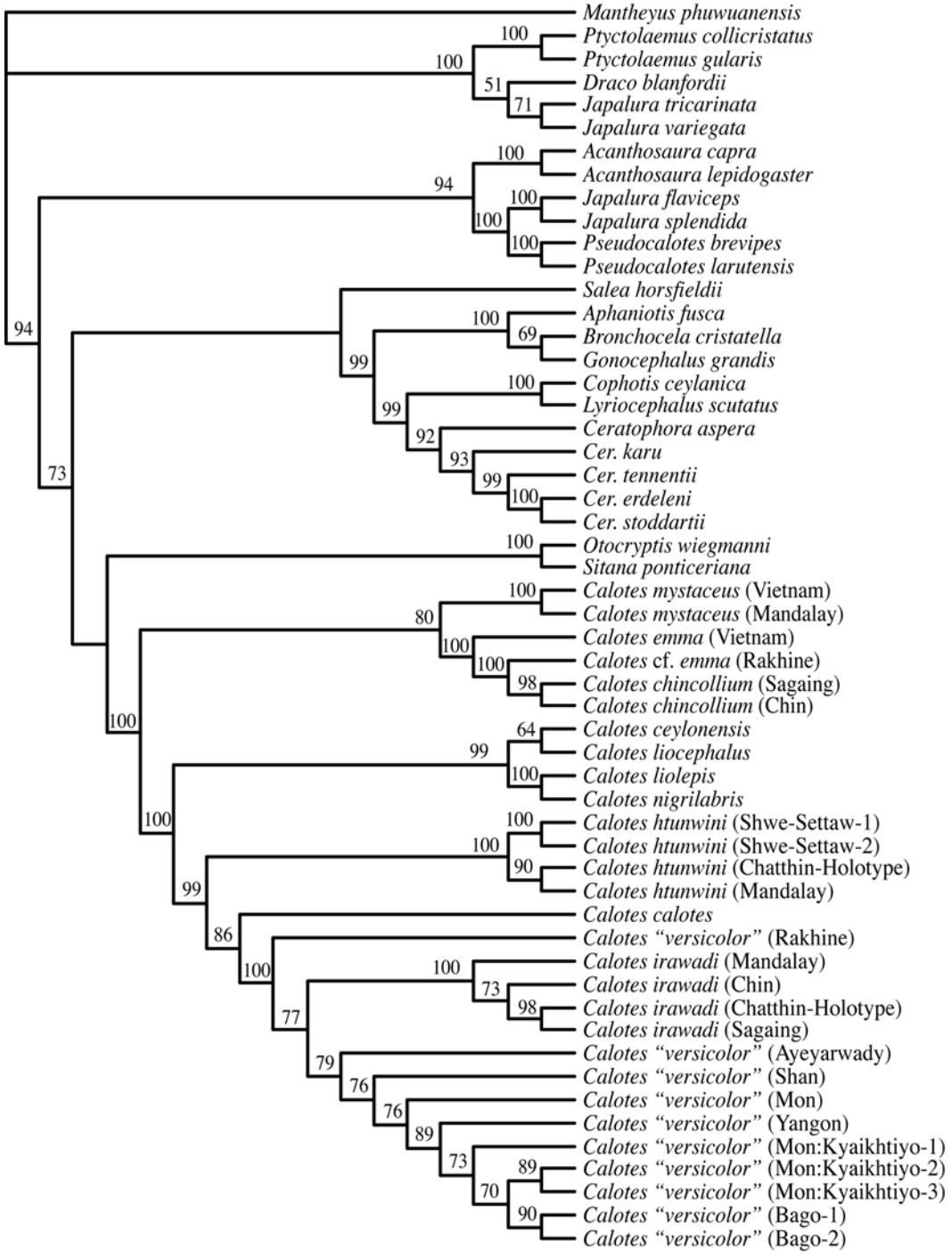

FIGURE 2. Phylogenetic relationships among agamid lizards based on maximum likelihood analysis using GTR + I + G model (mean -log-likelihood = 27680.88). Outgroups are identical to those presented in figure 1.

ly supported as a monophyletic group (bootstrap 84%, decay index 5).

Hierarchical likelihood ratio tests conducted using ModelTest found that the most complex model (GTR + I + G) best explains the aligned sequences and a neighbor joining topology. Model selected was identical when using the overall most parsimonious tree. Model parameters identified using successive approximations were as follows: a= 0.658; proportion of invariant sites = 0.238; substitution rates R(a) = 0.314, R(b) = 4.742, R(c) = 0.345, R(d) = 0.295, R(e) = 2.55, and R(f) = 1.000; and estimated base frequencies A = 0.383, C = 0.330, G = 0.075, and T = 0.212. Using the aligned DNA sequence data (992 unique site patterns) and model parameters from the successive approximations ML analysis, a single topology (Fig. 2) was found (-lnL = 27680.88). Relationships among most sequences representing *Calotes* species in ML analyses were identical to those found from MP analyses. Topological differences between these hypotheses are restricted to weakly supported intergeneric relationships at deeper nodes in the trees. There are several nodes within *Calotes* where ML bootstraps are noticeably higher than MP bootstraps including the group composed of *C. ceylonensis, C. liocephalus, C. liolepis,* and *C. nigrilabris* and the clade containing *C. calotes, C. irawadi*, and all *C.* "*versicolor*" populations, whereas ML bootstraps support for the class containing *C. irawadi* sequences from Chin, Chatthin, and Sagaing was much lower than the MP bootstrap value.

Maximum likelihood-corrected distances between previously published sequences of *Calotes* species, the *C. versicolor* group, *C. htunwini,* and *C. irawadi* exhibited extensive molecular variation (Fig. 3). The average pairwise genetic difference between *C. htunwini* and all other samples of *Calotes* was 25.8% whereas average pairwise differences between *C. irawadi* and all other samples of *Calotes* were 29.5%. Within the group previously referred to as *C. versicolor,* sequences of *C. htunwini* and *C. irawadi* compared to all other specimens were 21.3% and 9.5% different, respectively. Within the clade containing all populations of *C.* "*versicolor*" and *C. irawadi,* the latter species was 4.6% different based on maximum likelihood corrected distances. Interestingly, the specimen of *C.* "*versicolor*" from Rakhine State was found to be 20.6% divergent from *C. htunwini,* 4.4% different from *C. irawadi,* and 3.8% different from the remaining specimens of *C.* "*versicolor.*"

Observations on Morphological Variation in Myanmar *Calotes versicolor* Group

Preliminary analysis delineated six OTUs (operational taxonomic units) among ten sample localities, two of which (Htunwini and Irawadi) are described subsequent to this examination of morphological variation within and among samples. The latter two OTUs occur together broadly throughout the Central Dry Zone from Chatthin Wildlife Sanctuary southward to Shwe-Settaw W.S.; the Irawadi morphotype also occurs alone on the western edge of the Shan Plateau in the Pyin-Oo-Lwin area (900–1000 m). The garden lizards at the other Myanmar sample localities (Moyingyi and Nat-Ma-Taung), Pondicherry, and Thai-East, each represents a different OTU. Subsequent remarks on morphological variation use these OTU labels (Htunwini, Irawadi, and locality names).

Sexual dimorphism.— None of the individual locality samples is sufficiently large to reliably test (Students' *t* for measurements and scalation, χ^2 for coloration) for sexual or juvenile-adult dimorphism. We, nonetheless, present the result (Table 1) because these dimorphisms regularly occur in other *Calotes* and our preliminary data indicate that these dimorphisms also occur widely in Myanmar *Calotes* "*versicolor.*"

Adult females and males differ in size. Females average smaller than males, and this feature is statistically significant for most measurements in the combined samples of Htunwini and Irawadi

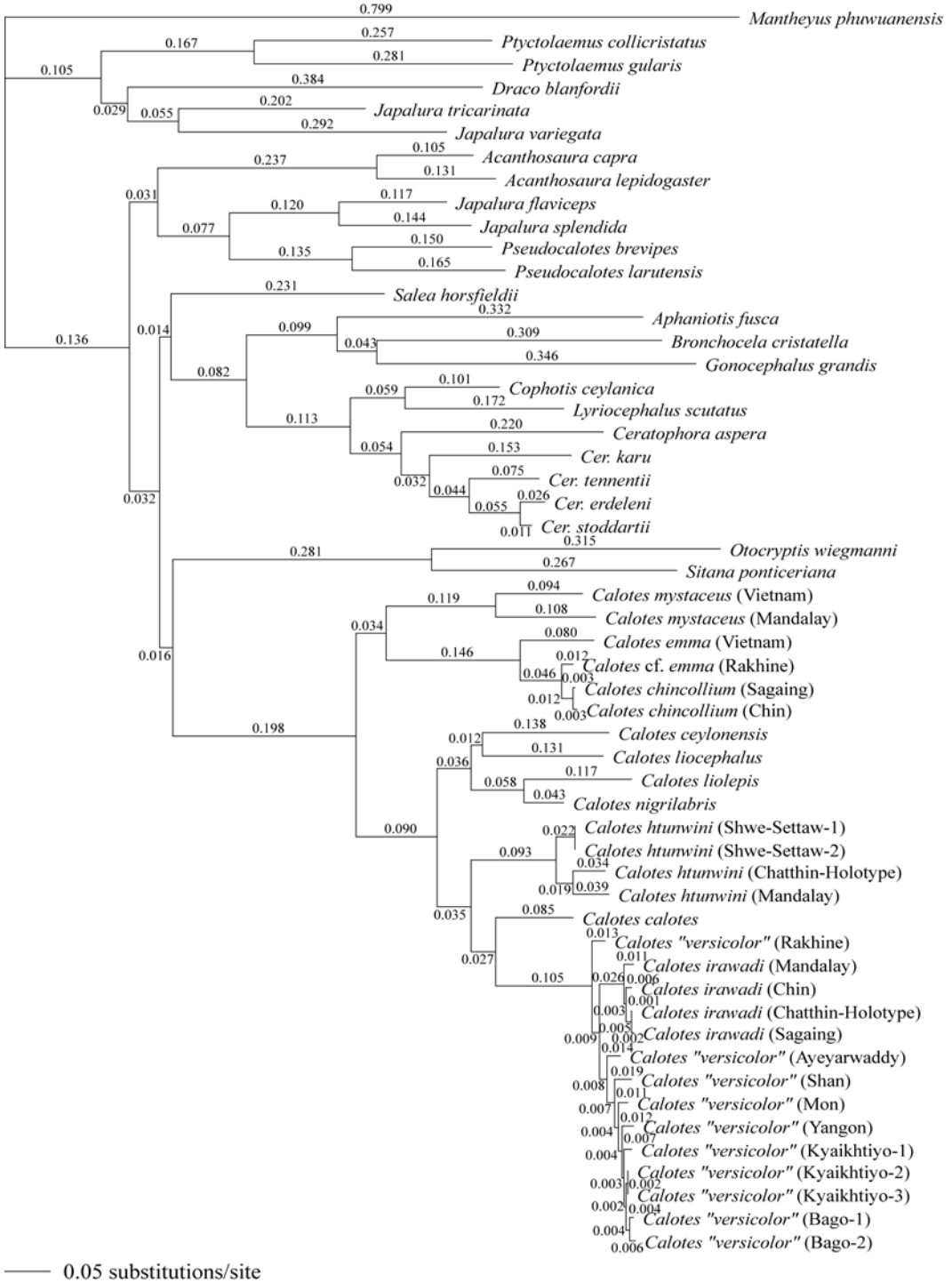

FIGURE 3. A phylogram depicting the phylogenetic relationships and relative divergence of DNA sequence data between species of draconine lizards and populations of the *Calotes versicolor* group. Branch length values represented by estimated number of nucleotide substitutions per site are depicted adjacent to branches.

TABLE 1. Summary of sexual dimorphic traits in *Calotes* "*versicolor*" samples. Character abbreviations are defined in the Appendix. Sample sizes are in parentheses: adult females, adult males, juveniles.

Htunwini

Alaungdaw Kathapa (4, 3, 1). TailW, 4ToeLng; Dorsal; ForearmSt.
Chatthin (3, 0, 7). Not testable.
Popa (0, 1, 3). Not testable.
Shin-Ma-Taung (5, 4, 0). EyeEar, TailH, TailW, UpArmL, UpLegL; Dorsal; color - ForearSt.
Shwe-Settaw (0, 0, 12). Not testable.
combined samples (14, 11, 21). HeadL, HeadW, JawW, HeadH, SnEye, NarEye, EyeEar, SnW, Interorb, SVL, TrunkL, TailH, TailW, PectW, SnForel, UpArmL, LoArmL, UpLegL, CrusL, HindfL, 4ToeLng; Dorsal, 4ToeLm; color – MidvLine, ForearSt.

Irawadi

Alaungdaw Kathapa (2, 14, 1). HeadL, HeadW, JawW, HeadH, SnEye, NarEye, EyeEar, Interorb, SVL, TrunkL, TailL, TailH, TailW, PectW, PelvW, SnForel, UpArmL, LoArmL, 4FingLng, UpLegL, CrusL, HindfL; 4ToeLm; color – DorsSt, TrnkBand.
Chatthin (2, 1, 4). Not testable.
Popa (3, 4, 3). TailL, HindfL, 4ToeLng; no scalation dimorphism; no color dimorphism.
Pyin-Oo-Lwin (5, 0, 1). Not testable
Shwe-Settaw (1, 7, 1). Not testable
combined samples (14, 30, 13). HeadL, HeadW, JawW, HeadH, SnEye, NarEye, EyeEar, Interorb, TailL, TailH, TailW, PectW, SnForel, UpArmL, LoArmL, UpLegL, CrusL, HindfL, 4ToeLng; Eyelid, Dorsal, 4FingLm, 4ToeLm; color – ThroatSt, ThroatPa, CheekCol, DorsSt, TrnkBand.

Moyingyi (3, 7, 1). HeadL, HeadW, JawW, HeadH, EyeEar, SnW, TailH, TailW, PectW, PelvW, SnForel, UpLegL, HindfLng; Dorsal; color - CheekCol.

Nat-Ma-Taung (5, 3, 7). EyeEar, TailH, HindfLng; no scalation dimorphism; DorsSt, ForearSt

Pondicherry (2, 11, 2). HeadL, HeadW, JawW, HeadH, SnEye, NarEye, EyeEar, Interorb; SVL, TrunkL, TailL, TailH, TailW, PectW, PelvW, SnForel, LoArmL, ForefL, 4FingLng, UpLegL, CrusL, HindfLng, 4ToeLng; no scalation dimorphism; state of preservation prevented test of color dimorphism.

Thai-East (2, 10, 1). JawW, HeadH, NarEye, EyeEar, SnW, Interorb, TailH, TailW, SnForel, UparmL; Dorsal, 4ToeLm; no color dimorphism.

(Table 1). Overall size differences between the sexes would presumably cause all component measurements to differ in average lengths. That a number of traits do not is noteworthy, and especially so when the differences are shared between the Htunwini and Irawadi samples. The shared non-dimorphic traits are: ForelL, 4FingLng, PelvW. Additional non-dimorphic traits are 4ToeLng for Htunwini and SnW, SVL for Irawadi. An explanation for this non-dimorphism is not immediately evident; perhaps larger samples and covariance analyses would determine if it is a biological reality. Size dimorphism is evident in the other two Myanmar samples (Table 1) as well as the extralimital ones.

Male *Calotes* "*versicolor*" are the larger sex, strikingly so in the Pondicherry sample, in which there is no overlap in SVL of adult females and males (Table 2). Tiwari and Aurofilio (1990) reported similar results from a Chennai (approx. 120 km N of Pondicherry) sample (10–12 females, 19–23 males). Overlap in SVL and other measurements occurs in all our other samples. This SVL overlap occurred also in Auffenberg's and Rehman's (1993) Myanmar sample. Their Myanmar sample consisted mainly of Yangon individuals, and the size dimorphism (SVL marginally significant difference) was diluted by the inclusion of specimens from three other distant Burmese localities, representing different OTUs.

The sexual differences in scalation are slight (Table 1).The widespread occurrence of Dorsal differences in Htunwini, Irawadi, Moyingyi, and Thai-East samples suggest that this difference is not a statistical artifact. Females have more Dorsals (means of females and males: 50.0, 44.6

TABLE 2. Summary of select measurement characters in adults of the *Calotes* "*versicolor*" samples. Character abbreviations are defined in the Appendix. Sample sizes are in parentheses. All measurements are in mm: mean ± s, minimum and maximum values.

Sample	*SVL*	*TrunkL*	*SnForel*	*HindfLng*	*HeadL*	*HeadW*	*EyeEar*	*Interorb*
Htunwini								
F(14)	69.9±6.12	34.7±2.73	25.0±2.59	21.1±2.14	16.5±1.51	13.8±2.34	3.9±0.42	8.6±1.21
	61.3–84.3	30.3–41.9	20.9–28.8	17.4–23.9	14.6–20.6	10.2–17.5	3.2–5.0	6.2–11.0
M(11)	78.5±6.89	37.4±3.51	28.4±2.50	24.3±2.36	18.5±3.03	16.6±2.64	4.9±0.60	9.8±0.76
	67.9–91.4	31.9–44.7	25.5–32.3	20.6–27.8	10.6–21.6	12.5–21.1	4.0–6.0	8.4–11.0
Irawadi								
F (14)	77.4±7.91	40.6±4.3	26.6±3.32	24.5±1.59	17.6±1.82	14.3±1.92	4.3±0.60	8.3±1.04
	64.3–90.3	32.1–44.9	20.8–32.1	21.0–26.5	13.9–21.4	11.2–17.8	3.1–5.5	6.9–10.7
M (30)	82.4±8.09	41.4±5.34	29.2±2.17	26.8±2.22	20.1±1.78	19.1±3.60	5.8±0.86	9.4±0.88
	66.4–106.8	31.7–56.9	25.4–33.7	23.0–34.1	16.9–24.9	13.3–28.3	4.2–7.9	7.9–11.3
Nat-Ma-Taung								
F (5)	79.4±13.63	41.6±8.72	28.2±4.12	24.5±2.77	18.1±2.85	17.1±4.04	4.8±0.75	8.5±1.21
	56.1–89.4	27.7–49.3	21.2–31.2	19.6–26.3	13.0–19.8	9.9–19.4	3.5–5.3	6.4–9.3
M (3)	88.3±1.17	46.2±1.07	31.2±0.92	28.6±0.61	21.7±0.62	21.0±1.77	6.4±0.10	10.1±0.40
	87.0–89.3	45.5–47.4	30.2–32.0	28.2–29.3	21.0–22.0	19.0–22.2	6.3–6.5	9.6–10.3
Moyingyi								
F (3)	83.4±4.92	41.4±2.65	30.7±1.47	27.0±1.22	17.9±1.34	14.4±1.77	4.2±0.35	8.9±0.91
	78.2–88.0	38.5–43.7	29.0–31.8	26.2–28.4	16.9–19.4	13.2–16.4	4.0–4.6	8.1–9.9
M (7)	91.4±4.52	43.5±2.97	35.4±2.50	30.1±1.35	21.0±1.34	20.1±2.03	6.1±0.71	9.6±0.36
	82.9–97.5	39.9–47.3	31.6–37.7	27.5–31.8	19.1–23.5	17.7–24.1	4.7–6.8	9.1–10.0
Pondicherry								
F (2)	92.9	45.2	31.3	28.4	21	18.1	5.5	11
	89.9–95.9	44.6–45.8	30.2–32.3	27.3–29.4	20.5–21.4	17.6–18.6	5.5	10.6–11.3
M (11)	119.3±8.69	52.5±4.23	45.7±4.88	37.2±2.00	28.3±1.91	29.4±4.05	9.6±1.26	14.0±0.93
	106.7–131.2	46.0–59.5	38.0–52.9	33.7–40.0	25.2–30.9	22.4–33.7	7.3–11.0	12.3–15.1
Thai-east								
F (2)	73.6	35.8	27.5	22.9	17.9	14.2	4.3	9.2
	71.2–76.0	34.4–37.1	26.3–28.6	22.1–23.7	17.7–18.0	13.5–14.8	4.2–4.3	9.1–9.3
M (10)	81.2±6.11	35.6±3.20	32.5±3.01	25.6±2.18	20.0±1.41	18.9±2.77	5.8±0.54	10.5±0.77
	69.9–90.1	30.2–41.1	26.8–36.1	23.2–30.0	17.9–22.8	13.8–23.3	4.8–6.7	8.9–11.6

Htunwini; 51.6, 48.2 Irawadi; 56.3, 49.5 Moyingyi; 47.5, 44.2 Thai-East). Presumably, the higher number of Dorsal in females reflects an increased abdominal volume, although circumference is not enlarged relative to an increase in Midbody. An explanation for slightly more 4ToeLm in males is not immediately evident.

Calotes "*versicolor*" are well known for bright head, neck, and fore-trunk coloration in sexually ready males. These bright reds and oranges soon disappear in preserved specimens; however, we have not observed these bold shades in mature males of the Htunwini, Irawadi, Moyingyi, and Nat-Ma-Taung populations. The preserved sexual coloration differences of the four dimorphic Burmese populations are largely non-overlapping (Table 1 and 4) except for the usual presence of ForearSt in Htunwini and Nat-Ma-Taung females, and the distinct DorsSt in Irawadi and Nat-Ma-Taung females. Clearly, the coloration of living adults of all Myanmar populations requires more attention and better cataloging.

Mensural traits.— Amidst the four Burmese OTUs, the Moyingyi population has the largest average body size even though the Moyingyi sample does not contain the largest Burmese individual (an Irawadi male; Table 2) among our Burmese samples. Htunwini adults are the smallest garden lizard of the four Burmese OTUs. Nat-Ma-Taung and Irawadi adults are approximately equal in size and the Moyingyi lizards the largest. We anticipate that these relative size differences will only be strengthened as sample sizes are enlarged.

There is a strong positive linear association among all the mensural traits and SVL, usually with coefficients of determination (R^2) greater than 0.80, confirming that regression equations account for a significant percentage of the variation. Regression slopes were not compared statistically. Visually, body-segment lengths appear to increase proportionately faster (i.e., higher slope values) in males than females for both Htunwini and Irawadi samples. Regression slopes for female Htunwini and Irawadi, and for male Htunwini, Irawadi, and Pondicherry samples are also similar. Thus, assuming that regressions reflect growth trajectories, females and males within a population possess different growth allometries, whereas the same sexes from different populations have similar allometries. This interpretation requires testing.

The Irawadi OTU is represented by individuals from seven areas (Alaungdaw Kathapa [AK], Chatthin, Popa, Pyin-Oo-Lwin, Yamethin, Yin Mar Bin, and Shwe-Settaw), but adults are available from six areas and only two (AK, Shwe-S) have enough adult males to hint that the more northerly populations might average somewhat smaller (SVL) than the Shwe-S area. The availability of adequate adults of Htunwini is similar and limits the evaluation of geographic variation. There are no adults from Shwe-S, and AK has the largest (mean SVL) males, and Chatthin the smallest females.

Because of the correlation among all the measurements, principal components analysis (PCA) results reflect only aspects of body size, and expectedly, the major loading variable is SVL, whose loading is double or more that of any other measurement. Preliminary PCA comparison of all adults and all measurements identified SVL, TrunkL, HeadW, and SnForel (ordered by loading rank) as the major loadings on the first component (PC1), and TrunkL for the second component (PC2) in adult females; PC1 explains 80% of total variance and PC2 the remaining variance. Results were similar for adult males: PC1 loading—SVL, TrunkL, UpLegL, PectW, and HindfL; PC2—TrunkL; PC1 80.6% of variance, PC2 22.4%. We used the preceding seven measurements and JawW in PC analysis to examine regional variation individually in adult females and males of the Htunwini and Irawadi samples. These four comparisons revealed no geographic structuring of either sex of each OTU (see Fig. 4A).

A PCA of adult males (n = 71) of the combined "*versicolor*" sample (n = 160) shows a segregation of the Pondicherry males from the Myanmar and Thai males (Fig. 4B). SVL is the major loading on PC1, TrunkL and HindfL on PC2, 93.6% and 3.4% of variance, respectively. Hence, the PC graph emphasizes the significantly larger bodied Pondicherry males on the PC1 axis and the similarity of body proportions on the PC2 axis. This size difference is best evaluated by minimum size at attainment of sexual maturity: males—106.7 mm SVL Pondicherry, 69.8 mm Thailand, 82.9 mm Moyingyi, 87.0 mm Nat-Ma-Taung, 67.9 mm Htunwini, and 66.4 mm Irawadi; females—89.9 mm SVL Pondicherry, 71.2 mm Thailand, 78.2 mm Moyingyi, 56.1 mm Nat-Ma-Taung, 61.3 mm Htunwini, and 64.3 mm Irawadi. The minimum mature sizes highlight the major size difference of the Pondicherry OTU in contrast to the Burmese and Thai OTUs.

Scalation.— Of the 12 scalation traits recorded, no sample displays a unique meristic aspect of scalation, i.e., unique in the sense of no or minimal overlap of one or a set of traits among the OTUs. All traits have either broad overlap or near identity of range of values (see Table 3). Although ranges overlap, four meristic traits (Dorsal, Midbody, 4FingLm, 4ToeLm) show differ-

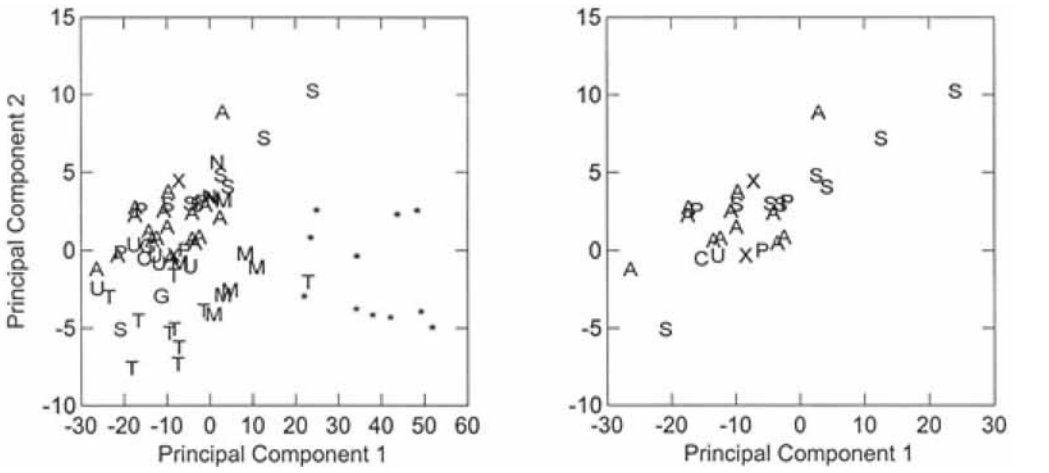

FIGURE 4. Principal components comparisons of *Calotes* "*versicolor*" samples using select mensural traits (JawW, SVL, TrunkL, PectW, SnForel, UpLegL, HindfL). Left. Adult males of the combined regional samples. Right. Adult males of the Irawadi regional samples. Abbreviations: *, Pondicherry, India; A, Alaungdaw Kathapa; C, Chatthin; G, Min-Gon-Taung; M, Moyingyi; N, Nat-Ma-Taung; P, Popa; S, Shwe-Settaw; T, eastern Thailand;. U, Shin-Ma-Taung; X, Yamethin.

ences of means among the six OTUs. Nat-Ma-Taung has the highest number of Dorsal (mean, 52.2) and Pondicherry the lowest (40.8). Table 3 shows the distribution of the Dorsal means, and a mean of the means is 48.2, confirming the outlier status of Nat-Ma-Taung. Neither of these samples displays sexual dimorphism of Dorsal or other scalation traits (Table 1). Pondicherry has the lowest Midbody meristic (42.8), and it is similarly distant from the mean of means (46.3). *Htunwini* has the lowest means for 4FingLm (16.9) and 4ToeLm (22.7), contrasting to the mean of means, 20.0 and 24.8, respectively.

Regional or intrapopulational variation can be examined only in Htunwini and Irawadi, and even in these OTUs, the data must be viewed cautiously owing to small sample sizes. For Htunwini, the means of the scalation traits for the five sample localities (Alaungdaw Kathapa, Chatthin, Popa, Shin-Ma-Taung, Shwe-Settaw) are very similar with a range of 1 or less for head scalation traits, and five or less for Dorsal and Midbody. The ranges are also small for 4FingLm (<1.5) and 4ToeL (<1.3), although the Chatthin sample is an outlier (difference > half of range) for both traits (16.4,

TABLE 3. Summary of select scalation characters in juvenile and adults of the *Calotes* "*versicolor*" samples. Character abbreviations are defined in the Appendix. Sample sizes are in parentheses.

Sample	*HeadSTr*	*Dorsal*	*Midbody*	*4FingLm*	*4ToeLm*
Htunwini (49)	12.3±1.23	47.3±4.37	47.1±2.73	16.9±1.47	22.7±1.83
	10–15	38–57	39–53	15–20	18–26
Irawadi (57)	12.1±1.24	48.9±3.92	45.6±2.22	20.2±1.52	24.9±1.46
	10–15	36–59	40–51	17–24	22–29
Nat-Ma-Taung (15)	11.7±1.10	55.2±3.91	49.4±2.67	20.6±0.91	25.9±1.60
	10–14	49–60	45–55	19–23	24–29
Moyingyi (11)	12.4±1.21	52.1±4.81	48.7±2.10	21.1±1.81	24.8±1.53
	11–15	46–61	46–53	18–24	23–28
Pondicherry (15)	12.7±1.22	40.8±3.08	42.8±2.37	21.5±1.92	26.5±1.89
	11–14	36–45	37–46	16–24	23–30
Thai-east (13)	13.2±0.80	44.9±2.22	44.6±2.47	19.5±1.39	24.0±1.08
	12–15	41–48	41–48	17–22	22–26

20.9). The uniformity of ranges and means is similar for the Irawadi samples (AK, Chatthin, Popa, Pyin-Oo-L, Shwe-S). Outlier values occur only for HeadSTr (AK, Chatthin) and Midbody (Pyin-Oo-L).

A PCA of all juveniles and adults of the combined "*versicolor*" sample shows a broad clustering (Fig. 5A; components 1 and 2) of the OTUs with no individual OTU separated by a hiatus from the other OTUs; however, internal structuring or aggregation is present. Pondicherry lizards lie largely in the upper left quadrant of the graph, overlapping somewhat with Irawadi lizards. Htunwini lizards occupy the bottom half of the cluster with little overlap with the other OTUs, and especially with minimal overlap (Fig. 5B) with sympatric Irawadi. There are four moderately strong loadings of traits on the first four components; these PCs accounts for 58, 16, 11, and 4% (= 89%) of the total variance. Dorsal and Midbody are major loading traits on PC1, 4FingLm and 4ToeLm on PC2, Midbody on PC3, and HeadSL on PC4. Thus, PCA discerns the lower values of Dorsal and Midbody for Pondicherry and similarly the low 4FingLm and 4ToeLm of Htunwini in the placement of these two OTUs in multicharacter hyperspace, that is, PC1 is a vector principally of trunk scalation and PC2 of digital lamellae.

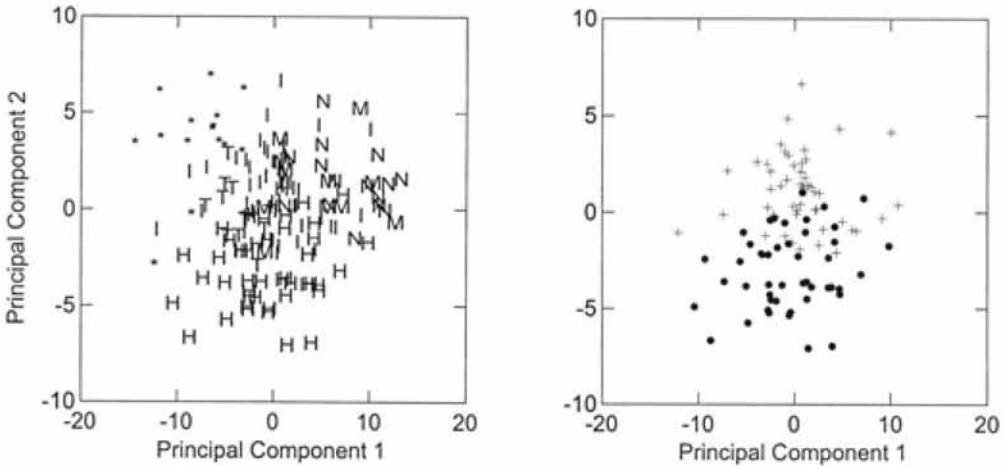

FIGURE 5. Principal components comparisons of *Calotes* "*versicolor*" samples using all scalation traits. Left. Juvenile and adult lizards of the combined regional samples. Right. Juveniles and adults of the Htunwini and Irawadi OTUs. Abbreviations: *, Pondicherry, India; H, circle, Htunwini OTU; I, +, Irawadi OTU; M, Moyingyi; N, Nat-Ma-Taung; T, eastern Thailand;.circle, H, Htunwini OTU; +, I, Irawadi OTU.

Other scalation features are less easily quantified and several of these traits are strikingly different among the "*versicolor*" OTUs examined in this study. The orientation of scales on the side of the neck and adjacent supra-axillary area is obliquely upward to vertical (Fig. 8) in all OTUs except Htunwini. Scale orientation in the latter is horizontal to slightly upward oblique. This orientation feature is confined to the cervical and supra-axillary area; posteriorly on the anterior trunk, the trunk scale orientation of Irawadi and all other "*versicolor*" lizards is obliquely upward.

Keels are variously developed on the neck, trunk, limbs, and caudal scales. Within a sample or OTU, the relative height of keels is usually equivalent in adult females and males. All OTUs share distinctly keeled caudal scales (dorsally and ventrally), although keeling seems slight to modest in Nat-Ma-Taung individuals. The extent of limb scale keeling varies among the OTUs. On the forelimb, keels are well developed on the dorsal and ventral surfaces of the upper and lower arms in Htunwini, Irawadi, Moyingyi, and Thai OTUs. Keels are similarly present on these surfaces in Nat-Ma-Taung individuals although seemingly lower than in the geographically adjacent Htunwini and

Irawadi. The relative height and their body location of keels may be sexually dimorphic in Pondicherry lizards; however, the state of preservation and the few females of our samples may have biased our observation. Adult Pondicherry females have low to modest keeling on all limb surfaces, adult males have reduced or no keeling on dorsal surface of the upper arm. For hindlimbs, the general pattern (Htunwini, Irawadi, Moyingyi, Thai, Pondicherry) is distinct keels on dorsal surface of thigh and crus, distinct keels ventrally on crus, and weak to no keels on underside of thigh. Nat-Ma-Taung individuals match the general pattern but with weaker keels. Keeling is well developed on the ventral scales, from throat to vent, of all OTUs. The strengthening of keeling on the dorsal and lateral surface of the neck and trunk is more variable. For Htunwini and Moyingyi, keels are well developed throughout. Keel height is moderate to low on these surfaces in Irawadi. Some Thai specimens match the Irawadi condition, others have no to low keels, and Pondicherry individuals have smooth dorsal scales.

Description and comparison of the dorsal crest in "*versicolor*" lizards represent a challenge. The degree of development of crest is ontogenetically and sexually variable. Adult males definitely have the strongest development of the crest in each of OTUs, but our observations suggest that crest-scale development is also affected by the hormonal or territorial status of individual males because slightly smaller adult males have less well-developed crests. Another challenge is determining the last "true" crest-scale. The anterior crest-scales are unquestionably present; however, there is a gradual transformation in shape and size diminution posteriorly. As we began data collection, we assumed that our Dorsal trait would delineate some of the differences in dorsal crests; however, it became evident quickly that Dorsal simply was a count of the number of middorsal scales from the first distinct, although short, spine to the middorsal scale above the vent. We have not yet developed a reliable means of defining where "spines" end and the first peaked middorsal scales begin. This ambiguity is reflected in the subsequent description of crest variation.

Of the six OTUs, the crest is best developed in the Pondicherry males. The crest begins with one or two short spines, then jumps to a spine with a length equal to tympanum diameter, quickly grading upward to spines of 2.5–3.0 × diameters at the rear of the neck and then gradually decreasing in length to about 0.75–1.0 × diameters at the base of the tail. The crest of adult Pondicherry females is less well-developed; the longest spines are slightly greater than tympanum diameter on the anterior neck declining to half that length on the anterior trunk, and flat middorsal scales by mid-trunk. The nature of dorsal spines in Myanmar OTUs is similar to the Pondcherry females except the crest does run with elevated spines to base of the tail in most males. The crest is modestly developed in Moyingyi males. The spines quickly reach a length of 75–100% tympanum diameter and remain a constant length to the supra-axillary and then shorten gradually to the base of the tail where the middorsal scale tips are still pointed and slightly elevated. Moyingyi females have slightly shorter spines anteriorly and largely mimic the male condition until midtrunk where the middorsal scales flatten and match the parasagittal dorsal scales in appearance. The preceding male and female patterns occur in Htunwini and Irawadi. In the former, the neck spine-lengths are less than tympanum diameter; in the latter, lengths equal the diameter. The neck spine in Irawadi are straighter and more numerous on the neck than in Htunwini (compare in Fig. 8) and other OTUs. The condition in Nat-Ma-Taung is similar to the Pondicherry lizards, although the maximum spine length never exceeds 1.5 × tympanum diameter in adult males and barely larger than a diameter in females. Thai males have a pattern like Moyingyi males, although an occasional Thai male can have one or two larger (to 2 × diam.) neck spines.

Initially, we had the impression that Htunwini lizards had somewhat larger surpaocular scales than those of Irawadi individuals. The HeadSTr trait was an attempt to quantify this difference but did not succeed. To ensure consistency in data collection, we used a transverse axis defined by ante-

rior border of the interparietal scale. Because of posterior position of the axis, it inadequately addressed the supraocular size issue. The poorly defined medial supraocular ring does not permit consistency in data-gathering. A difference in supraocular size might be a diagnostic feature; however, our current impression is that variation within the Htunwini or Irawadi OTU encompasses the variation of a combined sample. The Pondicherry, Thai, and Moyingyi samples match the preceding observation. Nat-Ma-Taung lizards appear to have the largest, hence fewer, supraoculars, but this appearance cannot be confirmed without a consistent quantitative measure.

The interparietal scale is typically the largest dorsal head scale. It is variously rectangular in shape. The shape variation in one OTU seemingly encompasses the variation in the total sample.

Calotes versicolor group members are characterized by a pair of supratympanic spines (= paroccipital spines of Moody) on each side of the head. Each spine is actually a cluster of scales with a single large center spine surrounded by lower spine-like scales. The anteriormost spine is also the dorsalmost one, lying well above the anterior half of the tympanum. The posterior spine is closer to the tympanum (3–4 scales separation) and commonly level with the posterior edge of the tympanum. The spines vary ontogenetically, becoming distinctly enlarged as an individual approaches maturity. They are also somewhat larger in adult males than in females, but this dimorphism is not great in our samples. With maturity, the basal scales become increasingly pointed and projecting. The Thai and Myanmar OTUs have modestly developed spines, their lengths half or less the maximum diameter of the tympanum. The spines in both female and male Pondicherry lizards are two-thirds or more tympanum diameter.

Coloration.— Our samples and coloration coding permit an explicit comparison of coloration differences in five OTUs. The Pondicherry sample presumably was held too long in formalin, and all specimens are a unicolor dark butterscotch brown. The quantification of coloration traits (Table 4) reveals that each OTU has a unique set of traits and that most adult females and males can be distinguish from each other in each OTU (except Thailand). This sexual differentiation is often not statistically significant (hence unreported above) when examining single color traits but is functional when using sets of traits. For example, Htunwini females (adult) regularly have ForearSt, NucSpot, TrnkBand, and MidvLine, which occur less frequently in males. Irawadi females typically lack CheekCol and have DorsSt and TrnkBand, the opposite condition in males. Nat-Ma-Taung males lack DorsSt and ForearSt, and these traits are almost always present in females. Moyingyi males regularly have CheekCol and ThroatPa, which are absent in females.

Geographic variation in coloration among Htunwini and Irawadi sample-localities cannot be accurately assessed owing to low numbers of adults at most localities. Possibly, Alaungdaw-Kathapa male Irawadi have darker and more frequent CheekCol than other Irawadi populations. No other regional coloration differences were noted in other Irawadi populations or in any Htunwini populations.

Amongst the OTUs, the Thai sample is the most readily differentiated. No Thai adults have DorsSt, ForearSt, NucSpot, ThroatPa, and TrunkSt; most adults have CheekCol. Except for Htunwini, males commonly have CheekCol; however, the intensity and size seemingly varies among the OTUs. Htunwini females and males also have reduced ThroatSt and TrunkSt. In contrast, Irawadi, Nat-Ma-T, and Moyingyi adults almost always have ThroatSt, and roughly half of the adult Irawadi and Nat-Ma-T females have TrunkSt.

Morphological differentiation.— We noted in the introduction that we recognized two genetically distinct "*versicolor*" lizards at Chatthin. The preceding genetic and morphological analyses confirm the distinctiveness of these lizards and demonstrate that the two lizards co-occur broadly throughout Myanmar's Central Dry Zone. These analyses also demonstrate the presence of other populations of "*versicolor*" lizards, representing distinct lineages.

TABLE 4. Summary of occurrence of color traits in adults of the *Calotes* "*versicolor*" samples. Character abbreviations are defined in the Appendix. Sample sizes are in parentheses. All values are percent present.

Sample	*CheekCol*	*DorsSt*	*ForearSt*	*NucSpot*	*TrnkBand*	*MidvLine*	*ThroatSt*	*ThroatPa*	*TrunkSt*
Htunwini									
F (14)	0	64	57	93	86	100	29	14	14
M (11)	0	73	18	64	45	64	9	0	0
Irawadi									
F (14)	7	50	78	86	100	93	100	29	50
M (30)	50	20	67	60	43	90	100	3	40
Nat-Ma-Taung									
F (5)	60	80	100	80	100	100	100	0	40
M (3)	67	0	0	100	67	67	100	0	0
Moyingyi									
F (3)	0	67	100	100	100	100	100	0	0
M (7)	86	43	86	100	43	100	86	57	0
Thai-east									
F (2)	100	0	0	0	100	50	100	0	0
M (10)	60	0	0	0	100	50	100	0	0

A variety of morphological traits allows us to differentiate these lineages. Briefly those traits are: 1) body size at sexual maturity and degree of sexual dimorphism of adults; 2) Dorsal, Midbody, 4FingLm, and 4ToeLm of scalation; and 3) a variety of coloration traits. Because our study focuses on the Central Dry Zone "*versicolor*", these two species are described below. A subsequent study will examine the more "peripheral" populations in the bordering mountain ranges and the coastal/southern populations from Rakhine to Mon State.

SPECIES DESCRIPTIONS

Calotes htunwini Zug and Vindum, sp. nov.

Figs. 6–8.

HOLOTYPE.— USNM 524044, an adult female from MYANMAR: **Sagaing Division**, Chatthin Wildlife Sanctuary, San Myaung Camp (23°34′27.6″N, 95°44′15.6″E; ca. 110 m), approx. 2 km WNW of Chatthin, collected by Htun Win, 22 May 1998.

PARATYPES.— MYANMAR: **Sagaing Division**, Alaungdaw Kathapa National Park CAS 215741, USNM 562980; Chatthin Wildlife Sanctuary CAS 231832, USNM 520545, 524045, 562967–968; Kabaing CAS 215811; Mintaingbin CAS 215368; Yin Ma Bin CAS 215347–348, 215448, 215457–458, USNM 562981; **Magway Division**, Shwe-Settaw Wildlife Sanctuary CAS 213607, 213620, 213741, 213786, 213789, USNM 562974–975.

DIAGNOSIS.— *Calotes htunwini* is a member of the *C. versicolor* species group and differs from all other members of this group by the horizontal orientation of the scale-rows on the side of the neck and adjacent supra-axillary area; scale-row orientation in the other *C. versicolor* members is obliquely posteriorad or vertical. Further, it differs from the sympatric *C. irawadi* by its slightly smaller adult body size (means 69.9, 78.5 mm SVL; female, male respectively), fewer 4FingLm (mean 16.9), absence of CheekCol, and infrequent presence of ThroatSt.

ETYMOLOGY.— We name this species in fond memory of Htun Win and to honor him for his contribution to Burmese herpetology. Htun Win grew up in Chatthin village and joined the Chatthin Wildlife Sanctuary in January 1993 as a day-worker and was appointed as a NWCD forester in January 1995. He began his herpetological work as the team leader of GZ's Chatthin W.S. herpetofauna monitoring-inventory project in August 1997 and then became the leader of our CAS-

NWCD-SI Herpetological Survey team in November 1999. His commitment to our survey project and his expanding knowledge of the Burmese herpetofauna were major factors for the success of the survey. He became ill while surveying the herpetofauna of Kachin State and died in June 2004. The epithet is proposed as a noun in apposition.

DESCRIPTION OF HOLOTYPE.— An adult female of 64.0 mm SVL, 22.2 mm SnForel, 33.8 mm TrunkL, 135 mm TailL (about ⅛ tip regenerated, tail now in 2 pieces), 6.4 mm TailH, 5.6 mm TailW, 9.1 mm PectW, 11.2 mm UpArmL, 11.0 mm LoArmL, 10.2 mm ForefL, 6.8 mm 4FingLng, 13.5 mm UpLegL, 12.8 mm CrusL, 18.2 mm HindfL, and 9.5 mm 4ToeLng. Head pentagonal (dorsal outline) covered largely with small, mostly smooth scales slightly overlapping; 14.7 mm HeadL, 10.3 mm HeadW, 10.0 mm JawW, 12.1 mm HeadH, 6.6 mm SnEye, 3.5 mm NarEye, 3.7 mm EyeEar, 4.6 mm SnW, and 6.7 mm InterOrb.

Head distinct from neck; snout to eye broadly acute and triangular, snout-tip blunt; head behind eyes with edges slightly bowed outward by jaw muscles but edges largely parallel; sides of head flat, descending perpendicular downward from sharp canthus rostralis and supraciliary edge to lips, posterior to eye slightly rotund; eyes, slightly protruding, just barely extending beyond canthus-supraciliary border; chin and throat generally flat. Dorsal head scales (Fig.7) variably sized and smooth surfaced, most equivalent in size to dorsal trunk scales; no distinct plates, rostral equivalent to supralabials in height above lip with 7 SnS; 8/8 (left/right) elongate and sharply folded CanthR, scales somewhat enlarged in supraocular area but not forming distinct supraocular plates; 13 HeadSL and 12 HeadSTr; posteriorly slightly enlarged, irregularly diamond-shaped interparietal with distinct medial parietal eye. Laterally head with single large nasal scale on each side abutting rostral and perforated by large naris; loreal and preocular area with small scales, those above supralabials arranged in two parallel longitudinal rows extending to posterior margin of orbit; 11/11 Suplab; eye covered with "sock" of small, nearly granular-sized scales and opening border by double row of eyelid scales, outermost row of ridged scales, inner row smooth and flat 12/13 Eyelid; postocular and temporal scales modest sized, smooth laterally and lightly keeled dorsolaterally; tympanum large (subequal eye-opening diameter) and naked; pair of spines or spine-clusters in supratympanum area, anterior one dorsolaterally directly above anterior half of tympanum separated by 6 scales, posterior one level with posterior edge of tympanum separated by 3 scales, a single narrow, dagger-like scale (length about ⅛ tympanum maximum diameter) projecting upward; 10/11 rectangular Inflab along mouth margin, bordered below by 3–4 rows of narrow and elongate, longitudinally arranged smooth scales; medially the chin throat scales triangular and strongly keeled; single median pentagonal mental scale between left and right Suplab.

Trunk scalation generally keeled dorsally and laterally; middorsal crest of elongate scales, occiput origin separated from interparietal by 3 rows of dorsal scales, dorsal spine-scales relatively small (lengths about 1.5 × length of adjacent parasagittal scales) and first 5–6 more equilateral-triangular than spine-like, length of crest-scales decreasing by midneck and flattened like adjacent dorsal scales by anterior trunk; 49 Dorsal, 48 Midbody; all trunk scales keeled, increasing in size from neck onto trunk, neck and supra-axillary scales horizontal (Fig. 8) with orientation gradually shifting diagonally upward although not near-vertical; dorsal trunk scales large and subequal ventral trunk scales; preaxillary scales modest sized and most smooth; ventral scales large and uniform sized from throat to vent and strongly keeled.

Limbs with modest to large scales, all keeled; fingers (21/21 4FingLm) and toes (27/28 4ToeLm) each with 3–4 modestly keeled scales dorsally and strongly bicarinate lamellae ventrally; claws long, thin and sharply pointed on all digits. Tail scalation similar to trunk with progressive loss of scale rows distally.

Coloration in preservation beige to light tan background dorsally and laterally; head scales

FIGURE 6. *Calotes htunwini* in life. Upper. Holotype, adult female [USNM 524044] – Chatthin (photographed by G. Zug). Left Paratype, adult female [USNM 524045] – Chatthin (G. Zug). Right. Paratype, subadult male [USNM 562997] – Shwe-Settaw (G. Zug).

speckled with dark brown dorsally; pair of dark brown, cream-centered nuchal spots, one on each side of posterior border of interparietal scale and not contacting one another; 4 dark brown line radiating posteriorly and ventrally from the orbit. Indistinct and discontinuous middorsal light line, broader dorsolateral light stripes also discontinuous; eight dark brown dorsal blotches cleft by light middorsal line and edged laterally by the dorsolateral light stripe on each side, each of the blotches separated front and behind by narrow light bar, which extends onto sides of trunk; 1 blotch on neck, 6 on trunk, and smaller and narrower onto tail base; laterally neck dark above and lighter below, trunk similar except generally darker. Fore- and hindlimbs banded, narrow light edges define

broader dark bands; banding lighter on forelimb in contrast to darker, more distinct banding on hindlimb; pale stripe along posterior margin of crus. Ventrally dusky beige with faded palmate dark striping on throat (ThroatSt) and faded dark midventral stripe on trunk (MidvLine). In life (Fig. 6), colors brighter and bolder; distinct orange to rufous tint on top and side of head, dorsally on neck and anterior trunk; ventrally white with beige tint and brown markings, throat faded orange.

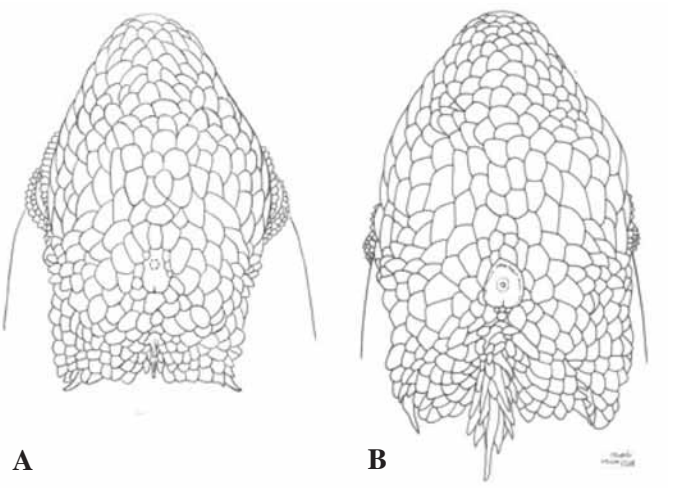

FIGURE 7. Dorsal view of the top of the head of (A) *Calotes htunwini* (USNM 5240440) and (B) *Calotes irawadi* (USNM 520543). Drawn by Molly Dwyer Griffin, 2005.

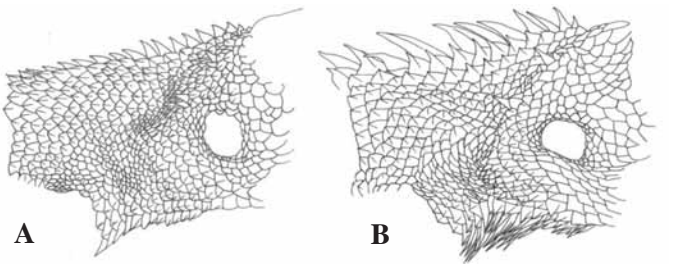

FIGURE 8. Lateral view of the side of the neck and shoulder of (A) *Calotes htunwini* (USNM 5240440) and (B) *Calotes irawadi* (USNM 520543). Drawn by Molly Dwyer Griffin, 2005.

VARIATION OF PARATYPES.— The paratypic series contains 7 adult females, 4 adult males, and 15 juveniles. The juveniles range in SVL from 34.5 to 75.7. The adult females range in SVL from 61.3 to 84.3 mm (mean, 69.6). Means for the females other measurements (all in mm) are: TrunkL 34.5; TailL 152; TailH 7.3; TailW 7.4; PecW 11.4; PelvW 7.4; SnForeL 25.0; UpArmL 13.7; LoArmL 12.3; ForefL 12.6; 4FingLng 8.2; UpLegL 15.6; CrusL 15.8; HindfL 21.1; 4ToeLng 11.5; HeadL 16.6; HeadW 13.4; JawW 11.7; HeadH 13.3; SnEye 6.8; Nareye 3.6; EyeEar 3.9; SnW 4.7; Interorb 8.5. The adult males range in SVL from 71.6 to 91.4 mm (mean, 81.4). Means for the males other measurements (all in mm) are: TrunkL 39.6; TailL 148.6; TailH 11.8; TailW 10.9; PecW 14.9; PelvW 8.2; SnForeL 28.8; UpArmL 15.5; LoArmL14.1; ForefL 14.0; 4FingLng 9.3; UpLegL 18.3; CrusL 18.3; HindfL 25.1; 4ToeLng 14.2; HeadL 19.9; HeadW 17.8; JawW 14.0; HeadH 13.3; SnEye 5.3; Nareye 4.2; EyeEar 5.1; SnW 5.3; Interorb 10.0.

Means for scalation traits for the entire paratypic sample is: SnS 6.7; HeadSTr 12.3; HeadSL 14.1; Canthr 8.0; EyeLd 11.2; Suplab 11.1; Inflab 10.1; TempSp 2.0; Dorsal 48.1; Midbody 47.4; 4FingLm 17.0; 4ToeLm 22.5.

Coloration in adults has a few sexual dimorphic aspects: MidvLine present in all females and half of the males; ForearSt in half of females and in no males. Both sexes lack ThroatPa and CheekCo, and TrunkSt are regularly absent. NucSpot occurs in most adults.

DISTRIBUTION AND NATURAL HISTORY.— *Calotes htunwini* occurs throughout the lower elevations of Myanmar's Central Dry Zone (Fig. 9). It is represented by vouchers from Chatthin W.S. southward to Shwe-Settaw W.S. and from Alaungdaw Kathapa N.P. eastward to the base of the Shan Plateau in the vicinity of Mandalay. Our field notes indicate that *C. htunwini* is a forest lizard.

At Chatthin, it occurs within the indaing forest. At Shwe-Settaw, it co-occurs with *C. irawadi* in the scrubby woodland bordering the Namada River. It was also found along a dry forest stream in the center of of the Shwe-Settaw reserve. At Popa and AK, the field notes are inadequate to differentiate between in forest and roadside-agricultural habitats. All the preceding forest records are of open forest, commonly with a scattered grass understory.

***Calotes irawadi* Zug, Brown, Schulte, and Vindum, sp. nov.**
Fig. 7–8, 10

Holotype.— USNM 520543, an adult male from Myanmar: **Sagaing Division**, Chatthin Wildlife Sanctuary, San Myaung Camp (23°34′27.6″N, 95°44′15.6″E; ca. 110 m), approx. 2 km WNW of Chatthin by local collector, 17 July 1997.

Paratypes.— Myanmar: **Sagaing Division**, Alaungdaw Kathapa National Park CAS 215535, 215641, 215709, USNM 562986–990, 562993; Chatthin Wildlife Sanctuary CAS 231833, USNM 520546, 524043, 562994; Kabaing CAS 215787; Khim Aye CAS 215423, 215426–429, USNM 562991–992. Magway Divis., Le Kaing CAS 213663, 213685, 213726–727; Shwe-Settaw Wildlife Sanctuary CAS 213865, 213891, 213899 USNM 562997–999; **Mandalay Division**, Popa Mountain Park USNM 562995-996.

Diagnosis.— *Calotes irawadi* is a member of the *versicolor* species group and shares the obliquely posteriorad or vertical scale-row orientation on the neck and adjacent supra-axillary area with all other *versicolor* group members except *C. htunwini*. It differs from *C. versicolor* (Pondicherry population) by a much smaller body size (female, male means 77.4, 82.4 mm SVL vs. 93 mm, 119 mm, respectively), and more Dorsal (means 48.9 vs. 40.8) and Midbody (47.1 vs 42.8).

Middorsal crest scales in *C. irawadi* are smaller (equal to tympanum diameter) and are straighter and more numerous than *C. versicolor* (Pondicherry) with crest scales to 2.5–3.0 × diameter of tympanum. Lengths of supratympanic spines in *C. irawadi* are half or less the diameter of tympanum and ⅔ or more tympanum diameter in *C. versicolor* (Pondicherry). *C. irawadi* averages smaller than Moyingyi and Nat-Ma-Taung "*versicolor*" and has fewer Dorsal. It differs from eastern Thailand "*versicolor*" by more Dorsal and in coloration by the usual presence of DorsalSt and NucSpot.

Etymology.— Irawadi is a variant spelling of Ayeyarwaddy and is used as a noun in apposition. Our use of Irawadi refers to the broad distribution of this species in the central portion of the Ayeyarwaddy River basin.

Description of holotype.— An adult male of 75.7 mm SVL, 28.0 mm SnForel, 36.7 mm TrunkL, 218 mm TailL (entire), 10.0 mm TailH, 9.4 mm TailW, 10.9 mm PectW, 14.9 mm UpArmL, 14.5 mm LoArmL, 14.6 mm ForefL, 9.7 mm 4FingLng, 20.3 mm UpLegL, 19.0 mm CrusL, 27.3 mm HindfL, and 15.9 mm 4ToeLng. Head pentagonal (dorsal outline) covered largely with small, mostly smooth scales slightly overlapping; 17.9 mm HeadL, 15.5 mm HeadW, 12.8 mm JawW, 14.0 mm HeadH, 7.6 mm SnEye, 3.7 mm NarEye, 4.5 mm EyeEar, 4.6 mm SnW, and 8.4 mm InterOrb.

Head distinct from neck; snout to eye broadly acute and triangular, snout-tip blunt; head behind eyes with edges slightly bowed outward by jaw muscles but edges largely parallel; sides of head flat, descending perpendicular downward from sharp canthus rostralis and supraciliary edge to lips, posterior to eye slightly rotund; eyes, slightly protruding, just barely extending beyond canthus-supraciliary border; chin and throat generally flat. Dorsally head scales (Fig.7) variably sized and smooth surfaced, most equivalent in size to dorsal trunk scales; no distinct plates, rostral equivalent to supralabials in height above lip with 7 SnS; 7/8 (left/right) elongate and sharply folded CanthR, scales somewhat enlarged in supraocular area but not forming distinct supraocular plates, 16 HeadSL and 15 HeadSTr, posteriorly slightly enlarged; irregularly bell-shaped interparietal with distinct medial parietal eye. Laterally head with single large nasal scale on each side abutting ros-

tral and perforated by large naris; loreal and preocular area with small scales, those above supralabials arranged in two parallel longitudinal rows extending to posterior margin of orbit; 11/10 Suplab; eye covered with "sock" of small, nearly granular-sized scales and opening border by double row of eyelid scales, outermost row of pyramidal scales, inner row smooth and flat 13/15 Eyelid; postocular and temporal scales modest to small, smooth laterally and dorsolaterally; tympanum large (subequal eye-opening diameter) and naked; pair of spines or clusters in supratympanum area, anterior one dorsolaterally directly above anterior half of tympanum separated by 5–6 scale rows, posterior one level with posterior edge of tympanum separated by 3 scale rows, a single narrow, spine-like scale (length about ¼ tympanum maximum diameter) projecting upward; 10/10 rectangular Inflab along mouth margin, bordered below by 3–4 rows of narrow and elongate, longitudinally arranged smooth scales; medially the chin throat scales triangular and smooth to lightly keeled; single median triangular mental scale between left and right 1st supralabials and barely larger than them.

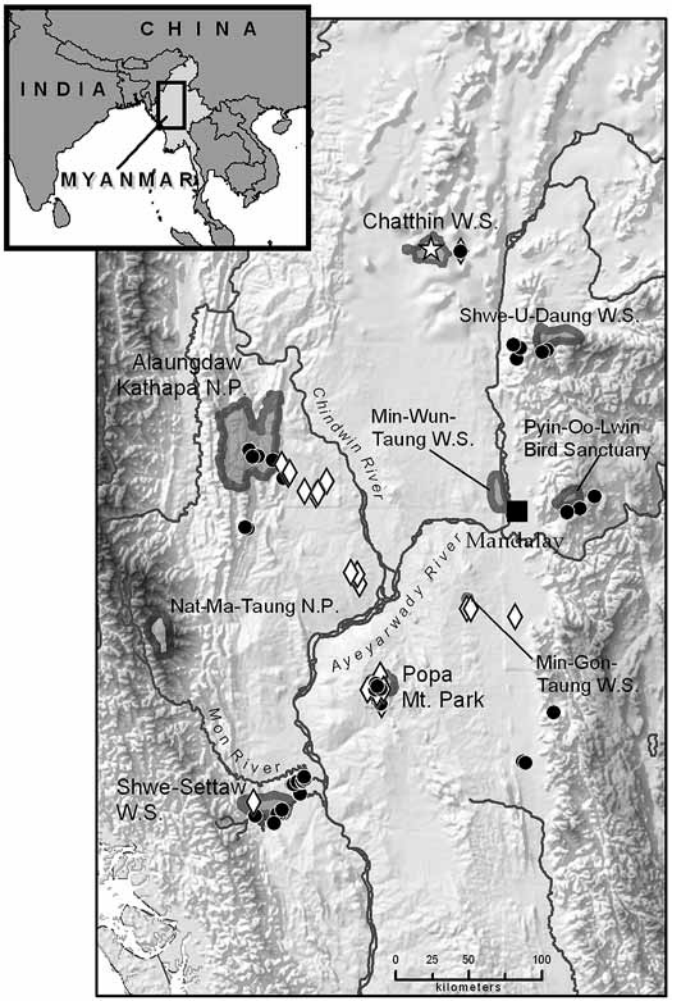

FIGURE 9. Geographic occurrence of *Calotes htunwini* and *Calotes irawadi* in the central dry zone of Myanmar. Symbols: star, type locality of both species, Chatthin Wildlife Sanctuary; solid circle, *Calotes htunwini*; diamond, *Calotes irawadi.* Map produced by Michelle Koo.

Trunk scalation generally keeled (moderately) dorsally and laterally; middorsal crest of elongate scales, occiput origin separated from interparietal by 2 rows of dorsal scales, dorsal spine-scales of moderate length (2–3 × length of adjacent parasagittal scales; midneck ones nearly equal maximum tympanum diameter) and blade-like, laterally compressed to supra-axillary as their lengths visibly decline, becoming more keeled scale-like but retaining projecting and hooked median tip to the base of the tail although flatten like adjacent dorsal scales; 49 Dorsal, 48 Midbody; all trunk scales keeled, weakly so on ventrolateral half of neck and trunk, keel and scale orientation diagonally upward from neck and supra-axillary area (Fig. 8) to base of tail, nearly vertical on anterodorsal surface of neck; preaxillary scales modest sized and most smooth; ventral scales large and uniform sized from throat to vent and strongly keeled.

Limbs with modest to large scales, all keeled; fingers (21/21 4FingLm) and toes (27/28 4ToeLm) each with 3–4 modestly keeled scales dorsally and strongly bicarinate lamellae ventrally; claws long, thin and sharply pointed on all digits. Tail scalation similar to trunk although more strongly keeled with progressive loss of scale rows distally.

Coloration in preservation dusky tan background dorsally and laterally; head scales speckled with dark brown dorsally; pair of dark brown nuchal spots, one on each posterolateral edge of interparietal scale and not contacting one another; 2 faded dark brown lines radiating posteroventrally from the orbit; dusky brown cheek patch (CheekCol). Indistinct small brown dorsal blotches across middorsal crest; none on neck, 6 on trunk, and darker, broader as regular bands on tail; laterally neck light above and dark below, trunk ground color mute brown throughout. Fore- and hindlimbs banded, narrow light defining broader dark bands; banding faded but distinct on fore- and hindlimb; faded pale stripe along posterior margin of crus. Ventrally light dusky beige with strongly faded palmate striping on throat (ThroatSt) and barely visible dark midventral stripe on trunk (MidvLine). In life (not photographed), brief color notes: "dorsum bronzy brown, ear drum and shoulder spot light green."

Variation of paratypes.— The paratypic series contains 5 adult females, 21 adult males, and 7 juveniles. The juveniles range in SVL from 41.9 to 81.5mm. The adult females range in SVL from 64.3 to 77.9 mm (mean, 71.6). Means for the females other measurements (all in mm) are: TrunkL 38.5; TailL 203.0; TailH 6.8; TailW 6.7; PecW 11.6; PelvW 7.4; SnForeL 23.4; UpArmL 14.1; LoArmL 13.2; ForefL 13.7; 4FingLng 9.7; UpLegL 16.9; CrusL 17.1; HindfL 23.8; 4ToeLng 13.8; HeadL 16.6; HeadW 13.6; JawW 11.8; HeadH 12.1; SnEye 7.5; Nareye 4.0; EyeEar 4.0; SnW 4.9; Interorb 8.0. The adult males range in SVL from 66.4 to 106.8 mm (mean, 83.3). Means for the males other measurements (all in mm) are: TrunkL 42.1; TailL 231.5; TailH 10.2; TailW 9.8; PecW 14.9; PelvW 8.6; SnForeL 29.3; UpArmL 17.1; LoArmL 15.8; ForefL 14.9; 4FingLng 10.7; UpLegL 20.1; CrusL 19.3; HindfL 26.5; 4ToeLng 16.1; HeadL 20.3; HeadW 19.6; JawW 16.3; HeadH 15.1; SnEye 8.6; Nareye 4.3; EyeEar 5.9; SnW 5.4; Interorb 9.5.

Means for scalation traits for the entire paratypic sample are: SnS 6.8; HeadSTr 12.3; HeadSL 14.3; Canthr 7.9; EyeLd 12.5; Suplab 10.9; Inflab 10.4; TempSp 2.0; Dorsal 48.4; Midbody 45.0; 4FingLm 20.1; 4ToeLm 24.8.

Coloration (Fig. 10) in adults shows no "either/or" sexual dimorphism. NucSpot is present in all females and only half of the males. Similarly ForeArSt is present in all females and ⅔ of males; TrunkSt is absent in half of females, ⅔ of males; and DorsSt is absent in most males and half of females. MidvLine is usually present in both sexes, ThroatSt always present, and ThroatPa commonly absent in both.

Distribution and natural history.— Of the two new taxa, *Calotes irawadi* has the broadest occurrence in Myanmar's Central Dry Zone (Fig. 9). It is represented by vouchers from Chatthin W.S. southward to Shwe-Settaw W.S. and from mid-elevations at Alaungdaw Kathapa N.P. eastward to edge of the Shan Plateau at Pyin-Oo-Lwin (approx. 1000 m elevation). Field observations indicate that *C. irawadi* is an open-forest lizard but also persists in fence-row habitats and cut-over woodland. Where it co-occurs with *C. htunwini* at Shwe-Settaw, the "forested" habitat is patches of secondary growth scrub <maximum tree height to 10 m> intermixed with small garden-field plots, and here it was found equally in both the forest and agricultural lands. At AK *C. irawadi* occurred mainly in forest habitats, at Popa in gardens and in the second-growth scrub adjacent to the more densely forested mountain-sides.

FIGURE 10. *Calotes irawadi* in life. Upper. Holotype, adult male [USNM 520543] – Chatthin (G. Zug). Left. Paratype, subadult male [USNM 562997] – Shwe-Settaw (G. Zug).Right. adult female [USNM 563004] – Pyin-Oo-Lwin (G. Zug).

Biogeographic Comments on Burmese Calotes

Geologically, Myanmar consists of several Gondwanan blocks that sequentially collided with the southeastern edge of the Laurasian plate beginning in the mid to late Triassic. The Sinoburmalayan (Sibumasu) block with smaller Gondwanan terranes moved "northeastward" closing the Mesotethys Sea and then collided with the Asian plate in the Late Cretaceous. This second collision produced the first stage of mountain building of the Sinoburman Range. The Burman plate collided with the southern edge of Sinoburmalayan block and continues to slide northward along the contact zone. This collision resulted in further mountain building and the initial uplift of the Shan Plateau on the Sinoburmalayan block. The collision of the Indian plate with the Eurasian plate at the end of the Early Eocene and its subsequent subduction beneath the Burman plate (late Miocene) initiated the building of the Indoburman Range and the isolation of the central lowlands of Myanmar from those of Indian and Indochina (Bender 1983; Hutchinson 1989; Hall 1998; Metcalfe 1998).

Acrodont lizard clades (Agamidae and Chamaeleonidae) are tightly associated with the Gondwanan tectonic plates (Macey et al. 2000). Of the three acrodont clades of Southeast Asia, two (the *Leiolepis* and *Hydrosaurus* clades) are hypothesized as faunal components of Gondwanan plates that joined Asia between 65 and 120 MYBP (Macey et al. 2000). The draconine clade (see Fig. 3) either entered Asia from the Indian plate (ca. 20 MYBP) or from an earlier terrane accretion; however, Macey et al. (2000) were unable to delimit the origin of the Draconinae as Southeast Asian or Indian. Our genetic data do not address the draconine origin question or whether *Calotes* arose in India or Southeast Asia. The data do demonstrate that the *Calotes versicolor* group has distinct Indian and Southeast Asian branches. We cannot address the origins of these two branches or when they arrived in Burma, because the data of phylogenetic relationships and estimates of branching age among the various *C. versicolor* populations and species are still too incomplete.

The central lowlands of Myanmar (the Central Dry Zone) is a distinct climatic zone, created by the previously mentioned mountain building. The Central Dry Zone and its flora and fauna had gained its isolation and likely its strong seasonal aridity by, at least, the Late Miocene. Falling and rising sea-levels during the Pleistocene (embayment to Mandalay at least once during this period) regularly changed the landscape of the central Ayeyarwaddy River Valley. Exactly how these briefly described geological events affected the dispersal and isolation of the biota remains unknown. Our growing knowledge of the biodiversity of this central valley attests to major landscape changes producing multiple isolation events and opportunities for differentiation and speciation.

Reporting the discovery of *Naja mandalayensis*, Slowinski and Wüster (2000:269) noted "likely that additional field work will reveal that the central dry zone is a [*sic*] area of significant herpetological endemism." Field and laboratory studies are demonstrating that this central dryland and adjacent foothills have a more species-rich herpetofauna and more

TABLE 5. Amphibians and reptiles confined to the Central Dry Zone of Myanmar. Herein, this zone is the area between 19.5°to 24.5°N and elevations below 1000 m.

Amphibia
Microhylidae
Microhyla sp-miniature
Ranidae
Fejervarya limnocharis complex sp
Reptilia
Agamidae
Calotes htunwini
Calotes irawadi
Liolepis peguensis
Gekkonidae
Cyrtodactylus brevidactylus
Cyrtodactylus chrysopylos
Colubridae
Oligodon splendidus
Elapidae
Bungarus magnimaculatus
Naja mandalayensis

endemics (Table 5) than previously reported. Much of the evidence for this endemicity remains unpublished, although some reports are in various stages of analysis and writing. For example, our surveys regularly reveal that most areas have two sympatric *Fejervarya limnocharis* group frogs, either a large and medium-sized frog pair or a medium-sized and small frog pair. A miniature *Microhyla* sp. occurs at least from Chatthin to Mandalay. These taxa, along with *Calotes htunwini*, *C. irawadi*, and *N. mandalayensis* highlight the Central Dry Zone as a center of speciation and, further, suggest the ability of this herpetofauna to withstand major human perturbations, because all of preceding taxa are found in paddies and other human-disturbed habitats as well as fragments of natural habitats.

A historical explanation is not presently available to offer a sequence of isolation events to permit regional differentiation and eventual speciation in this area. We doubt that the various embayments of the Pleistocene offer an appropriate isolation mechanism. We have not found any detailed geologic histories of central Burma that might offer clues to a landscape history with the appearance and disappearance of habitat islands for biotic differentiation. The present dry zone is not floristically uniform. It contains three major forest types and a Euphorbia semi-desert in its center (Kress et al. 2003). Our data on the habitat occurrence of *Calotes htunwini* and *C. irawadi* are not sufficiently precise to identify the habitat preference or restriction of these two species, but the broad dry zone distribution of both shows that they occupy a variety of forests within the broader classification of mixed deciduous and dry forest.

On a broader scale, the phylogenetic hypothesis generated herein and preliminary unpublished data show these newly recognized species represent different evolutionary lineages. *Calotes htunwini* and its ancestor represent an early branching within the *C. versicolor* group with affinities to Indian species and populations. *Calotes irawadi* is more closely allied with populations of *C.* "*versicolor*" from Myanmar and East Asia, i.e., China, Cambodia, Laos, and Vietnam (Schulte, Stuart, and Bauer, unpublished data). That these two species share a similar distribution indicates that their ancestors were likely central Burma residents and shared the same history of geographic isolation.

Key to Myanmar[6] *Calotes*

1. Scales on side of trunk obliquely upward. 2
1. Scales on side of trunk obliquely downward. . . . . *C. kingdonwardi*

2. Crescent-shaped patch of small granular scales in front of forelimb insertion 6
2. No patch of granular scales in front of forelimb insertion; this preaxillary area with moderate to large scales (*C. versicolor* group). 3

3. Scales on side of neck and adjacent shoulder area horizontal; keels on these scales modestly to strongly developed . . . . . *C. htunwini* sp. nov.
3. Scales on side of neck and adjacent shoulder area obliquely upward; keels on these scales weakly to strongly developed 4

4. Females and males sexually mature at SVL of 78 mm or larger; adult females and male without diagonal dark stripes on chest and belly . . . . . Yangon-Moyinge OTU
4. Females and males sexually mature at SVL of 60 mm or larger; some adults with diagonal dark stripes on chest and belly 5

5. Adults with narrow dorsal bars middorsally, bars often offset on opposite sides of dorsal crest . . . . . *C. irawadi* sp. nov.

[6] For *C. versicolor* group from central Myanmar, 16°N to 24°N.

5. Adults with broad dorsal bars middorsally, bars commonly congruent on opposite sides of dorsal crest . . . . . Nat-Ma-Taung OTU

6. Two parallel rows of compressed scales above tympanum . . . . . *C. jerdoni*
6. No parallel rows of compressed scales above tympanum 7

7. Large postorbital spine present. . . . . *C. emma*
7. No postorbital spine 8

8. Midbody scale rows 47-57, tail not swollen posterior to base in males . . . . . *C. mystaceus*
8. Midbody scale rows 59-74, tail swollen posterior to base in males. . . . . *C. chincollium*

Acknowledgments

The Myanmar Herpetological Survey is a country-wide species inventory designed to uncover the full diversity of the Burmese herpetofauna by surveying broadly but focusing on the forest and wildlife reserves of the Myanmar Forestry Department, Ministry of Forestry. The Survey owes it success to the administrative and logistic support of U Shwe Kyaw, Director General, Forestry Department, and U Khin Maung Zaw, Director, and U Tin Tun, Deputy Director, of the Nature and Wildlife Conservation Division (NWCD, Forestry Dept.), and critically to the NWCD staff (U Htun Win, Daw Thin Thin, U Kyi Soe Lwin, U Awan Khwi Shein, U San Lwin Oo, Sai Wunna Kyi) who have been the core of our survey team. The Survey is a collaborative effort among the staff of NWCD, the California Academy of Sciences, and the Smithsonian's National Museum of Natural History (SI-NMNH). The latter two institutions have provided a variety of administrative and financial support. We thank all the above individuals and institutions for their past and ongoing support.

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Literature Cited

Anderson, S., A.T. Bankier, and I.G. Young. 1981. Sequence and organization of the human mitochondrial genome. *Nature* 290:457–465.

Auffenberg, W., and H. Rehman. 1993. Studies on Pakistan reptiles. Pt. 3. *Calotes versicolor*. *Asiatic Herpetological Research* 5:14–30.

Auffenberg, W., and H. Rehman. 1995. *Calotes versicolor nigrigularis* Auffenberg and Rehman 1993 a junior primary homonym. *Asiatic Herpetological Research* 6:27.

Bender, F. 1983. *Geology of Burma*. Gebrüder Borntraeger, Berlin, Germany. 293 pp.

BREMER, K. 1994. Branch support and tree stability. *Cladistics* 10:295–304.

DAUDIN, F.M. 1802. *Histoire Naturelle, Génerale et Pariculierère des Reptiles*; Ouvvrage . . . Société savantes. Tome Troisième. F. Dufar, Paris. 452 pp.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

FELSENSTEIN, J., AND H. KISHINO. 1993. Is there something wrong with the bootstrap on phylogenies? A reply to Hillis and Bull. *Systematic Biology* 42:193–200.

HALL, R. 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. Pages 99–131 *in* R. Hall and J.D. Holloway, eds., *Biogeography and Geological Evolution of SE Asia*. Backhuys Publ., Leiden, Netherlands.

HALLERMANN, J. 2005. A taxonomic review of the genus *Bronchocela* (Squamata: Agamidae), with description of a new species from Vietnam. *Russian Journal of Herpetology* 12:167–182.

HALLERMANN, J., AND W. BÖHME. 2000. A review of the genus *Pseudocalotes* (Sauria: Agamidae), with description of a new species from West Malaysia. *Amphibia-Reptilia* 21:193–210.

HUTCHISON, C.S. 1989. *Geological Evolution of South-East Asia*. Clarendon Press, Oxford, UK. xv + 368 pp.

KÄSTLE, W. 2002. Family Agamidae (agamids). Pages 575–670 *in* H.H. Schleich and W. Kästle, eds., *Amphibians and Reptiles of Nepal*. Biology, Systematics, Field Guide. A.R.G. Gantner Verlag Kommanditgesellschaft, Ruggell, Germany.

KRESS, W.J., R.A. DEFILIPPS, E. FARR, AND YIN YIN KYI. 2003. *A Checklist of the Trees, Shrubs, Herbs, and Climbers of Myanmar*. Contribution from the United States National Herbarium, vol. 45. Washington, D.C., USA. 590 pp.

KUMAZAWA, Y., AND M. NISHIDA.1993. Sequence evolution of mitochondrial tRNA genes and deep-branch animal phylogenetics. *Journal of Molecular Evolution* 37:380–398.

MACEY, J.R., A. LARSON, N.B. ANANJEVA, Z. FANG, AND T.J. PAPENFUSS. 1997. Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution* 14:91–104.

MACEY, J.R., J.A. SCHULTE II, A. LARSON, Z. FANG, Y. WANG, B.S. TUNIYEV, AND T.J. PAPENFUSS. 1998. Phylogenetic relationships of toads in the *Bufo bufo* species group from the eastern escarpment of the Tibetan Plateau: a case of vicariance and dispersal. *Molecular Phylogenetics and Evolution* 9:80–87.

MACEY, J.R., J.A. SCHULTE, II, A. LARSON, N.B. ANANJEVA, Y. WANG, R. PETHIYAGODA, N. RASTEGAR-POUYANI, AND T.J. PAPENFUSS. 2000. Evaluating trans-Tethys migration: an example using acrodont lizard phylogenetics. *Systematic Biology* 49:233–256.

MADDISON, W.P., AND D.R. MADDISON. 2003. *MacClade: Analysis of Phylogeny and Character Evolution*, Version 4.0. Sinauer, Sunderland, Massachusetts, USA.

MANTHEY, U., AND W. DENZER. 2000. Description of a new genus, *Hypsicalotes* gen. nov. (Sauria: Agamidae) from Mount Kinabalu, north Borneo, with remarks on the generic identity of *Gonocephalus schultzewestrumi* Urban, 1999. *Hamadryad* 25:13-20.

MANTHEY, U., AND W. GROSSMANN. 1997. *Amphibien & Reptilien Südostasiens*. Natur u. Tier Verlang, Münster, Germany. 512 pp.

METCALF, I. 1998. Paleozoic and Mesozoic geological evolution of the SE Asian region: multidisciplinary constraints and implications for biogeography. Pages 25–41 *in* R. Hall and J.D. Holloway, eds., *Biogeography and Geological Evolution of SE Asia*. Backhuys Publishers, Leiden, Netherlands.

MOODY, S.M. 1980. *Phylogenetic and Historical Biogeographical Relationships of the Genera in the Family Agamidae* (*Reptilia: Lacertilia*). Ph.D. dissertation. University of Michigan, Ann Arbor, Michigan, USA. xv + 373 pp.

OTA, H., AND T. HIKIDA. 1991. Taxonomic review of the lizards of the genus *Calotes* Cuvier 1817 (Agamidae Squamata) from Sabah, Malaysia. *Tropical Zoology* 4:179–192.

POSADA, D., AND K.A. CRANDALL. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817–818.

POSADA, D., AND K.A. CRANDALL. 2001. Selecting the best-fit model of nucleotide substitution. *Systematic Biology* 50:580–601.

SCHULTE, J.A., II, J.R. MACEY, R. PETHIYAGODA, AND A. LARSON. 2002. Rostral horn evolution among agamid

lizards of the genus *Ceratophora* endemic to Sri Lanka. *Molecular Phylogenetics and Evolution* 22:111–117.

SCHULTE, J.A., II, J.P. VALLADARES, AND A. LARSON. 2003. Phylogenetic relationships within Iguanidae, inferred using molecular and morphological data and a phylogenetic taxonomy of iguanian lizards. *Herpetologica* 59:399–419.

SCHULTE, J.A., II, J.V. VINDUM, HTUN WIN, THIN THIN, KYI SOE LWIN, AND AWAN KHWI SHEIN. 2004. Phylogenetic relationships of the genus *Ptyctolaemus* (Squamata: Agamidae), with a description of a new species from the Chin Hills of western Myanmar. *Proceedings of the California Academy of Sciences*, ser. 4, 55(12):227–247.

SLOWINSKI, J.B., AND W. WÜSTER. 2000. A new cobra (Elapidae: *Naja*) from Myanmar (Burma). *Herpetologica* 56(2):257–270.

SMITH, M.A. 1935. *The Fauna of British India, including Ceylon and Burma. Reptilia and Amphibia*. Vol. *II—Sauria*. Taylor & Francis Ltd., London, UK. xii + 445 pp.

SORENSON, M.D. 1999. *TreeRot*, Version 2. Boston University, Boston, Massachusetts, USA.

SULLIVAN, J., Z. ABDO, P. JOYCE, AND L. SWOFFORD. 2005. Evaluating the performance of a successive-approximations approach to parameter optimization in maximum-likelihood phylogeny estimation. *Molecular Biology and Evolution* 22:1386–1392.

SWOFFORD, D.L. 2002. *PAUP**. Phylogenetic Analysis Using Parsimony (* and Other Methods), Version 4.0b10. Sinauer, Sunderland, Massachusetts, USA.

SWOFFORD, D.L., G.J. OLSEN, P.J. WADDELL, AND D.M. HILLIS. 1996. Phylogenetic inference. Pages 407–543 *in* D.M. Hillis, C. Moritz, and B.K. Mable, eds., *Molecular Systematcs*, 2nd ed. Sinauer Associates, Sunderland, Massachusetts, USA.

TIWARA, M., AND A. SCHIAVINA. 1990. Biology of the Indian garden lizard, *Calotes versicolor* (Daudin). Part I: Morphometrics. *Hamadryad* 15(1):30–33.

VINDUM, J.V., HTUN WIN, THIN THIN, KYI SOE LWIN, AWAN KHWI SHEIN, AND HLA TUN. 2003. A new *Calotes* (Squamata: Agamidae) from the Indo-Burman Range of western Myanmar (Burma). *Proceedings of the California Academy of Sciences*, ser. 4, 54(1):1–16.

WEISROCK, D.W., J.R. MACEY, I.H. UGURTAS, A. LARSON, AND T.J. PAPENFUSS. 2001. Molecular phylogenetics and historical biogeography among salamandrids of the "true" salamander clade: Rapid branching of numerous highly divergent lineages in *Mertensiella luschani* associated with the rise of Anatolia. *Molecular Phylogenetics and Evolution* 18:434–448.

WERMUTH, HEINZ. 1967. Liste der rezenten Amphibien und Reptilien. Agamidae. *Das Tierreich* 86:1–127.

ZUG, GEORGE R. 1998. Australian populations of the *Nactus pelagicus* complex (Reptilia: Gekkonidae). *Memoirs of the Queensland Museum* 42(2):613–626.

ZUG, GEORGE R., HTUN WIN, THIN THIN, THAN ZAW MIN, WIN ZAW LHON, AND KYAW KYAW. 1998. Herpetofauna of the Chatthin Wildlife Sanctuary, north-central Myanmar with preliminary observations of their natural history. *Hamadryad* 23:111–120.

Appendix

A. Methodology for Obtaining Molecular Data

Genomic DNA was extracted from liver using the DNeasy Tissue Kit® (Qiagen, Inc.). Amplification of genomic DNA was conducted in a DNA Engine® (PTC-200TM) Peltier Thermal Cycler (MJ Research) using a denaturation at 94C for 35 s, annealing at between 45–54°C for 35 s, and extension at 70C for 150 s for 30–35 cycles with Life Technologies (Gibco) Taq polymerase. Negative controls were run on all amplifications to check for contamination. Amplified products were purified with AMPure® magnetic beads (Agencourt). Cycle-sequencing reactions were run using ABI Prism Big Dye Terminator chemistry version 3.1 (Perkin-Elmer) with a denaturation at 96C for 10 s, annealing at 50C for 10 s, and extension at 60C for 4 min for 35–40 cycles. Sequencing reactions were run on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems).

Amplifications of the mitochondrial ND1 gene through the COI gene from genomic DNA were prepared with several primer combinations. All samples were amplified with L3914 in combination with H4980 or H5617a, as well as L4437 in combination with H5934a or H6159. Both strands were sequenced using L3914, L4160, L4178a, H4419b, H4419d, L4437, H4618b, L4831a, L4831c, L4882b, H4980, L5002, L5417, L5549b, H5617a, L5631, L5638b, H5692, H5934a, H5937c, H6030, and H6159. Most primers are as described by Macey et al. (1997) except L3914, which is reported in Macey et al. (1998) as L3878. Additional primers used include L4160 (Kumazawa and Nishida 1993), H4419b and L4882b (Macey et al. 2000), L5549b (Schulte et al. 2003), and H6159 (Weisrock et al. 2001). Several new primers were designed for this study: H4419d (5' – GGYATGGGCCCAAYTGCTT – 3'); H4618b (5' – TTGTGGCAGCTTCRATTGCNCGTGG – 3'); L4831c (5' – TGACTACCAGAAGTACTNCAAGG – 3'); L5417 (5' – ACATCAGCAACAAARTGACG – 3'); L5631 (5' – CATCAYCTGAATGCAACYCAG – 3'); H5937c (5' – TAYAATGTTCCRATATCTTTRTG – 3'); and H6030 (5' – CCMARAGCTTGTCCTGGTTG – 3'). Primer numbers refer to the 3' end on the human mitochondrial genome (Anderson et al. 1981), where L and H denote primers whose extension produces the light and heavy strands, respectively. Voucher specimen information and GenBank accession numbers for newly reported sequences are provided in the material examined section. Aligned DNA sequences are available in TreeBASE (Study accession number = S1461; Matrix accession number = M2627).

DNA sequences were aligned initially by eye. Positions encoding part of ND1, all of ND2, and part of COI were translated to amino acids using MacClade 4.08 (Maddison and Maddison 2003) for confirmation of alignment. Alignments of sequences encoding tRNAs were based on secondary structural models. Secondary structures of tRNAs were inferred from primary structures of the corresponding tRNA genes using these models. Gaps are treated as missing data. Unalignable regions were excluded from phylogenetic analyses due to ambiguity in our hypotheses of homology for these aligned data.

B. Definition of Morphological Characters

Each character and its abbreviation follow; we include a definition only where we record character differently than preceding researchers. Abbreviations follow Zug (1998) for ease of recognition. All characters reported for right side, all measurements in millimeters.

Mensural Characters

A. Head

Eye-ear length: **EyeEar —** Distance from anterior edge of tympanum to posterior of orbit (not pupil opening).

Head height: **HeadH** — Dorsoventral distance from top of head to underside of jaw at transverse plane intersecting angle of jaws.

Head length: **HeadL —** Distance from anterior edge of tympanum to tip of snout.

Head width: **HeadW** — Distance from left to right outer edge of temporal or jaw muscles at their widest point without compression of soft tissue.

Interorbital width: **Interorb** — Transverse distance between anterodorsal corners of left and right orbits.

Jaw width: **JawW —** Distance from left to right outer edge of jaw angles; this measurement excludes jaw musculature broadening of head.

Naris-eye length: **NarEye** — Distance from anterior edge of orbit to posterior edge of naris.

Snout-eye length: **SnEye** — Distance from anterior edge of orbit to tip of snout (rostral scale).

Snout width: **SnW** — Internasal or internarial distance of other authors; transverse distance between left and right nares.

B. Body and Limbs

4th finger: **4FingLng —** Distance from juncture of 3rd and 4th digits to distalmost extent (outer/distalmost surface of claw) of 4th finger.

4th toe: **4ToeLng —** Distance from juncture of 3rd and 4th digits to distal end of 4th digit on hindfoot.

Crus length: **CrusL** — Length of crus (tibia) from knee to heel.

Forefoot length: **ForefL —** Distance from proximal end of forefoot to tip of fourth digit.

Hindfoot length: **HindfL —** Distance from proximal end (heel) of hindfoot to distalmost surface of fourth toe.

Lower arm length: **LoArmL —** Distance from elbow to distal end of wrist, or just before underside of forefoot.

Pectoral width: **PectW —** Distance between left and right axilla (posterior to forelimb insertions) measured on ventral side.

Pelvic width: **PelvW —** Distance between left and right inguen (posterior to hindlimb insertions).

Snout-vent length: **SVL**.

Snout-forelimb length: **SnForel** — Distance from anterior of forelimb, or shoulder, to tip of snout.

Tail height: **TailH —** Distance from dorsal to ventral surface of tail base measured just posterior to vent.

Tail length: **TailL —** Distance from vent to distal end of tail; noting completeness or regeneration of tail.

Tail width: **TailW —** Distance from left to right side of tail base just posterior to vent.

Trunk length: **TrunkL** — Body length or axilla-groin length of others; distance between posterior edge of forelimb insertion (axilla) to anterior edge of hindlimb insertion (inguen).

Upper arm length: **UpArmL —** Distance from anterior insertion of forelimb, or shoulder, to elbow.

Upper leg length: **UpLegL —** Distance from anterior edge of hindlimb insertion to knee.

Meristic Characters

A. Head

Canthus rostralis: **CanthR —** number of elongate scales along 'dorsolateral snout ridge' from above posterodorsal corner of nasal scale to and including posteriormost supraciliary scale.

Dorsal eyelid scales: **Eyelid —** Number of scales found along dorsal edge of eyelid.

Dorsal head scales: **HeadSLn —** Number of scales longitudinally on midline between interparietal and rostral scale.

Head scales: **HeadSTr —** Number of scales in transverse line between posteriormost left and right supraciliary scales, just anterior of interparietal.

Infralabials: **Inflab** — posterior end defined by posteriormost enlarged scales that touches with Suplab at rear corner of mouth.

Snout scales: **SnS —** Number of scales on line transversally between left and right nasal scales (single scale surrounding naris).

Supralabials: **Suplab —** posterior end defined by posteriormost enlarged scales that touches Inflab at rear corner of mouth.

Temporal spines: **TempSp —** Number of distinctly enlarged spine-like scales in patches above and posterior of tympanum, exclusive of dorsal or head crest spines.

B. Body and Limbs

Forefoot lamellae (scansors): **4FingLm** — Number of 4^{th} digit lamellae; from 1^{st} lamella at digits' cleft that is wider than deep and touches dorsal digital scale (on at least one side) to most distal lamella; fragmented proximal scales are excluded.

Hindfoot lamellae (scansors): **4ToeLm** — As for 4FingLm.

Dorsal scales or spines: **Dorsal —** Number of middorsal scales (spines or not), beginning with first enlarged spine-like scale on nape to above vent.

Midbody scale rows: **Midbody —** Number of scale rows around trunk at midbody.

Coloration of Preserved Specimens

A. Dorsal color characters

Cheek Color: **CheekCol —** Presence (1) or absence (0) of dark patches on jowl muscles.

Paired Dorsolateral Stripes: **DorsSt —** Presence (1) or absence (0) of pair of dorsolateral light stripes, one on each side of trunk.

Forearm Stripe: **ForearSt** — Presence (1) or absence (0) of longitudinal light stripe on the outer surface of forearm.

Paired Nuchal Spots: **NucSpot —** Presence (1) or absence (0) of pair of dark spots just posterior and abutting interparietal scale.

Dark Bands on Trunk: **TrnkBand —** Number of dark bands (bars) on dorsum of trunk between axilla and inguen, not including bands over shoulder or pelvis.

B. Ventral color characters

Midventral Dark Line: **MidvLine —** Presence (1) or absence (0) of dark line on venter midline from throat to pelvis.

Throat Stripes: **ThroatSt —** Presence (1) or absence (0) of striping on throat.

Colored Throat Patch: **ThroatPa —** Presence (1) or absence (0) of colored patch or band on throat.

Ventral Trunk Striping: **TrunkSt —** Striping ventrally on trunk, none (0), irregular or broken striping (1), or continuous striping (2). This character excludes MidvLine.

Ventral Color: **VenColor —** Ventral background coloration, white to cream (0), light tan to beige (1), or pinkish to light brown or dusky (2).

SEX AND MATURITY.— Examination of gonads revealed sex and maturity. Females were considered mature when they possessed vitellogenic follicles, typically >1.5 mm diameter, oviducal eggs, or stretched oviducts; males when testes and epididymides were enlarged, supplemented by presence of secreting precloacal or femoral pores.

COMMENTS ON CHARACTERS.— Several researchers have attempted to quantify digit shape and length, as well as other traits. Although we support quantification because it permits statistical analysis and presumably removes a degree of bias or subjectivity, many voucher specimens are not carefully prepared resulting in bent or folded specimens or parts thereof. Thus, we believe that quantification of some characters implies a degree of accuracy that does not exist. Our selection of mensural characters emphasizes those possessing termini ending on bone and along axes that have rigorous bony struts reducing compression or bending. SnForel and TrunkL, for example, are two useful measurements but also two that can have significant variation resulting from poor preparation.

C. Specimens Examined

Museum symbolic codes follow Leviton et al. (1985) except for the Wildlife Heritage Trust, Colombo, Sri Lanka (WHT), Bombay Natural History Society (BNHS), and the newly established Myanmar Biodiversity Museum (MBM). The code BNHS-AMB is followed by the field number for Aaron M. Bauer for an uncatalogued specimen being deposited at the designated institution.

1. Tissue vouchers

The DNA sequence data derives from new sequences and previously reported data
(Type specimens in bold)

Newly reported sequences are: *Calotes chincollium* (Chin – CAS 220582, DQ289458; Sagaing – CAS 215505, DQ289459); *Calotes* cf. *emma* (Rakhine – CAS 223062, DQ289460); *Calotes htunwini* (Chatthin – USNM **524044**, DQ289461; Mandalay – CAS 204851, DQ289462; Shwe-Settaw1 – USNM **562976**, DQ289463; Shwe-Settaw2 USNM **562977**, DQ289464); *Calotes irawadi* (Chatthin – USNM **520543**, DQ289465; Chin – CAS 219911, DQ289466; Mandalay – USNM 563005, DQ289467; Sagaing – CAS 204862, DQ289468); *Calotes* "*versicolor*" (Ayeyarwaddy – CAS 205008, DQ289469; Bago1 – CAS 206551, DQ289470; Bago2 – USNM563012, DQ289471; Mon – CAS 222606, DQ289472; Mon:Kyaik.1 – MBM.USNM/fs 35783, DQ289473; Mon:Kyaik.2 – MBM.USNM/fs 35815, DQ289474; Mon:Kyaik.3 – MBM.USNM/fs 35831, DQ289475; Rahkine – CAS 204991, DQ289476; Shan – CAS 230481, DQ289477; Yangon – CAS 208157, DQ289478).

Previously reported sequences used here are reported in Macey et al. (2000) and Schulte et al. (2002, 2004): *Acanthosaura capra* (MVZ 222130, AF128498); *Acanthosaura lepidogaster* (MVZ 224090, AF128499); *Aphaniotis fusca* (TNHC 57874, AF128497); *Bronchocela cristatella* (TNHC 57943, AF128495); *Calotes calotes* (WHT 1679, AF128482); *Calotes ceylonensis* (WHT 1624, AF128483); *Calotes emma* Vietnam (MVZ 224102, AF128489); *Calotes liocephalus* (WHT 1632, AF128484); *Calotes liolepis* (WHT 1808, AF128485); *Calotes mystaceus* Myanmar (CAS 204848, AF128488); *Calotes mystaceus* Vietnam (MVZ 222144, AF128487); *Calotes nigrilabris* (WHT 1680, AF128486); *Ceratophora aspera* (WHT 1825, AF128491); *Ceratophora erdeleni* (WHT 1808, AF128522); *Ceratophora karu* (WHT 2259, AF128520); *Ceratophora stoddartii* (WHT 1512, AF128492); *Ceratophora tennentii* (WHT 1633, AF128521); *Cophotis ceylanica* (WHT 2061, AF128493); *Draco blanfordii* (MVZ 222156, AF128477); *Gonocephalus grandis* (TNHC 56500, AF128496); *Japalura tricarinata* (CAS 177397, AF128478); *Japalura variegata* (ZIL 20922, AF128479); *Japalura flaviceps* (MVZ 216622, AF128500); *Japalura splendida* (CAS 194476, AF128501); *Lyriocephalus scutatus* (WHT 2196, AF128494); *Mantheyus phuwuanensis* (FMNH 255495, AY555836); *Otocryptis wiegmanni* (WHT 2262, AF128480); *Pseudocalotes brevipes* (MVZ 224106, AF128502); *Pseudocalotes larutensis* (previously reported as *Pseudocalotes flavigula* – TNHC 58040, AF128503); *Ptyctolaemus collicristatus (*USNM 559811, AY555837) *Ptyctolaemus gularis* (CAS 221515, AY555838)*; Salea horsfieldii* (BNHS-AMB5739, AF128490); *Sitana ponticeriana* (WHT 2060, AF128481).

Several corrections are made to the identifications as reported in Macey et al. (2000). *Calotes emma* (MVZ 222144) is *Calotes mystaceus; Calotes versicolor* (MVZ 224102) is *Calotes emma*; sequences reported as *Aphaniotis fusca* and *Bronchocela cristatella* should be switched, that is AF128497 is *Aphaniotis fusca* and. AF128495 is *Bronchocela cristatella*.

2. Morphological vouchers

(Type specimens in bold)

Calotes htunwini: Myanmar: **Sagaing Division**, Alaungdaw Kathapa National Park CAS **215741**, 215764, USNM **562980**; Chatthin Wildlife Sanctuary CAS **231832,** USNM **520545**, 520547, **524044–045**, **562967–968,** 562983–985; Kabaing CAS 210517, 215801, **215811**; Mintaingbin CAS **215368**; Yin Ma Bin CAS **215347–348**, **215448, 215457–458**, USNM **562981**; Yingpaungtaing CAS 215381–382. **Magway Division**, Shin-Ma-Taung Forest Reserve CAS 210709, 215836, 215838–839, 215870; Shwe-Settaw Wildlife Sanctuary CAS **213607**, **213620**, **213741**, **213786**, **213789**, 213841, USNM **562974–975**. **Mandalay**

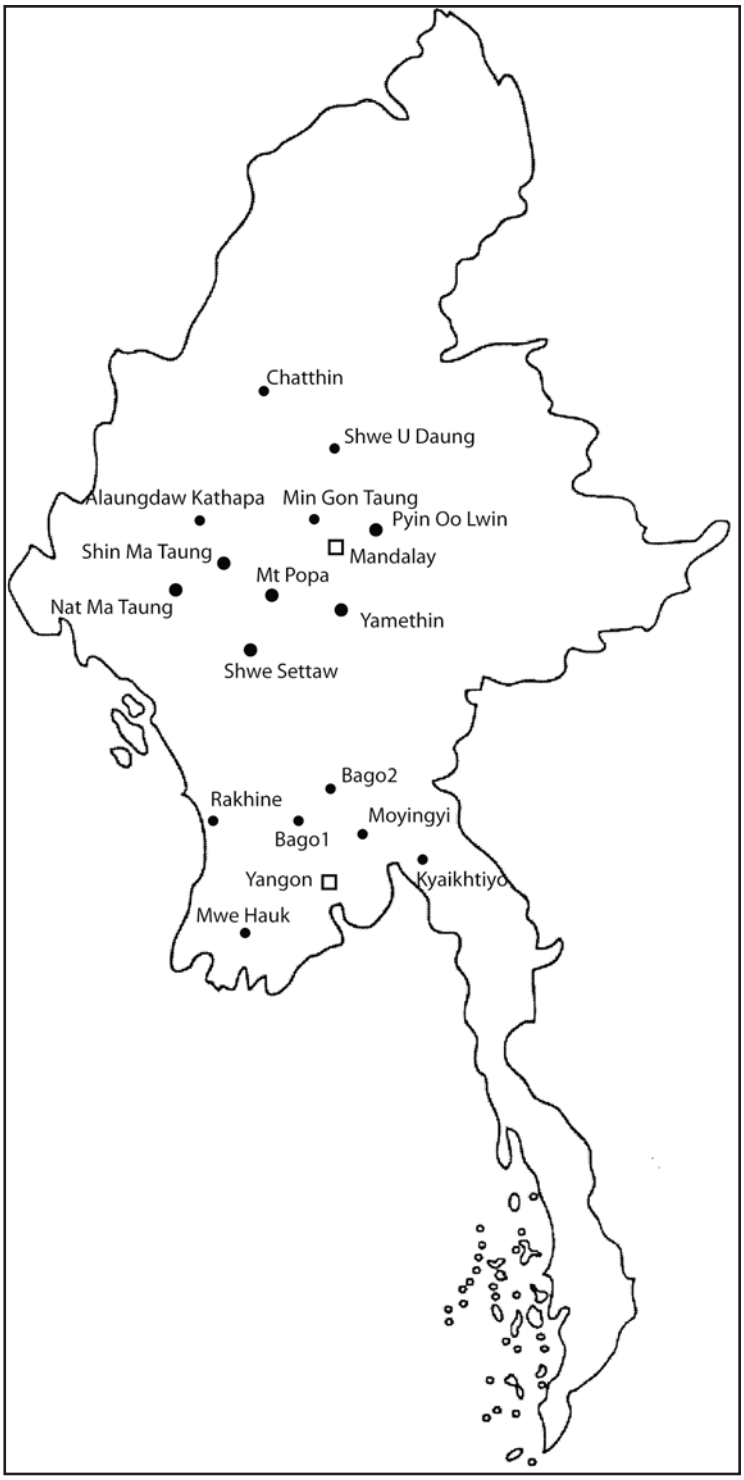

FIGURE 11. The localities identified on the map represent the major samples of the Specimens Examined section. DNA samples are identified in the above list by abbreviated names. Their equivalents are: Ayeyarwady = Mwe Hauk; Chin = Nat-Ma-Taung; Mon &/or Kyaik = Kyaikhtiyo; Sagaing = Alaungda Kathapa; Shan (not on map) = Pyadalin Cave W.S. (21°06'N 96°21'E).

Division, 96 km S of Mandalay CAS 204851; Min-Gon-Taung Wildlife Sanctuary CAS 216013, 216045, USNM 562982; Popa Mountain Park CAS 214021–022, 214090, 214114.

Calotes irawadi: MYANMAR: **Sagaing Division**, Alaungdaw Kathapa National Park CAS **215535**, **215641**, **215709,** USNM **562986–990, 562993**; Chatthin Wildlife Sanctuary CAS **231833**, USNM **520542, 520543, 520546, 524043, 562994**, 563000; Kabaing CAS 215787; Khim Aye CAS **215423, 215426–429**, USNM **562991–992**. **Magway Division**, Le Kaing CAS **213663, 213685**, 213702, **213726–727**; Shin-Ma-Taung Forest Reserve CAS 216136; Shwe-Settaw Wildlife Sanctuary CAS **213865, 213891, 213899,** USNM **562997–999**. **Mandalay Division**, Popa Mountain Park CAS 213954, 214009, 214015, 214086, 214140, 231230, USNM **562995–996**, 563001–002; Pyin-Oo-Lwin USNM 563003–008; Yamethin CAS 210565, 210605; Yin Ma Bin CAS 215293.

Calotes "tiedemanni-versicolor": INDIA: **Tamil Nadu State**, Pondicherry [11°57′N, 79°48′E] CM 152047–054, 152068–072, USNM cm152066–067.

Calotes "*versicolor*": MYANMAR: **Bago Division**, Moyingyi Wetland Bird Sanctuary [17°35′N, 96°34′E] USNM 563012–014, fs 36572, 36579–581, 36589–590, 36606–607; **Chin State**, Nat-Ma-Taung Wildlife Sanctuary. [21°12′N, 94°5′E) CAS 219911–916, 219918–919, 219921–927. THAILAND: Ubon Ratchathani [15°14′N, 104°53′E] USNM 206049–050, 206052–054, 206057, 206059–62, 206071–072, 206080.