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Burmese *Hemidactylus* (Reptilia, Squamata, Gekkonidae): Geographic Variation in the Morphology of *Hemidactylus bowringii* in Myanmar and Yunnan, China

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Six species of the gecko genus Hemidactylus are reported currently from Myanmar. This genus, in the family Gekkonidae, is the most geographically widespread and one of the most speciose. Morphological analysis within one Burmese species, H. bowringii, is concordant with the geographic pattern of genetic differentiation revealed by Carranza's and Arnold's (2006) phylogram based on mtDNA sequence data. Our analysis shows additional foci of regional differentiation within Burmese H. bowringii at other localities not included in the aforementioned phylogeny. The regional differentiation among the populations examined indicates that two species occur in central and northern Myanmar. One species occurs across northern Myanmar from Sagaing and Kachin into western China and southward east of the Ayeyarwady River to at least the Bago-Mandalay division border; the southern species occurs from west of the Ayeyarwady River from central Magway to Yangon. Neither of these two populations appears conspecific with Hong Kong H. bowringii (type-locality), hence each is recognized as a new species. Hemidactylus bowringii proper is the species occurring in South China. The status of Hemidactylus berdmorei (Blyth, 1853), an assumed synonym of H. bowringii, of southern Tanintharyi remains unresolved.

Myanmar (Burma) hosts six species of *Hemidactylus* geckos. This genus is among the most speciose of the gekkonids (~85 known species), as well as the most widely distributed gecko genus (Kluge 2001). Morphologically, *Hemidactylus* geckos are united by derived traits in toe morphology. These traits include varying numbers and degrees of divisions in lamellae of the manus and pes (Boulenger 1885). However, there is also sizeable variation among species in traits such as head proportions, body and limb size, and scalation patterns (Loveridge 1947; Smith 1935); nevertheless, the unique aspects of foot morphology reflect the monophyly of *Hemidactylus*. This monophyly was recently confirmed by mtDNA sequence analysis of 33 *Hemidactylus* taxa from more than 90 localities throughout the worldwide distribution of this genus (Carranza and Arnold 2006). Their study showed that *Hemidactylus* consisted of five clades, one of which contained all tropical Asian species. They further demonstrated that Burmese populations of *H. bowringii* and *H. brookii* each consist of more than a single genetic lineage (Fig. 1).

The presence of multiple genetic lineages within supposed single species suggests hidden biodiversity within the known and seemingly morphological uniform Burmese species. This seeming uniformity, however, has not been examined closely in any of the Burmese *Hemidactylus* or for that

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matter in any tropical Asian Hemidactylus. Our goal was two-fold, first to test the assumed uniformity in Burmese H. bowringii, which is well represented by vouchers of the joint CAS-NWCD-SI Myanmar Herpetofaunal Survey. We examined the external morphology of Burmese populations for regional differentiation. If regional differentiation exists, our second goal was to determine the degree of concordance between the observed regional morphological differentiation and the genetic lineages revealed by Carranza's and Arnold's mtDNA analysis.

MATERIALS AND METHODS

Our study focused on samples of Hemidactylus bowringii from throughout Myanmar and an adjacent locality in Yunnan, China. The specimen localities lie between ~26° and 17°N and at elevations from 5 to 1000 m. The distribution of the Myanmar H. bowringii-like geckos is depicted in Zug et al. (2007, fig. 1). For this study, we organized the specimens into two sampling sets: 1) locality samples, based largely on state or division of the specimens' origins; and 2) latitudinal samples by the latitude (rounded to the nearest integer) of the specimens. The total number of Burmese-Yunnan specimens examined is 108 individuals; they are identified in Appendix B, therein organized by locality sample. The numeric composition of the two sample sets is depicted in Table 1.

Our preliminary examination for morphological differences between geographically distinct individuals from Yunnan (Southwest China) and Shwe-Settaw (west of the Ayeyarwady River in Magway Division) identified no striking scalation differences. However, a possible difference in body size and head proportions was recognized.

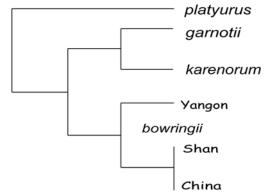


FIGURE 1. Stylized dendrogram displaying the proposed relationships among the Burmese members of the Hemidactylus bowringii species complex (fide Zug et al. 2007). The dendrogram derives from the maximum likelihood tree of Carranza and Arnold (2006: fig. 1). Tissue vouchers from the CAS-NWCD-SI survey are: platyurus CAS 204982, 215451, 222332; garnotii CAS 184322-323, 21059, 210280, 213517; karenorum CAS 210670; bowringii Yangon CAS 213333, Shan CAS 216345 [from Shan-Mandalay border, included in the Mandalay locality sample for this study], China (Yunnan) CAS 207483.

TABLE 1. Composition and coding of the two sets of the Burmese-western Chinese Hemidactylus bowringii samples. Localities arranged roughly north to south. Sample size, n. The names are used in the text and the codes in the figures to designate specific samples.

Sample	n	code	Sample	n	code
Yunnan	16	С	2.7°	5	7
Kachin	16	K	26°	16	Ċ
Sagaing	18	A	25°	11	5
Shin-Ma-Taung	7	T	24°	7	4
Mandalay	19	M	23°	4	3
Shwe-Settaw	28	S	22°	16	2
Yangon	4	Y	21°	17	1
			20°	28	0
			17°	4	Y

From this initial comparison and examination of current gekkonid literature, we developed a set of 12 mensural and 13 meristic (scalation) character traits. Most traits were adapted from Zug et al, 2003. Definitions of these traits are presented in Appendix A. Each trait has a unique abbreviation for ease of recognition of the traits within the text, tables, and figures of this report. Each specimen was dissected to examine the gonads to determine sex and maturity. Females were considered mature when they possessed vitellogenic follicles, typically >1.5 mm diameter, oviducal eggs, or stretched oviducts; males were recorded as mature when testes and epididymides were enlarged, supplemented by presence of secreting precloacal pores.

SYSAT version 11 was used for all statistical analyses. Central-tendency statistics provided the baseline analysis. Dimorphism between adult females and males was examined by Student's t test and identified with a $p \le 0.05$ in the pooled-variance t test. The larger variance pool aids confidence in accepting or rejecting dimorphism in samples comprised of smaller sample sizes and/or an inequality of females-males. We use principal components analysis (PCA) and discriminant function analyses (DFA) to examine the distribution of individuals and samples within multi-character space as well as the relationships of the samples to one another. To enhance this examination, our PCA and DFA compare the mensural and meristic (scalation) character sets separately and the two sexes separately. None of the data sets is transformed; for PCA, we use correlation matrices, no axis rotation, and principal components scores. Both multivariate protocols serve in an exploratory manner to examine intersample character variation and to test for potential differentiation among the samples.

OBSERVATIONS OF MORPHOLOGICAL VARIATION IN BURMESE-YUNNAN HEMIDACTYLUS BOWRINGII

SEXUAL DIMORPHISM.— Few of the individual locality samples are sufficiently large to provide a robust test of dimorphism between females and males. The samples that we consider adequate to test (Table 2) reveal little evidence of dimorphism between the sexes. None of the tests suggests an overall size (SVL) differential of the two sexes within any sample. Body segment measurements show dimorphism in only two samples. The latitudinal 21° sample has males with statistically thicker heads (HeadH) and longer neck-head lengths (SnForeL). Mandalay males had longer EyeEar and CrusL than females.

Dimorphism is not evident in any scalation trait other than TotPore, with a single exception. All males have pores. All females lack secreting pores, and only a few females have some "pore-scales" with dimples but without evidence of a secretion beneath the dimple. Sagaing shows significant differences in all four digit traits (Table 2). Although this dimorphism might be real, the fractional difference in means of the two sexes and the unequal number of males and females suggest a stochastic event. None of the other traits in the Sagaing sample approaches significance.

MENSURAL TRAITS.— Three locality (Kachin, Sagaing, Mandalay) and three latitudinal (21°, 22°, 25°) samples are geographic composites (see Appendix B). These composite samples encompass broad geographic areas, hence it was necessary to address whether each composite represented a single population [in the broadest sense]. Our assumption is that if multiple populations (genetic lineages) are represented in a single locality sample, the means of several characters should be significantly different and/or the variance of several characters should be greater in composite samples compared to

TABLE 2. Summary of dimorphism in adult *Hemidactylus bowringii* of the Burmese-western Chinese samples. Character abbreviations defined in Appendix A; localities arranged roughly north to south. Results presented for samples with n>12 and/or one sex $n\geq 4$; sample size in parentheses – females, males.

Yunnan & 26° (9♀, 5♂)

Mensural: No dimorphism Scalation: Inflab, TotPore

Kachin (4 ♀, 12 ♂)

Mensural: No dimorphism Scalation: TotPore

25° (4♀, 7♂)

Mensural: No dimorphism Scalation: TotPore

Sagaing $(10\,\%, 5\,\%)$

Mensural: No dimorphism Scalation: TotPore, 4FingLm, 4FingDv, 4ToeLm, 4ToeDv

21° (9♀, 8♂)

Mensural: HeadH, SnForelL Scalation: TotPore

Mandalay (10♀, 8♂)

Mensural: EyeEar, CrusL Scalation: TotPore

Shwe-Settaw & 20° (14°, 14°) Mensural: No dimorphism

Scalation: TotPore

those traits in samples derived from a single geographic site. Because of the relatively small sizes of our composite samples, a few characters by chance can be expected to show differences, and occasionally as statistically significant. We tested difference in means with Student's t tests and the equality of character variance by visual comparison of the Coefficients of Variation (V). These tests were applied to both mensural and scalation characters, and where one or both suggests multiple populations, the mixed nature of sample is discussed within this section.

Intrasample comparison of the three composite locality samples indicates that each represents a single population. Neither Mandalay nor Sagaing has any mensural or scalation traits displaying significant differences ($p \le 0.05$ for Student's t tests) among the multiple localities. Kachin has one to three traits with statistically significant t values in the three pair-wise analyses. Only EyeEar is common between two localities. Further, the Vs of Kachin's measurements equal or are less than those of Yunnan, in which all individuals derived from the walls of a single hotel in Liuku. This discordance of only a few characters supports the interpretation that the Kachin sample represents a single population. The three sites (Appendix B) comprising this sample are a maximum of 230 km distant on a N-S axis. For comparison the most distant sites for Mandalay and Sagaing are each about 300 km apart. Two of the composite latitudinal samples (25°, 22°) have one (NarEye) or no traits with significant differences. In contrast, the 21° sample displays major differences for most mensural and scalation traits between the sites east of the Ayeyarwady River and a single site (Shin-Ma-Taung) west of the river, clearly demonstrating that this composite represents two distinct populations. These differences will be identified later in the appropriate sections.

The Burmese-Yunnan *Hemidactylus bowringii* are not large geckos. Their mean body sizes range from 49.1 mm (Yunnan) to 37.5 mm SVL (Shwe-Settaw). Other mensural traits (Table 3) have moderate to high association with overall body length. Correlation is greatest with long-axis measurements, such as TrunkL (r = 0.82), SnForel (0.87), HeadL (0.79), SnEye (0.80), and least

TABLE 3. Summary of select mensural traits in adults of the Burmese-western Chinese *Hemidactylus bowringii* samples. Character abbreviations are defined in Appendix A. Sample sizes are in parentheses. All measurements are in mm: mean $\pm s$, minimum and maximum values.

SVL	TrunkL	SnForel	HeadL	JawW	SnEye	ForeaL	CrusL
49.1±3.32	24.0±2.11	17.3±1.31	12.1±0.81	7.2±0.55	5.0±0.39	5.8±0.53	6.4±0.29
43.7-56.3	18.6-27.4	14.2-19.0	10.9-13.6	6.2-8.0	4.4-5.6	4.9-6.5	5.8-7.0
49.0±3.32	23.3±2.12	19.0±1.73	12.1±0.73	7.4 ± 0.42	5.2±0.33	5.9±0.41	6.7±0.34
45.0-53.2	20.3-27.4	16.7-22.6	10.7-13.3	6.8-8.4	4.6-6.1	5.2-6.5	6.1-7.5
48.3±2.40	23.6±1.99	18.3±1.28	11.8±0.69	7.3 ± 0.36	5.1±0.23	5.9 ± 0.37	6.7±0.21
45.0-51.6	20.3-27.4	16.7-20.4	10.7-12.9	6.8-7.8	4.6-5.4	5.2-6.4	6.3-7.0
43.8±2.99	20.7±2.10	16.0±1.33	11.0±0.68	7.0 ± 0.47	4.6±0.33	5.2±0.54	5.8 ± 0.68
39.7-50.7	16.9-25.6	13.7-17.8	9.9-12.4	6.1-8.0	4.1-5.1	4.4-6.4	5.0-7.1
45.6±3.44	21.4±1.68	16.8±1.16	11.2±0.68	7.1±0.53	4.7±0.39	5.7±0.58	6.4 ± 0.70
39.7-51.4	18.8-25.6	14.9-19.1	9.9-12.4	6.1-8.0	4.1-5.4	4.9-6.7	5.4-7.6
41.1±1.99	19.0±1.70	15.9±1.20	10.2±0.54	8.9±1.67	4.1±0.31	4.5±0.33	5.1±0.46
37.2-43.9	16.3-20.5	13.6-17.4	9.4-10.8	6.8-10.7	3.7-4.7	3.9-4.9	4.3-5.7
47.3±2.72	21.5±1.68	17.7±1.02	11.6±0.76	7.0 ± 0.54	4.8±0.39	6.0 ± 0.35	6.9 ± 0.49
40.6-51.9	18.8-24.6	15.9-19.9	10.2-13.4	5.8-7.8	3.9-5.4	5.4-6.7	6.1-8.0
37.5±2.10	16.6±1.43	14.1±0.91	9.4 ± 0.74	5.9±0.38	3.7±0.24	4.5±0.35	5.0±0.45
34.4-43.3	13.9-19.9	12.5-16.0	8.3-11.0	4.9-6.9	3.4-4.4	3.8-5.2	4.0-5.8
38.1±2.65	17.1±1.17	15.1±1.27	9.7±1.02	6.1±0.49	3.9±0.31	4.7±0.29	5.5±0.61
35.7-41.6	16.1-18.8	13.4-16.3	8.8-11.1	5.5-6.7	3.6-4.3	4.4-5.1	5.0-6.4
	49.1±3.32 43.7-56.3 49.0±3.32 45.0-53.2 48.3±2.40 45.0-51.6 43.8±2.99 39.7-50.7 45.6±3.44 39.7-51.4 41.1±1.99 37.2-43.9 47.3±2.72 40.6-51.9 37.5±2.10 34.4-43.3 38.1±2.65	49.1±3.32 24.0±2.11 43.7–56.3 18.6–27.4 49.0±3.32 23.3±2.12 45.0–53.2 20.3–27.4 48.3±2.40 23.6±1.99 45.0–51.6 20.3–27.4 43.8±2.99 20.7±2.10 39.7–50.7 16.9–25.6 45.6±3.44 21.4±1.68 39.7–51.4 18.8–25.6 41.1±1.99 19.0±1.70 37.2–43.9 16.3–20.5 47.3±2.72 21.5±1.68 40.6–51.9 18.8–24.6 37.5±2.10 16.6±1.43 34.4–43.3 13.9–19.9 38.1±2.65 17.1±1.17	49.1±3.32 24.0±2.11 17.3±1.31 43.7-56.3 18.6-27.4 14.2-19.0 49.0±3.32 23.3±2.12 19.0±1.73 45.0-53.2 20.3-27.4 16.7-22.6 48.3±2.40 23.6±1.99 18.3±1.28 45.0-51.6 20.3-27.4 16.7-20.4 43.8±2.99 20.7±2.10 16.0±1.33 39.7-50.7 16.9-25.6 13.7-17.8 45.6±3.44 21.4±1.68 16.8±1.16 39.7-51.4 18.8-25.6 14.9-19.1 41.1±1.99 19.0±1.70 15.9±1.20 37.2-43.9 16.3-20.5 13.6-17.4 47.3±2.72 21.5±1.68 17.7±1.02 40.6-51.9 18.8-24.6 15.9-19.9 37.5±2.10 16.6±1.43 14.1±0.91 34.4-43.3 13.9-19.9 12.5-16.0 38.1±2.65 17.1±1.17 15.1±1.27	49.1±3.32 24.0±2.11 17.3±1.31 12.1±0.81 43.7-56.3 18.6-27.4 14.2-19.0 10.9-13.6 49.0±3.32 23.3±2.12 19.0±1.73 12.1±0.73 45.0-53.2 20.3-27.4 16.7-22.6 10.7-13.3 48.3±2.40 23.6±1.99 18.3±1.28 11.8±0.69 45.0-51.6 20.3-27.4 16.7-20.4 10.7-12.9 43.8±2.99 20.7±2.10 16.0±1.33 11.0±0.68 39.7-50.7 16.9-25.6 13.7-17.8 9.9-12.4 45.6±3.44 21.4±1.68 16.8±1.16 11.2±0.68 39.7-51.4 18.8-25.6 14.9-19.1 9.9-12.4 41.1±1.99 19.0±1.70 15.9±1.20 10.2±0.54 37.2-43.9 16.3-20.5 13.6-17.4 9.4-10.8 47.3±2.72 21.5±1.68 17.7±1.02 11.6±0.76 40.6-51.9 18.8-24.6 15.9-19.9 10.2-13.4 37.5±2.10 16.6±1.43 14.1±0.91 9.4±0.74 34.4-43.3 13.9-19.9 12.5-16.0 8.3-11.0	49.1±3.32 24.0±2.11 17.3±1.31 12.1±0.81 7.2±0.55 43.7–56.3 18.6–27.4 14.2–19.0 10.9–13.6 6.2–8.0 49.0±3.32 23.3±2.12 19.0±1.73 12.1±0.73 7.4±0.42 45.0–53.2 20.3–27.4 16.7–22.6 10.7–13.3 6.8–8.4 48.3±2.40 23.6±1.99 18.3±1.28 11.8±0.69 7.3±0.36 45.0–51.6 20.3–27.4 16.7–20.4 10.7–12.9 6.8–7.8 43.8±2.99 20.7±2.10 16.0±1.33 11.0±0.68 7.0±0.47 39.7–50.7 16.9–25.6 13.7–17.8 9.9–12.4 6.1–8.0 45.6±3.44 21.4±1.68 16.8±1.16 11.2±0.68 7.1±0.53 39.7–51.4 18.8–25.6 14.9–19.1 9.9–12.4 6.1–8.0 41.1±1.99 19.0±1.70 15.9±1.20 10.2±0.54 8.9±1.67 37.2–43.9 16.3–20.5 13.6–17.4 9.4–10.8 6.8–10.7 47.3±2.72 21.5±1.68 17.7±1.02 11.6±0.76 7.0±0.54 40.6–51.9 18.8–24.6	49.1±3.32 24.0±2.11 17.3±1.31 12.1±0.81 7.2±0.55 5.0±0.39 43.7-56.3 18.6-27.4 14.2-19.0 10.9-13.6 6.2-8.0 4.4-5.6 49.0±3.32 23.3±2.12 19.0±1.73 12.1±0.73 7.4±0.42 5.2±0.33 45.0-53.2 20.3-27.4 16.7-22.6 10.7-13.3 6.8-8.4 4.6-6.1 48.3±2.40 23.6±1.99 18.3±1.28 11.8±0.69 7.3±0.36 5.1±0.23 45.0-51.6 20.3-27.4 16.7-20.4 10.7-12.9 6.8-7.8 4.6-5.4 43.8±2.99 20.7±2.10 16.0±1.33 11.0±0.68 7.0±0.47 4.6±0.33 39.7-50.7 16.9-25.6 13.7-17.8 9.9-12.4 6.1-8.0 4.1-5.1 45.6±3.44 21.4±1.68 16.8±1.16 11.2±0.68 7.1±0.53 4.7±0.39 39.7-51.4 18.8-25.6 14.9-19.1 9.9-12.4 6.1-8.0 4.1-5.4 41.1±1.99 19.0±1.70 15.9±1.20 10.2±0.54 8.9±1.67 4.1±0.31 37.2-43.9 16.3-20.5 13.6-17.4 9.4-10.8 6.8-10.7 3.7-4.7 47.3±2.72 21.5±1.68 17.7±1.02 11.6±0.76 7.0±0.54 4.8±0.39 40.6-51.9 18.8-24.6 15.9-19.9 10.2-13.4 5.8-7.8 3.9-5.4 37.5±2.10 16.6±1.43 14.1±0.91 9.4±0.74 5.9±0.38 3.7±0.24 34.4-43.3 13.9-19.9 12.5-16.0 8.3-11.0 4.9-6.9 3.4-4.4 38.1±2.65 17.1±1.17 15.1±1.27 9.7±1.02 6.1±0.49 3.9±0.31	49.1±3.32 24.0±2.11 17.3±1.31 12.1±0.81 7.2±0.55 5.0±0.39 5.8±0.53 43.7-56.3 18.6-27.4 14.2-19.0 10.9-13.6 6.2-8.0 4.4-5.6 4.9-6.5 49.0±3.32 23.3±2.12 19.0±1.73 12.1±0.73 7.4±0.42 5.2±0.33 5.9±0.41 45.0-53.2 20.3-27.4 16.7-22.6 10.7-13.3 6.8-8.4 4.6-6.1 5.2-6.5 48.3±2.40 23.6±1.99 18.3±1.28 11.8±0.69 7.3±0.36 5.1±0.23 5.9±0.37 45.0-51.6 20.3-27.4 16.7-20.4 10.7-12.9 6.8-7.8 4.6-5.4 5.2-6.4 43.8±2.99 20.7±2.10 16.0±1.33 11.0±0.68 7.0±0.47 4.6±0.33 5.2±0.54 39.7-50.7 16.9-25.6 13.7-17.8 9.9-12.4 6.1-8.0 4.1-5.1 4.4-6.4 45.6±3.44 21.4±1.68 16.8±1.16 11.2±0.68 7.1±0.53 4.7±0.39 5.7±0.58 39.7-51.4 18.8-25.6 14.9-19.1 9.9-12.4 6.1-8.0 4.1-5.4 4.9-6.7 41.1±1.99 19.0±1.70 15.9±1.20 10.2±0.54 8.9±1.67 <t< td=""></t<>

for JawW (0.42). The preceding pattern from the Mandalay sample is matched in the other larger samples (Yunnan, Kachin, Shwe-Settaw). The similarity in correlations among the four largest locality and two largest latitudinal (22°, 25°) samples is also displayed in their normal levels of variation. All show Vs ranging between 3–10% for all measurements except NarEye and SnW. Usually (>75%), the Vs are \leq 8% including the latter two measurements. These data are consistent with the interpretation that only the 21° sample is mixed, i.e., contains representatives of two distinct populations.

The trend, evident from visual examination of the data (Table 3), is the largest adults occur in the more northerly and/or mountainous localities (> 48 mm mean SVL; Yunnan, Kachin, 25°). Average body size declines southward with the smallest H. bowringii in Shwe-Settaw and Yangon. Ranges of body sizes overlap in adjacent samples, but 24° (Chatthin Wildlife Sanctuary) adults average 42.2 mm SVL (39.8–43.7 mm, n =5), not overlapping with the more northerly ones. The Sagaing sample (containing the Chatthin [22°N] specimens) overlaps with the northern samples as do the 22° and Mandalay ones. Shin-Ma-Taung barely overlaps with Yunnan, and Shwe-Settaw and Yangon have no overlap with Yunnan. Maturity is attained at a smaller SVL (~35 mm) in the southern population on the west side of the Ayeyarwady River. The Mandalay sample (east of Ayeyarwady) has a minimum size of maturity at 40.6 mm SVL. Owing to the association of the other measurements with SVL, the preceding pattern is displayed similarly in each of those traits.

Examining the measurements and samples in multidimensional space reveals a similar, although somewhat more revealing, pattern of geographic differentiation. We have maximized the exploratory aspect of DFA and PCA by the examination of adults only and females and males separately. SnW is excluded from these analyses owing to measuring difference of the two authors.

PCA and DFA identify different sets of "significant" traits, i.e., those accounting for variance in PCA and those contributing to group discrimination in DFA. The PCA sets are similar for adult females and males. All measurements except JawW load strongly on the first component (PC1) in females and roughly equally. This loading of the first 10 measurements declines slowly with a distinct drop in loading value for JawW. SVL, HeadL, and SnEye are the three highest loading traits (i.e., 0.96–0.98) on the females' first component; JawW is the major loading trait for PC2 and all others of minor weight. The same three traits form the top loading cluster in males with nearly identical loading values; subsequent loading value and position are somewhat, but not greatly, different, and again JawW has the lowest loading with a distinct gap from the other 11 traits. JawW is again the major loading trait for PC2.

The DFA sets for females and males share a single character (JawW) strongly influencing the discrimination function (i.e., high F-to-remove values). For females, TrunkL and NarEye also are significant traits, but only the CrusL in males. After these three and two traits, respectively, trait influence in discrimination drops sharply. The resulting classification matrices display similar results. Examining only the results of the Jackknife classifications, China (Yunnan) females are 100% correctly classified, Shwe-Settaw 73%, Yangon 67%, and Mandalay and Shin-Ma-Taung 60%; the mean classification for the seven samples is 65%, see Fig. 2; for males, accuracy of classification is Shwe-Settaw 79%, Mandalay 63%, and all others are at or below 50% (mean 55%). Classification accuracy is considerably higher (means 88 and 85%, respectively) in the nonjack-knived matrices.

The misclassifications are informative by their suggestion of regional relationships. For females, Shwe-Settaw misclassified individuals were assigned to Yangon and Sagaing; Mandalay's broadly to China, Kachin, Sagaing, and Shwe-Settaw; Shin-Ma-Taung to Sagaing; Sagaing's also broadly to Kachin, Mandalay, Shwe-Settaw, and Yangon; Kachin's to China and Sagaing; and Yangon's to Shwe-Settaw. For males, Shwe-Settaw misclassified individuals were placed in Yangon

and Sagaing; Mandalay's misclassified in Kachin and Yangon; China's in Kachin; Shin-Ma-Taung's in Sagaing; Sagaing's in Kachin and Shwe-Settaw; and Kachin's in China, Sagaing, and Mandalay. The single Yangon male was assigned to the Sagaing group. The relative distribution or relationship of the individuals is depicted in Fig. 2.

A DFA examination of the latitudinal samples of adult males and females did not reveal a drastically different pattern from the

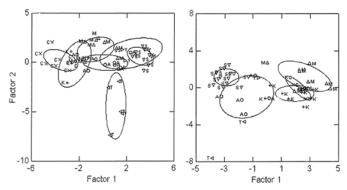


FIGURE 2. DFA canonical scores plots for mensural data of adult females (left) and males (right) of the *Hemidactylus bowringii* locality samples. The ellipses define the 50% probability limits of each sample locality; capital letters denote locality and are identified in Table 1

DFAs of the regional samples, although a considerably lower level of overall accuracy (48%). The lessening of accuracy results from an increase in samples and a concomitant reduction in their sample sizes, i.e., latitudinal 19° (n=1) sample misclassified, accuracy 0%, and also the number of samples (10) nearly equals the number of traits (11) in the model. Nevertheless, the results show some regional robustness: 25° (=Chatthin W.S.) has 100% accuracy; and 20° (Shwe-Settaw) and 26° (China) each displays 70% accuracy. Again, Shwe-Settaw's misclassifications are Yangon (17°) assignments, and China's with Kachin (25° , 27°). Sample 21° misclassifications (21% accuracy) are to latitudinal samples to the north (22° – 26°).

Meristic traits— Of the 13 scalation traits recorded, no sample displays a unique aspect of scalation, i.e., unique in the sense there is no or minimal overlap of one or a set of traits among localities. All traits have either broad overlap or near identity of ranges of values (see Table 4). Although overlap occurs, some trends can be observed, usually with a slight reduction in means from north to south. All populations contain individuals with three SnS, two large scales on each side abutting the nasal scale and a variable-sized median scale; Mandalay and southern samples (Shin-Ma-Taung, Shwe-Settaw) have numerous individuals without a median scale. In most Burmese H. bowringii, the first infralabial scale has a triangular extension that touches the naris/nasal scale (NaInf). Southern populations have numerous individuals in which the extension does not reach the nasal scale. For the Suplab, there is a slight reduction from north to south. A reduction trend is not evident in the Inflab. In most H. bowringii, the first pair of chin scales is large and broadly in contact on the midline behind the mental scale; however, some individuals in the China and Yangon samples have smaller scales and no medial contact. TotPore (males only) shows a distinct north-south cline with fewer pores in the southern samples. The number of finger and toe lamellae (4FingLm, 4ToeLm) is nearly uniform in all samples except Shin-Ma-Taung. These characters are examined in more detail later in this section.

Unlike in the mensural characters, PCA and DFA identify overlapping sets of "significant" scalation traits. The PCA sets are nearly identical for adult females and males. For females, component loading (PC1) is highest for 4ToeDv; 4FingLm, Suplab, 4FingDv, and 4ToeLm (in order of decreasing loading; 0.84 to 0.70) and in males, 4ToeDv; 4FingLm, 4FingDv, 4ToeLm, and TotPore (0.84–0.74). Suplab in females, Suplab and Inflab in males have moderate loading; all other head scalation traits load weakly on PC1. Females have SnS strongly loading on PC2; other traits load "significantly" less. Inflab has the highest loading in male PC2.

The DFA sets for females and males share some of the same characters strongly influencing

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Sample	SnS	NaInf	Suplab	ChinSD	TotPore	4FingLm	4FingDv	4ToeLm	4ToeDv
Yunnan (16)	3.4±0.62	0.8±0.40	9.5±0.63	0.2±0.45	29.6±1.67	7.7±0.45	5.2±0.43	9.5±0.82	5.9±0.50
[also 26°]	3-5	0-1	9-11	0-1	28-32	7–8	5–6	8-11	5-7
Kachin (16)	3.2 ± 0.40	0.6 ± 0.50	10.7 ± 0.73	0.2 ± 0.45	28.7±1.56	8.1 ± 0.81	5.3 ± 0.48	10.4 ± 0.51	6.0 ± 0.63
	3-4	0-1	9-11	0-1	26-28	7–9	4–6	9-11	5–6
25° (11)	3.2±0.40	0.7 ± 0.47	10.8 ± 0.40	0.3 ± 0.47	29.1±1.68	7.8 ± 0.60	5.2±0.40	10.4±0.50	5.9±0.54
	3-4	0-1	9-11	0-1	27-31	7–9	5–6	10-11	5-7
Sagaing (18)	3.2±0.52	0.9 ± 0.32	9.8 ± 0.81	0.2 ± 0.43	25.6±1.81	7.6 ± 0.62	4.8 ± 0.94	9.7 ± 0.69	5.3±0.69
	3-5	0-1	8-11	0-1	23-28	7–9	3–6	8-11	4–6
22° (14)	3.1±0.27	1.0 ± 0.0	9.9 ± 0.54	0.1 ± 0.36	26.7±2.06	7.8 ± 0.58	5.1±0.62	10.0 ± 0.55	5.7±0.47
	3-4	1	9-11	0-1	23-28	7–9	4–6	9-11	5–6
Shin-Ma-Taung	2.9 ± 0.38	0.14 ± 0.38	8.1 ± 0.69	0.0 ± 0.0	21.0 ± 2.83	6.6 ± 0.54	3.6 ± 0.53	8.3 ± 0.95	4.1±0.90
(7)	2-3	0-1	7–9	0	19-23	6–7	3-4	7–9	3–6
Mandalay (18)	2.9 ± 0.24	1.0 ± 0.0	9.9 ± 0.47	0.2 ± 0.38	25.7±2.31	7.8 ± 0.39	4.9 ± 0.24	9.9 ± 0.58	5.8 ± 0.38
	2-3	1	9-11	0-1	21-28	7–8	4–5	8-11	5–6
Shwe-Settaw (28)	3.1±0.44	0.6 ± 0.51	9.2 ± 0.83	0.1 ± 0.28	23.3±2.13	7.1 ± 0.60	4.2 ± 0.60	9.4 ± 0.96	4.7±0.61
[also 20°]	2-4	0-1	8-11	0-1	18-26	6–9	3–6	7-11	4–6
Yangon (4)	3.0 ± 0.0	0.0 ± 0.0	9.7 ± 0.96	0.0 ± 0.0	25.0 ± 0.0	8.0 ± 0.0	4.2 ± 0.50	10.0 ± 0.0	5.2 ± 0.0
	3	0	9-11	0	25	8	4-5	10	5–6

TABLE 4. Summary of select scalation characters in Burmese-western Chinese *Hemidactylus bowringii* samples. Character abbreviations are defined in the Appendix A. Sample sizes are in parentheses. TotPore for adult males only.

the discrimination function. NaInf is the highest for both males and females. For females, 4ToeDv, 4ToeLm, and 4FingDv comprise the next, not distant, set of important discrimination traits; for males, the next set is Chin, 4ToeLm, TotPore, and 4FingLm. The resulting Jackknife classification matrices display dissimilar results with strikingly different accuracy (average accuracy 52% females, 67% males). For females, only Mandalay (accuracy 80%) and China (67%) exceeds 60% (Fig. 3). In females, Sagaing and China misclassifications are assigned widely in other northern samples, although Mandalay receives the most individuals. The misclassifications for Shwe-Settaw are in Yangon; Yangon's in Shwe-Settaw and Shin-Ma-Taung, and Shin-Ma-Taung in Shwe-Settaw. In males, four samples (Kachin, Mandalay, Shwe-Settaw, Shin-Ma-Taung) have accuracy >75%. Shin-Ma-Taung's two males are correctly assigned, only two Shwe-Settaw males (n=14)

are incorrectly assigned (Sagaing) and similar misclassification for Mandalay (n=7) with one individual to Kachin (Fig. 3). China's misclassifications are to Kachin and Mandalay; Sagaing's to China, Mandalay, and Shwe-Settaw; and the single Yangon male is classified with Shwe-Settaw males.

DFA of the latitudinal samples was performed only on adult males, owing to the likely importance of TotPore in male discrimination. TotPore was the most

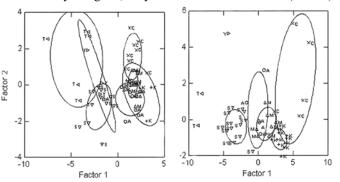


FIGURE 3. DFA canonical score plots for scalation data of adult females (left) and males (right) of the *Hemidactylus bowringii* locality samples. The ellipses define the 50% probability limits of each sample locality; capital letters denote locality and are identified in Table 1

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important discriminator for males, although Chin and 4ToeLm had near equal Fs; SnS was less but still weighed heavily. The average accuracy (30%) was low with only the 25° sample (57%) exceeding 50% accuracy, and in four of the nine latitudinal samples, no individuals were correctly classified.

Several scalation traits were not quantified during the initial character selection and definition. The aforementioned analyses suggested that some samples were consistently differentiated, and this result urged a re-examination of scalation features. That re-examination revealed several features related to the traits characterized. Our recorded data had three chin (postmentals) characters (Chin, ChinSAs, ChinSD). Two other chin scale morphologies are observed in our samples. The recorded chin characters are uniform or nearly so across all samples, hence show no evidence of regional differentiation. The medial contact of left and right 1st postmental scales (Chin) is vari-

able, usually greatest when postmental scales are large; 2nd postmental scales do not contact medially in any of *H. bowringii* examined. Of the uncoded chin morphologies, the first concerns the relative size of the first postmentals and the nature of the posterior edge formed by the abutting 1st postmental scales. Large scales are elongate pentagons producing a convex to slightly angular posterior edge (Fig. 4) in association with the 2nd postmentals. The small condition has squarish scales posteriorly forming a straight edge, often the edge is continuous across rearward edge of the 1st and 2nd postmental scales (Fig. 4). The large scale-convex edge condition occurs in nearly all

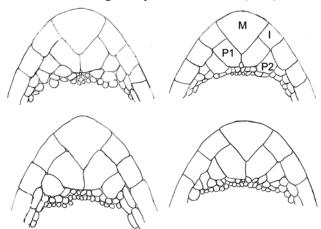


FIGURE 4. Schematic illustration of size and arrangement of chin scales in Burmese-China Hemidactylus bowringii. Clockwise from upper left: Kachin - CAS 233019; Shwe-Settaw - USNM 564821; Shin-Ma-Taung - CAS 215841; Hong Kong - MCZ R172987. Abbreviations: I, infralabial; M, mental; P, postmentals (1 primary or anterior, 2 secondary or posterior).

Kachin and Yunnan individuals and the majority of the Sagaing and Mandalay ones; all Shin-Ma-Taung individuals display the small-straight edge condition, and this condition occurs in a few individuals in the Sagaing and Shwe-Settaw samples. In the latter two samples, the 1st postmental is an elongate pentagon but seemingly intermediate in size between the Kachin large and the Shin-Ma-Taung small condition.

The second chin morphology relates to ChinSD and also involves size, i.e., the relative size of 2nd postmental scale to 1st. Because the 2nd is almost always smaller than the 1st, ChinSD data are uniform across our samples (Table 4); however, relative size segregates into two states, i.e., $2^{\text{nd}} \le \text{or} \ge \text{half}$ area of 1^{st} postmental. The greater-than state is most frequent one in Yunnan, Sagaing, Mandalay, and Yangon samples, somewhat less than 50% in Kachin and Sagaing, and 100% in Shwe-Settaw and Shin-Ma-Taung. This relative size feature also is seen in the number of chin scales touching an infralabial and lying between the 2nd postmental scale and the 2nd-3rd infralabial suture: 1, occasionally 2, scales in specimens with the larger postmentals; and 2 or 3 postmentals in individuals with small 2nd postmental scales.

Suplab is regionally uninformative as we defined it. The supralabials of Shin-Ma-Taung seem larger than those of most individuals from elsewhere. The number of entire supralabials in front of the anterior edge of the exposed eyeball is 4 (mode) to 5 for Shin-Ma-Taung and, modally, 5 or 6, (range 5 to 7, except 4–7 for Shwe-Settaw) for the other samples.

Subdigital lamellae display regional differentiation among the samples. Shin-Ma-Taung [SMT] possesses the lowest lamellar counts (mean and range) of the seven locality samples (Table 4). The other six localities share similar means and ranges for the hand – 4FingLm and 4FingDv – although Shwe-Settaw [SS] and Yangon are intermediate between SMT and the other northern and eastern localities. A nearly identical pattern exists for the hindfoot lamellar characters (Table 4) with SMT lowest, SS and Yangon intermediate, and the other samples highest. The only difference is the mean and range of 4ToeDv of

difference is the mean and range of 4ToeDv of Sagaing sharing the intermediate position with SS and Yangon. Reduced lamellae on the first toe also show a similar distributional pattern with SMT lowest (3–5), SS and Yangon intermediate (4–5), and the other samples highest (5 or 5–6).

The preceding results add morphological support to the presence of two "bowringii" species in Myanmar and encourage the formal recognition of both; however, that path requires the resolution of what is true *H. bowringii*. Zug et al. (2007) suggested, on distributional data only, that the South China-Hong Kong populations were invasives. Because Hong Kong is the type-locality (restricted by M. Smith, 1935) of *H. bowringii*, a comparison of the morphology of representatives from this area with those from Burma is essential.

Lazell (2002) observed that Hong Kong area (Shek Kwu Chau; SKC) male H. bowringii ranged between 26.5 and 52.5 mm SVL, with the smallest mature male at 36 mm SVL. He did not provide a size range for adult SKC females, although he noted that six gravid females were 49-54 (mean, 50) mm SVL and that gravid females from other Hong Kong localities ranged 42-49 (mean 46) mm SVL. Our examination of a small sample (n = 10) from Hong Kong yields an adult SVL range of 40 to 47 mm (mean, 44 mm), generally equivalent to Lazell's data. Other morphometric aspects are summarized in Table 5 and compared to the Burmese samples [hereafter combined into a North (Yunnan, Kachin, Sagaing and Mandalay samples) and a South (Shin-Ma-Taung, Shwe-Settaw and Yangon samples) sample. Hong Kong [HK] males are generally intermediate in size between the males of the two Burmese populations, although somewhat closer to the North population. The heads of the HK males appear somewhat broader than the heads of either of the two

TABLE 5. Comparison of select mensural and scalation characters among adult males of the three samples of the Burmese and South Chinese *Hemidactylus bowringii* complex. Abbreviations as in Table 3 and 4.

	North	South	Hong Kong
n	30	17	8
CVII	48.0±3.69	38.2 ± 2.92	44.4±2.67
SVL	39.8-53.2	34.4-43.9	39.9-46.9
TrunkL	22.1±2.36	17.0 ± 1.64	19.8 ± 2.31
	16.9-26.2	13.9-20.5	15.4-22.2
SnForel	18.3 ± 1.86	14.5 ± 1.39	16.4 ± 1.37
	13.7-22.6	12.5-17.4	15.0-18.6
HeadL	12.1 ± 0.85	9.7 ± 0.95	11.3 ± 0.83
neauL	10.2 - 13.4	8.3-11.1	10.2 - 12.7
JawW	7.3 ± 0.59	6.3 ± 1.20	7.5 ± 0.38
Jaw W	5.8-8.4	5.6-10.3	6.9 - 7.9
SnEye	5.1 ± 0.44	3.9 ± 0.38	4.7 ± 0.43
Sillye	3.9-6.1	3.4-4.7	4.2 - 5.4
ForeaL	5.8 ± 0.54	4.6 ± 0.26	5.2 ± 0.5
TOTCAL	4.4 - 6.7	4.1 - 5.1	4.1 - 5.9
CrusL	6.6 ± 0.66	5.2 ± 0.44	5.5 ± 0.42
Clush	5.0-8.0	4.6–6.4	4.8 - 6.0
SnS	3.1 ± 0.51	3.0 ± 0.35	2.6 ± 0.52
5115	2-5	2–4	2–3
NaInf	0.8 ± 0.41	0.6 ± 0.51	0.7 ± 0.46
11441111	0-1	0-1	0-1
Sublab	10.0 ± 0.72	9.4 ± 0.86	9.4 ± 0.52
Suoluo	9–11	8-11	9–10
Chin	1.9 ± 0.43	1.9 ± 0.48	1.2 ± 0.46
Cillii	0–2	0–2	1–2
TotPore	27.5 ± 2.42	23.1 ± 2.23	28.2 ± 1.91
1011 010	21–32	18–26	24–30
4FingLm	7.9 ± 0.72	6.9 ± 0.56	8.2 ± 0.46
4FIIIgLIII	7–10	6–8	8–9
4FingDv	5.1 ± 0.72	3.9 ± 0.43	5.6 ± 0.74
	3–6	3–5	4–6
4ToeLm	9.9 ± 0.84	9.2 ± 1.03	10.2 ± 0.46
. 1002111	8–11	7–11	10–11
4ToeDv	5.7 ± 0.65	4.6 ± 0.61	6.6 ± 0.74
41000	4–7	4–6	5–7

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Burmese populations. This broadness is suggested by the HeadW to HeadL proportion (Table 6). Pairwise Student's *t* test comparisons among the three samples demonstrate significant differences between one or more pairs for each proportion; however, the ranges of all three samples overlap in all proportions even though the means appear distinct. The situation is likely identical for females but our HK sample contained only two adult females. The means for the HK females are nearly identical to Burmese females.

Comparison of scalation among the three samples also demonstrates overlapping ranges in all recorded traits of scalation. Some characters (SnS, Chin, TotPore, and all lamellae characters) show contrasting differences in means (Table 5). The

TABLE 6. Comparison of mean body proportions (%) among adults of three samples of the Burmese and South Chinese *Hemidactylus bowringii* complex. Character abbreviations for the proportions are identified in the Appendix A. Symbols: *n*, sample size; Student's *t* test probabilities <0.05 in pairwise comparison - * North to South samples, ° North to Hong Kong, ^ South to Hong Kong.

	3.7 .1	α .1	
	North	South	Hong Kong
n	63	36	10
Trunk/SV	0.472*	0.447*	0.445°
SnFor/SV	0.371*	0.38*	0.374
Forea/SV	0.121°	0.118	0.116°
CrusL/SV	0.137°	0.134^	0.125°^
HeadL/SV	0.248°	0.249	0.253°
HeadW/HL	0.402°	0.407^	0.435°^
SnEy/HL	0.418*	0.396*^	0.417^
NarEy/HL	0.297*	0.281*^	0.331°^
EyEar/HL	0.315*	0.33*	0.337°

degree of differences among the three samples tends to be greater between the South and HK samples. The uncoded chin scale pattern for HK is typically large pentagonal 1^{st} postmentals forming a straight posterior edge. The 2^{nd} postmentals are almost always small, $\leq 0.5~1^{st}$ postmentals and occasionally very small and circular.

The syntypes of *Doryura Bowringii* Gray, 1845 are two juveniles (BMNH 1[1]34a – 20.4 mm and 32.2 mm SVL). They are faded to a uniform light beige and are flaccid, although the skin remains firm (Fig. 5). Body proportions lie within the ranges of those of the recent HK sample. The scalation traits that could be seen clearly (head scalation) also matched the HK sample. Digit lamellae characteristics could not be determined with certainty.

Coloration— Our initial examination to identified characters found no color or pattern features that could be seen on most specimens or precisely characterized for accurate data-capture in subsequent examination of specimens. Like most, perhaps all, *Hemidactylus*, *H. bowringii* lighten and darken their coloration in life. Half or more of the specimens examined were preserved in the light phase and appear nearly uniform grayish beige. In this phase, some individuals faintly display the longitudinal row of light spots on the side and the postocular stripe on cheek and anterior neck. Even in the dark phase, the pattern of dark dorsal marks is variably displayed.

In life, *H. bowringii* can be boldly patterned (Fig. 6). The general pattern for the dark phase is a tan to dusky tan background dorsally and laterally on head, neck, and trunk. Dark brown marks and cream spots create the *bowringii* pattern. Often a narrow dark V lies on the nuchal and diffuse dark markings occur on the neck and trunk. Dorsolaterally, and laterally, the dark marks form fragmented longitudinal stripes with the lateral one most sharply defined; this latter stripe extends from the nares to eye and from rear of eye to shoulder, thereafter broken by circular cream spots, and as a solid stripe onto the base of the tail. The dorsolateral stripe is always fragmented; it begins on the anterior neck and extends onto the base of the tail. Venter is immaculate from chin to the base of thetail, typically a light tannish white. The phase shift from dark to light causes a gradual loss of the intensity of the dark markings, with the light spots sometimes evident with the disappearance of the dark ones. Also the dark lateral stripe from eye to shoulder disappears more slowly, as also do the dorsal markings on the tail.

Differences between northern and southern populations are subtle. In northern individuals, the dark markings forming the dorsolateral stripe are anteroposterior elongate and yield a more discrete dorsolateral stripe; in southern individuals, these marks are transversely elongated, yielding a barred or ladder pattern on the dorsum of the trunk (compare the Shwe-Settaw and Pyin-Oo-Lwin individuals in Fig. 6). The transverse nature is more evident dorsally on the tail, with dark chevrons in southern individuals vs. dark spots in northern ones.

The general pattern description applies to the *H. bowringii* adults from Hong Kong. The HK pattern is more similar to that described above for northern Burmese individuals, although many HKs have dark chevrons or transverse bars on the tail dorsum. Also many HK individuals have a broad cream stripe on the neck

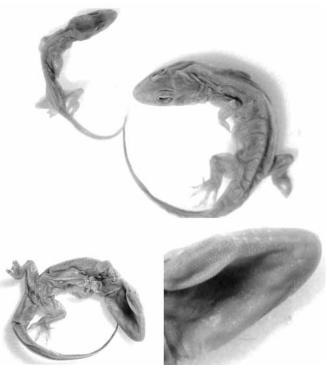


FIGURE 5. Syntypes of *Hemidactylus bowringii*. Top: right large juvenile (BMNH 2007.1, lectotype; 32.2 mm SVL); left, small juvenile (BMNH 2007.2 paralectotype; 20.4 mm SVL). Bottom: ventral view and chin of lectotype (BMNH 2007.1).

above the lateral stripe (see Karsen 1986:84), and in a few individuals, the light area extends forward to the eye.

MORPHOLOGICAL DIFFERENTIATION—DISCUSSION

Sexual dimorphism.— The few samples and traits showing dimorphism in adults argue that Burmese-Yunnan populations lack sexual dimorphism, with the exception of the presence of femoral-precloacal pores (TotPore) in males, although the small sample sizes and the uneven representation of females and males in most samples do not lend robustness to this interpretation. These two factors would seem more likely to offer false positive identification of dimorphism than the opposite. Further the lack of concordance between the two samples with mensural-dimorphic traits (21° - HeadH, SnForelL; Mandalay – EyeEar, CrusL) and similarly between the two samples with scalation-dimorphic characters (Yunnan – Inflab; Sagaing – 4FingLm, 4FingDv, 4ToeLm, 4ToeDv) supports the likelihood these putative dimorphic traits are simply a stochastic result of measurement or sampling. This interpretation is supported by the overlap of individual specimens in the 21° and Mandalay samples; 12 Mandalay specimens (6 of each sex) are part of the 21° sample, yet the two samples do not share the same set of dimorphic characters. There are few comparable examinations of dimorphism in other populations of tropical Asian *Hemidactylus*. Brown and Alcala (1978) reported no sexual dimorphism in the Philippine *H. brookii*, *H. frenatus*, or *H. platyurus*. The size range of adult females and males in these three species overlapped broadly. Zug



(1991) observed only that females had narrower heads in Fijian *H. frenatus*. Lazell (2002) examined the reproductive biology of *Hemidactylus* from Shek Kwu Chau, an islet in the Hong Kong region. He found no sexual dimorphism other than presence-absence of precloacal-femoral pores. He specifically notes the absence of size dimorphism (adult females 42–49 mm, males 36–52 mm SVL). Our HK sample is too small to adequately test for dimorphism.

Males and females differ in the presence of the femoral-precloacal pore series. In our total sample, we observed no females with secreting pores and no adult males lacking pores. This dichotomy is a common attribute of many geckos.

MENSURAL TRAITS.— Both univariate and multivariate analyses reveal a trend in body size. This trend is displayed in all mensural characters, except JawW, because they are strongly correlated, i.e., $r \ge 0.75$ and usually > 0.80 because of the intercorrelation of the mensural traits. These correlations would have been stronger (higher r values) if our samples included the full range of life-stages. Our samples emphasized large juveniles and adults, both from a collecting bias and our data-gathering emphasis.

This emphasis on samples of large juveniles and adults has the advantage of reducing variation within each of the locality and latitudinal samples, hence permitting a more robust comparison among the samples. The samples, even the smaller ones, display low to normal variance as judged by low to moderate Vs (6 to 10%) for all characters, except SnW (commonly ~20%). As noted in the results section, we excluded SnW from our analyses owing to CM and GZ measuring this trait differently.

We noted in the results section the occurrence of larger geckos in the northern and Mandalay samples (Table 3). Although the measurement ranges of the northern and southern samples (Shin-Ma-Taung, Shwe-Settaw, Yangon) overlap, the means are significantly different, and only the Sagaing sample's mean approaches the maximum size (SVL) of the southern samples. This observation led to our combination of the individual Burmese-Yunnan samples into two regional samples for examination with the topotypic Hong Kong sample. These three samples (Table 5) proved significantly different from one another (SVL: N-S t = 13.41 df = 97 p < 0.001, N-H t = -2.64 df = 71 p = 0.01, S-H t = 6.62 df = 44 p < 0.001). We also observed that body proportion ranges overlapped among these three regional samples, yet the sample means show significant differences (Table 6).

MERISTIC TRAITS.— No aspect of scalation uniquely distinguishes a sample or set of samples. A few traits show a low-frequency of occurrence of one condition in a limited geographic area, such as the absence of a median 'supranasal' scale in southern samples. Others, e.g., Suplab, show a weak north-south cline. Only TotPore has a distinct clinal pattern with the northern-most and southern-most samples significantly different from one another, although their ranges overlap (Table 4). Subdigital lamellae are fewer and with more divided ones in the Shin-Ma-Taung sample. The other sample-localities broadly overlap, although the condition in Shwe-Settaw and Yangon is somewhat intermediate. Shin-Ma-Taung geckos also seem to differ from other Burmese *H. bowringii* by somewhat larger supralabial scales. Scale shape and size on the chin show two 1st postmental patterns. Yunnan and Kachin individuals have somewhat larger 1st postmentals and these scales form an angular (convex) posterior edge between the 2nd postmentals. All Shin-Ma-Taung and many Shwe-Settaw geckos have proportionately smaller 1st postmentals than in the northern samples; this condition and also often smaller 2nd postmental produce a straight posterior

FIGURE 6 (left). Color patterns of *H. bowringii* group geckos from Myanmar and China. Top: *H. bowringii* — China: Guangdong; Nan Ao Island, Tai Zhu Ao [photographer Hou Mian; © The Conservancy Agency]. Middle left/right: *H. aquilonius* — Myanmar: Mandalay Divis.; Pyin-Oo-Lwin [G. Zug; MBM-USfs 36837]. *H. aquilonius* — Myanmar: Sagaing Divis.; Chatthin Wildlife Sanctuary [G. Zug; USNM 520556]. Bottom: *H. thayene* — Myanmar: Magway Divis.; Shwe-Settaw Wildlife Sanctuary [G. Zug; USNM 564821-holotype].

edge of the postmentals. Sagaing and Mandalay samples show a mix of these two posterior-edge patterns.

COLORATION.— Both the faintness and uniformity of coloration in the light phase and the irregular-edging of the dark marks in the dark phase cloud coloration differences among the samples. At first glance, the reaction is to declare that all "bowringii" look the same; however, some subtle differences exist, although these differences require confirmation by image-documentation in samples of living geckos. We suggest that the north and south Burmese samples segregate on the nature of the dorsolateral dark stripe with the former possessing a better defined, more contiguous dorsolateral stripe vs. a slight transversely barred pattern in the latter. Hong Kong "bowringii" have a broad cream stripe or patch on each side of the neck, absent in the Burmese individuals.

Lazell (2002:21) observed that Boulenger's illustration (1885: pl. XII) was peculiar in the random scattering of irregular-sized light spots on the dorsum. We agree, perhaps Boulenger's illustrator depicted patches of loose [pre-shed] scales.

GEOGRAPHIC DIFFERENTIATION: CONCLUSIONS.— As mentioned above, no character has a unique state for the differentiation of the two Burmese genetic lineages of Hemidactylus bowringii identified by Carranza and Arnold (2006). Morphological differences, however subtle, exist and display geographic discontinuity between northern and southern samples. The most evident aspect is adult size, both mean and minimum size at maturity. Northern samples (Kachin, Yunnan, Sagaing, Mandalay) have larger adults (Table 3; means 44-49 mm SVL, minimum 40-45 mm) as compared to the smaller adults (Table 3; means 37-42 mm SVL, minimum 34-38 mm) of the southern samples (Shin-Ma-Taung, Shwe-Settaw, Yangon). [Note: The Shan specimen analyzed genetically by Carranza and Arnold derived from Shwe-U-Daung Wildlife Sanctuary which overlaps the border of Shan State and Mandalay Division. Because we had specimens from both sides of the sanctuary, we included the Shan specimen in the Mandalay locality-sample.] A few aspects of scalation also show populational differences. In males, the number of precloacal pores (TotPore) overlaps only slightly between northern and southern samples, with significant differences of the means (north -26-30, south -21-25). Digital lamellae also display north-south differentiation. Even though the means and ranges of 4FingLm and 4ToeLm strongly overlap, the number (means) of divided lamellae for both fore- and hindfeet (4FingDv, 4ToeDv; Table 4) do not.

In multivariate space (Figs. 2, 3), the locality samples regularly divide into sets of north and south clusters, although as in single character comparisons, overlap occurs among the northern and southern samples. The China and Kachin samples overlap strongly in all analyses, and Mandalay commonly shares this overlap. Sagaing often overlaps with both the northern and southern (Shwe-Settaw, Yangon) samples. Shin-Ma-Taung is the most distinct locality, with it specimens always well outside the 50% confidence ellipse of northern samples and slight overlap with the other two southern ones. This position suggests that the Shin-Ma-Taung population might be genetically distinct from the northern and other southern populations; however, we do not accept that interpretation presently. We, however, interpret the morphological differences reported above as concordant with the mtDNA sequence data of Carranza and Arnold (2006) and advocate the recognition of two species within Myanmar.

This interpretation is re-enforced by results from the comparison of Hong Kong *H. bowringii* with the Burmese samples. The Hong Kong sample is intermediate between the two Burmese combined samples (Table 5, Fig. 7). The three samples are well segregated in multivariate space with only a northern individual or two overlapping into the Hong Kong 50% confidence ellipse. This segregation indicates that the South China populations represent another species of the *H. bowringii* group.

TAXONOMIC NOTES AND DECISIONS

Our interpretation that Hemidactylus bowringii geckos Myanmar represent two species is restricted to populations from Yangon northward. Our examination of H. bowringii populations outside of central and northern Myanmar has been perfunctory, although sufficient to suggest that at least two of these populations deserve taxonomic recognition. Before preceding with this nomenclatural step, three taxonomic mat-

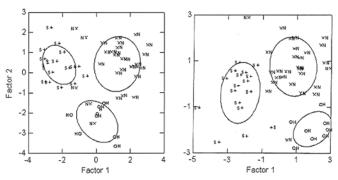


FIGURE 7. DFA canonical scores plots for mensural (left) and scalation (right) data of adult males of three *Hemidactylus bowringii* group samples. The ellipses define the 50% probability limits of each sample; capital letters denote locality (H, Hong Kong; N, northern Myanmar sample; S, southern Myanmar sample).

ters require resolution: 1) definition of the *H. bowringii* species group; 2) proof that Smith's (1935) restriction of the type-locality of *bowringii* to "Hong-Kong" is appropriate; that is, the type specimens match the morphology of the present Hong Kong *bowringii*; 3) demonstration that "*bowringii*" from Tanintharyi [Myeik Beik] are the same as one of central and northern populations or different from them in order that the name *Leiurus berdmorei* Blyth can be correctly applied.

The *bowringii* species group consists of the populations of *Hemidactylus* geckos previously labeled *H. bowringii*, which occurs from the terai of Nepal, northern India (Sikkim, West Bengal), adjacent Bangladesh, Myanmar, adjacent northwestern China (Yunnan), and southern China (Hainan eastward) to Taiwan and Ryukyu Islands (Zug et al. 2007). These geckos have a dorsal and lateral trunk surface of uniformly small granular scales; the tail oblong in cross-section, indistinctly segmented with a small spine-like scale ventrolaterally on each side at posterior edge of each segment; and 7 to 11 lamellae on the underside of the 4th toe, about half of these lamellae divided medially.

In spite of an earlier proposal (Zug et al. 2007) that the southern China populations were introduced, our current interpretation is that these populations are natural and further that they represent a different species from those of Myanmar. This interpretation is important because the Hong Kong population is topotypic. Although Gray (1845) did not provide a type-locality, Smith (1935) restricted the type-locality to Hong Kong. Smith did not explain his restriction; however, Lazell (2002) notes that the donor (C. Bowring [actually J.C. Bowring]) of the syntypes was in Macao and possibly Hong Kong by 1842, thus increasing the likelihood that the types did derive from that area of southern China. Our examination of the poorly preserved syntypes shows a tentative match with recently collected Hong Kong specimens. The deteriorating condition of the syntypes does not permit an unequivocal assignment. We designate the largest syntype as the lectotype.

The condition of the Zoological Survey of India holotype of *Hemidactylus berdmorei* is even worse than that of the *bowringii* syntypes. Blyth (1853) described a gecko *Leiurus Berdmorei* (subsequently synonymized with *H. bowringii*) from Mergui (=Myeik) of the Tenasserim coast. His description noted that the specimen matches Gray's African *Leiurus* with the exception of no webbing at base of the toes. Blyth's description, otherwise, concerns color and pattern. The description is generalized, mentioning "4 longitudinal blackish streaks along the back and sides, 3 or 4 interrupted cross-bands of the some on the upper surface of the tail, . . ." These two traits and the others mentioned by Blyth have a general match with the central and northern Burmese *H. bowringii*

group members. The coloration also matches that of *Hemidactylus garnotii*, which is more boldly striped than *bowringii* group members in the dark phase. The holotype was supposed lost but recently relocated by Das and Dattagupta (1998). Disastrously the specimen has disintegrated and is in fragments. We estimate the SVL of the holotype ZSI 6173 as approx. 56 mm [By assuming the museum tag in Das and Dattagupta (1998) fig. 1 is 19 mm long and SnForel 22 mm; SnForel/SVL averages 38% (Zug et al. 2007); these values yield the SVL estimate.]. At this time, we have no recent *H. bowringii* group specimens from southern Tanintharyi to verify this estimate; however, if our SVL estimate is correct, the Mergui geckos (type locality) are at the upper end of the SVL range of the northern Burmese and southern Chinese populations, and match the average SVL of Burmese *H. garnotii*.

Our study did not encompass samples from west of Myanmar, thus we cannot address the specific status of these populations. These populations are unlikely to be "true" *H. bowringii*. Possibly, they consist of one or both of the new Burmese species; however, for the present, we recommend that their uncertain status be identified by including the *bowringii* epithet in quotes.

Hemidactylus bowringii Species Group Members

Hemidactylus bowringii (Gray, 1845)

Figures 4-6.

Lectotype.—BMNH 2007.1 (formerly 1[1]34 a), an unsexed juvenile without specific locality, presented by C. Bowring in 1842. Smith (1935) restricted the type-locality to Hong Kong, see preceding Taxonomic Notes section for explanation.

PARALECTOTYPES.—BMNH 2007.2 (formerly 1[1]34 a), an unsexed juvenile without specific locality, presented by C. Bowring in 1842.

DIAGNOSIS.— *Hemidactylus bowringii* is a member of the *H. bowringii* species group and differs from other members of this group by the possession of the following set of traits: adult SVL averaging 44.4 mm (range, 40–47 mm); 8–9 fourth finger lamellae (mean, 8.2); 4–6 of fourth finger lamellae divided (5.6); 10–11 fourth toe lamellae (mean, 10.2); 5–7 of fourth toe lamellae divided (6.6); 24–30 precloacal pores in males (28.2); posterior edge of first postmental scales straight or smoothly convex; solid dark lateral stripe from snout to anterior trunk, series of dark dashes forming dorsolateral stripe on trunk, and dorsal surface of tail with dark chevrons bordered posteriorly by white bars.

ETYMOLOGY.— J.E. Gray named this species to acknowledge the donation of the syntypes and other specimens by John Charles Bowring, 1821–1893. See Lazell (2002) for a brief biography of J.C. Bowring.

DESCRIPTION OF THE LECTOTYPE.— The lectotype is the larger of the two syntypes. Both are poorly preserved and presently soft and flaccid, and faded to a uniform whitish tan.

An unsexed juvenile of 32.2 mm SVL, 15.9 mm TrunkL, 13.6 mm SnForel, 3.8 mm ForeaL, 3.8 mm CrusL, and 29 mm TailL (broken). Head pentagonal in outline, snout bluntly pointed, and covered dorsally with small granular scales in juxtaposition: 9.0 mm HeadL, 6.8 mm JawW, 4.0 mm HeadH, 3.6 mm SnEye, 2.7 mm NarEye, 2.7 mm EyeEar, 1.0 mm SnW. Bilateral measurements from right side.

Plate-like head scales confined to margin of mouth; rostral trapezoidal, top edge slightly concave and clefted, bordered behind by 3 internasal scales; naris surrounded by internasal, 2 nasal and rostral scales; 9 (right) Suplab; 7 Inflab; broad triangular mental scale bordered posteriorly by large 1° postmentals; latter abutting posteriorly on lateral half by 2° postmental on each side; posterior border of 1° postmental transversally straight; 2° postmental less than half area of 1° postmental.

Body slightly depressed, moderately robust, covered by small, smooth granular scales dorsally and laterally; scale size increasing gradually from middorsally to ventrolaterally and more abruptly to ventral scales; ventral scales several times larger than dorsal scales, smooth plate-like and slightly overlapping; indistinct ventrolateral fold on each side of trunk. Tail ellipsoidal in cross-section, indistinctly segmented; small granular scales dorsally, gradually enlarging laterally to become cycloid ventrolaterally onto ventral surface, and ventromedially large rectangular and slightly overlapping; ventrolateral fringe indistinct. Limbs well-developed; all digits well-developed, each bearing a claw and digital pad with rectangular lamellae, 7 4FingLm, 5 4FingDv, 10 4ToeLm, 6 ToeDv. 24 femoral and precloacal pores, continuous series on each side (13/11, left/rt), separated medially by 2 nonpore scales.

Coloration from Gray (1845:156): "Grey-brown, with minute specks; tail with narrow pale cross bands, darker-edged in front; limbs and tail white-speckled; . . "

Variation of Hong Kong population.— Adults range 36–52 mm SVL (Table 5; Lazell 2002) averaging ~44 mm. Other body measurements are highly correlated with SVL, and there is no apparent sexual dimorphism in mensural characters. Aside from the presence (males) and absence (females) of precloacal-femoral pores, scalation also appears non-dimorphic. Variance is low ($v \le 8$; Suplab, TotPore, 4FingLm, 4ToeLm) to modest ($v \le 14$; Inflab, 4FingDv, 4ToeDv). Scalation ranges are: 2–3 SnS, 0–1 NaInf, 9–10 Suplab, 6–8 Inflab, 24–30 TotPore, 8–9 4FingLm, 4–6 4FingDv, 10–11 4ToeLm, and 5–7 4ToeDv. We note that Ota's brief description (1989) of Taiwanese *H. bowringii* has 23–31 TotPore and tail without lateral denticulations. These minimal data offer tentative confirmation of *H. bowringii* occurring across southern China to Taiwan and Ryukyu islands.

DISTRIBUTION AND NATURAL HISTORY.— Because our study examined only specimens from the Hong Kong area, we cannot unequivocally claim that *H. bowringii* is the species occurring from eastern Indochina through southern China to Taiwan and the Ryukyus; nevertheless, we recommend that interpretation.

According to Lazell (2002; Hong Kong area), *H. bowringii* is one of the three most abundant reptiles and occurs widely from human dwellings to woodlands. Lazell's reproductive data show egg deposition begins in late March and extends to late August. Hatchlings first appear in late June and then through late September; incubation is approximately 30–45 days. Size-class growth data suggest that *H. bowringii* attain maturity in 9 to 11 mo from hatching.

Hemidactylus berdmorei (Blyth, 1853)

HOLOTYPE.— ZSI 6173. A fragmented specimen (Das and Dattagupta 1998) of questionable sex, derived from "Mergui, where procured by Capt. Berdmore." (Blyth 1853).

DIAGNOSIS.— The fragmentary nature of the type and the absence of a recent series of southern Tanintharyi specimens prevent a characterization of this species. Extrapolation from the dimensions of the head to shoulder fragment of the holotype indicate an approximate SVL of 56 mm.

ETYMOLOGY.— E. Blyth named this species and others for Capt. Thomas Matthew Berdmore, 1811–1859, in appreciation for Berdmore's donation of Burmese specimens. Although a soldier, Capt. Berdmore was in charge of the Forest Office, Calcutta, and in 1849, he accompanied Dr. Falconer of the Calcutta Botanical Garden on a trip to inventory forests in Tenasserim (biographic details *in litt*. C. Wemmer, 1 June 2007).

DESCRIPTION OF THE HOLOTYPE.—Fragmentary.

DISTRIBUTION.— The type derives from the southeastern tip of Myanmar, i.e., southern Tanintharyi State.

COMMENT.— This name is tentatively retained within the *Hemidactylus bowringii* species group. The disintegrating condition of the holotype and the absence of recently collected specimens from the vicinity of the type-locality of *Leiurus Berdmorei* Blyth, 1853 prevent a comparison of these geckos with the central and northern *H. bowringii* group members.

Hemidactylus aquilonius McMahan and Zug, sp. nov. Figures 4, 6, 8.

HOLOTYPE.— CAS 233019, adult male from MYANMAR, **Kachin State**, He Pu village (25°06′14″N 96°21′55″E, Mohnyin Township) collected by a He Pu villager, 17 May 2003.

PARATYPES.— MYANMAR, **Kachin State**, Putao – CAS 221204–205, 221208, USNM 564840; MYANMAR, **Kachin State**, Machanbaw 230218; MYANMAR, **Kachin State**, Pidaung Wildlife Sanctuary – CAS 230368, 230371–374; MYANMAR, **Kachin State**, He Pu village – CAS 232810–811, 232882, 232884, 233000, 233019.

DIAGNOSIS.— *Hemidactylus aquilonius* is a member of the *H. bowringii* species group and differs from other members of this group by the possession of the following set of traits: adult SVL averaging 48.0 mm (range, 40–53 mm); 7–10 fourth finger lamellae (mean, 7.9); 3–6 of fourth finger lamellae divided (5.1); 8–11 fourth toe lamellae (9.9); 4–7 of fourth toe lamellae divided (5.7); 21–32 precloacal pores in males (27.8); posterior edge of first postmental scales usually angular to smoothly convex; dark dorsolateral trunk stripe composed of elongate dash-like spots; and dorsal surface of tail with small, irregular dark spots rarely bordered by white.

ETYMOLOGY.— The specific name is derived from the Latin *aquilonius* for northern or northerly and refers to the northern distribution of this species in Myanmar and adjacent China. The name is proposed as an adjective.

DESCRIPTION OF THE HOLOTYPE.— An adult male of 51.3 mm SVL, 25.8 mm TrunkL, 19.1 mm SnForel, 6.2 mm ForeaL, 7.0 mm CrusL, and 44 mm TailL (reg). Head pentagonal in outline, snout bluntly pointed, and covered dorsally with small granular scales in juxtaposition: 12.9 mm HeadL, 7.8 mm JawW, 5.5 mm HeadH, 5.3 mm SnEye, 3.5 mm NarEye, 4.2 mm Eye-Ear, 1.0 mm SnW. Bilateral measurements from right side.

Plate-like head scales confined to margin of mouth; rostral trapezoidal, top edge slightly concave and depressed, bordered behind usually by 3 internasal scales; 36 interorbital scales; naris surrounded by 2 nasal scales, rostral, and extension of 1st supralabial; 10/9 (left/right) Suplab, 5/4 Suplab in front of anterior edge of eye; 8/8 Inflab; broad triangular mental scale bordered posteriorly by large 1° postmentals; latter bordered on lateral half by 2° postmental on each side; posterior border of 1° and 2° postmental angularly concave. 2° postmental about half area of 1° postmental, left and right postmentals equal sized.

Body slightly depressed, moderately robust, covered by small, smooth granular scales dorsally and laterally; scale size increasing gradually from middorsally to ventrolaterally and more abruptly to ventral scales; ventral scales $\geq 4X$ larger than dorsal scales, smooth cycloid and slightly overlapping; approximately 90 scales around midbody; ventrolateral fold on trunk indistinct. Tail ellipsoidal in cross-section, indistinctly segmented; small granular scales dorsally, gradually enlarging laterally to become cycloid ventrolaterally onto ventral surface, and ventromedially large rectangular and slightly overlapping; ventrolateral fringe not evident. Limbs well-developed; all digits well-developed, each bearing a claw and digital pad with rectangular lamellae, 8/7 4FingLm, 6/4 4FingDv, 10/9 4ToeLm, 6/6 4ToeDv. Femoral and precloacal pores (16/15) continuous on each side, separated medially by 2 nonpore scales.

Coloration in preservative tannish ground color with brown markings. Dorsally head lightly

speckled with tiny brown spots, small irregular brown spots dorsally on neck, trunk and tail; brown spots dorsolaterally and laterally forming vague longitudinal stripes, midlaterally brown stripe from front of eye to axilla through eye and above ear, highly interrupted on trunk and fading on base of tail; longitudinal white spots dorsolaterally from base of neck onto tail. Venter from chin onto tail unicolor light tan.

INTRASPECIFIC VARIATION.— The regional variation of H. aquilonius is described in the preceding Results and Discussion sections as the samples from Yunnan, Kachin, Sagaing, and Mandalay (or northern samples). Briefly, adult size ranges from 40 to 56 mm SVL (Table 5); other body measurements are strongly correlated to overall body size. Body size averages larger in the two northern-most samples (both 49 mm SVL), Mandalay is intermediate, and Sagaing the lowest (44 mm) (Table 3). The smallest adult H. aquilonius occurs at Chatthin. Scalation is generally similar (Table 4) in the four northern samples, and there is no evidence of a north-south or east-west cline with the exception of TotPore. The Yunnan sample averages 29.6 (TotPore), the hightest number of femoral-precloacal pores; Kachin is nearly the same; and Mandalay-Sagaing have a lower TotPore mean, nearly identical to one another (25.6, 25.7, respectively).

A large adult male (56.6 mm SVL) from Pyin-Oo-Lwin was excluded from the Mandalay sample owing to its size and atypical coloration, i.e., unicolor brown

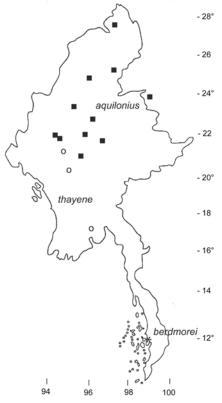


FIGURE 8. Distribution of *Hemidactylus* bowringii group members in Myanmar. *H. aquilonius*, squares; *H. thayene*, circles; *H. berdmorei*, star-burst

dorsally and laterally with the exception a dark brown (although faded) stripe on the trunk. The stripe is punctuated by a series of light tan spots. Its scalation matches other *H. aquilonius* and is now identified as that species.

DISTRIBUTION AND NATURAL HISTORY.—*H. aquilonius* occupies the northern half of Myanmar and adjacent western China (Fig. 9). It extends southward east of the Ayeyarwady River to the Mandalay-Bago border, which also roughly marks the southern limits of the Burmese central dry zone.

The habitat data for Yunnan and Kachin indicate that *H. aquilonius* is a house (commensal) gecko. In contrast, all Chatthin specimens were collected in the forest and on the forest floor amongst leaf litter. At Chatthin, *H. frenatus* was major gecko resident of the park headquarter buildings. At Alaungdaw Kathapa, *H. aquilonius* was collected both on buildings and in the forest. The AK collection notes indicate that individuals were found most frequently on bare banks of streams.

Hemidactylus thayene Zug and McMahan, sp. nov. Figures 4, 6, 8.

HOLOTYPE.— USNM 564821, adult male from MYANMAR, **Magway Division**, Shwe-Settaw Wildlife Sanctuary, Namada River bluff at main station (20°03′33″N 94°35′39″E, ~112 m) collected by Sai Wunna Kyi and George R. Zug, 22 February 2003.

PARATYPES.— MYANMAR: **Magway Division**, Shwe-Settaw Wildlife Sanctuary, in or vicinity of – CAS 213598–599, 213603, 213619, 213779, 213782–783, 213835, 213838, 213840, 213845, 213860–861, 213876–878, 213882, USNM 564822–823, 564825–832.

DIAGNOSIS.— *Hemidactylus thayene* is a member of the *H. bowringii* species group and differs from other members of this group by the possession of the following set of traits: adult SVL averaging 38.2 mm (range, 34–44 mm); 6–8 fourth finger lamellae (mean, 6.9); 3–5 of fourth finger lamellae divided (3.9); 7–11 fourth toe lamellae (mean, 9.2); 4–6 of fourth toe lamellae divided (4.6); 18–26 precloacal pores in males (23.1); posterior edge of first and second postmental scales usually transversally straight; dark dorsolateral trunk stripe of short segment transversely elongate; and dorsal surface of tail with dark chevrons with slight or no light posterior border.

ETYMOLOGY.— The name derives from the Burmese word for ghost, *thaye* – pronounced thayay – and *nge* or *ne* for small, hence yielding *thayenge* or *thayene*. The latter is more euphonious and is used as a noun in apposition. The little ghost epithet refers to the light rustling of leaves created by this gecko's nocturnal foraging on the forest floor during the dry season.

DESCRIPTION OF THE HOLOTYPE.— An adult male of 35.4 mm SVL, 15.5 mm TrunkL, 14.2 mm SnForel, 4.5 mm ForeaL, 5.0 mm CrusL, and 30 mm TailL (regenerated). Head pentagonal in outline, snout bluntly pointed, and covered dorsally with small granular scales in juxtaposition: 8.6 mm HeadL, 5.8 mm JawW, 3.6 mm HeadH, 3.5 mm SnEye, 2.7 mm NarEye, 2.3 mm EyeEar, 0.5 mm SnW. Bilateral measurements from right side.

Plate-like head scales confined to margin of mouth; rostral trapezoidal, top edge slightly concave and clefted, bordered behind by 3 internasal scales; 32 interorbital scales; naris surrounded by 3 nasal scales, and rostral; 10/10 (left/right) Suplab, 4/4 Suplab in front of anterior edge of eye; 9/8 Inflab; broad triangular mental scale bordered posteriorly by large 1° postmentals; latter bordered on lateral half by 2° postmental on each side; posterior border of 1° postmental straight 2° postmental about half area of 1° postmental, left and right postmentals equal sized.

Body slightly depressed, moderately robust, covered by small, smooth granular scales dorsally and laterally; scale size increasing gradually from middorsally to ventrolaterally and more abruptly to ventral scales; ventral scales several times larger than dorsal scales, smooth plate-like and slightly overlapping; approximately 96 scales around midbody; slight ventrolateral fold on trunk. Tail ellipsoidal in cross-section, segmented; small granular scales dorsally, gradually enlarging laterally to become cycloid ventrolaterally onto ventral surface, and ventromedially large rectangular and slightly overlapping; ventrolateral fringe barely evident although enlarged blunt scale on each side at posterior end of segment. Limbs well-developed; all digits well-developed, each bearing a claw and digital pad with rectangular lamellae, 7/7 4FingLm, 3/4 4FingDv, 10/10 4ToeLm, 5/5 4ToeDv. Femoral and precloacal pores (10/11) continuous on right, separated medially by 3 nonpore scales.

Coloration in preservative tannish ground color with brown markings. Dorsally head lightly speckled with tiny brown spots, brown spots dorsally on neck, trunk and tail; brown spots bordered posteriorly by white spots; dorsolaterally dark spots widely separated, midlaterally series of white spots not creating stripe; dark lateral stripe from mid-snout through eye and above ear and faintly to axilla. Venter from chin onto tail unicolor white.

INTRASPECIFIC VARIATION.— The regional variation of *H. thayene* is described in the preceding Results and Discussion sections as the samples from Shin-Ma-Taung, Shwe-Settaw, and Yangon (or southern samples). Briefly, adult size ranges from 34 to 44 mm SVL (Table 5), and most other body metrics are strongly correlated to SVL. Shwe-Settaw has the smallest average adult size (37.5 mm SVL), Yangon individuals are only slightly larger, and Shin-Ma-Taung *H. thayene* are the largest. Scalation is generally similar (Table 4) in the three samples. Shin-Ma-Taung geckos

have the lowest values for most scalation traits, although the ranges of these traits typically overlap broadly.

An adult male from Shwe-Settaw (USNM 564824; 41.1 mm SVL) possesses *H. aquilonius* scalation characteristics. Most striking is the 30 TotPore value, shared only with Yunnan sample geckos. Other scalation features are at the higher end of the range for the three *H. thayene* samples. This specimen was either preserved in the light phase, or if in the dark phase, its coloration is nearly unicolor. We have tentatively identified it as a *H. aquilonius*. Because a tissue sample was obtained when originally collected, our identification can be tested.

DISTRIBUTION AND NATURAL HISTORY.— *H. thayene* occurs from south-central Magway southward to the Ayeyarwady delta (Yangon area) (Fig. 9).

Field notes suggest that *H. thayene* is a forest-floor resident. It was found either at night moving among the leaf litter or during the day beneath litter such as logs and rocks.

Key to Hemidactylus in Myanmar

1a. Dorsally trunk with uniform scalation of small, nearly equal-sized granular scales2 1b. Dorsally trunk with enlarged smooth or keeled tubercles variously arranged among small granular scales5 2a. Adults ≥ 49 to ≤ 68 mm SVL. Secondary postmental scales separated from infralabial scales by one or two rows of small chin scales. Ten to 15 subdigital lamellae on fourth toe of each hindfoot; all lamellae, except terminal one, clefted or divided. Tail strongly dorsoventrally depressed, spindle-shape in cross-section, and with ventrolateral sawtooth-like fringe of point-2b. Adults ≥ 34 to ≤ 58 mm SVL. Secondary postmental scales touch infralabial scales. Six to 11 subdigital lamellae on fourth toe of each hindfoot; some proximal and terminal lamellae entire, mid-digit ones clefted or divided. Tail strongly or weakly depressed, spindle-shape or oblong 3a. Adults \geq 47 to \leq 58 mm SVL. Well-developed skin fold ventrolaterally on trunk and rear of thigh. Webbing between digits of fore- and hindfeet 1/4-1/3 length of digit. Tail strongly dorsally depressed, spindle-shape in cross-section, and with ventrolateral fringe of densely packed 3b. Adults ≥ 34 to ≤ 56 mm SVL. No or weak skin fold ventrolaterally on trunk. Webbing between digits of fore- and hindfeet, if present, limited to base of digits. Tail depressed, oblong in crosssection, without distinct ventrolateral fringe of scales. Adult males with 18-32 precloacal-4a. Adults \geq 39 to \leq 56 mm SVL. Posterior edge of first postmental scales usually angularly convex. Adult males with 21–32 precloacal-femoral pores, usually \geq 26. Dark dorsolateral trunk stripe of elongate dash-like spots; dorsal surface of tail with small, irregular dark spots rarely 4b. Adults ≥ 34 to ≤ 44 mm SVL. Posterior edge of first and second postmental scales usually transversally straight. Adult males with 18–26 precloacal-femoral pores, usually ≤ 24. Dark dorsolateral trunk stripe of short segment transversely elongate; dorsal surface of tail with dark

5a. Adults ≥ 42 to ≤ 59 mm SVL. Dorsally and laterally trunk with six or fewer longitudinal rows of small, widely spaced, smooth tubercles. Tail robust, oblong in cross-section, and strongly

- segmented; each segment with 6 (usually) enlarged, projecting cone-like scales along posterior border. Adult males with 23-34 (usually ≥ 29) precloacal-femoral pores H. frenatus

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Appendix

A. Definition of Morphological Characters

Each character and its abbreviation follow. Abbreviations follow Zug et al. (2003) for ease of recognition. All bilateral characters reported for right side, all measurements in millimeters.

MENSURAL CHARACTERS:

Crus length: CrusL—Length of tibia from knee to heel.

Forearm length: ForeaL—Length of ulna from elbow to wrist.

Eye-ear length: **EyeEar**—Distance from posterior edge of orbit to anterior edge of ear-opening. Head height: **HeadH**—Dorsoventral distance from the top of head to the underside of the jaw at the transverse plane intersecting the angle of jaws.

Head length: **HeadL**—Distance from tip of snout to anterior edge ear-opening.

Jaw width: **JawW**—Straight-line distance from left to right outer edge of jaw angles; this distance does not measure the jaw musculature broadening of the head.

Nares-eye length: NarEye—Distance from nares to anterior edge of orbit.

Snout-eye length: SnEye—Distance from tip of snout to anterior edge of orbit.

Snout-forelimb length: **SnForel**—Distance from tip of snout to anterior border of forelimb insertion.

Snout-vent length: SVL

Snout width: **SnW**—Distance across snout between left and right nares.

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

MERISTIC CHARACTERS:

Chin (postmental) scales: Chin—Medial contact of paired postmental scales.

Chin scale size: **ChinSD**—Size of enlarged or primary postmental scales relative to secondary postmentals.

Asymmetrical chin shield: **ChinSAs**—Comparative size of primary postmental scales, right to left one.

Infralabials: **Inflab**—Number of enlarged scales bordering the mouth from mental to below posterior border of eye.

Naris-infralabial contact: NaInf—Naris abuts or separated from first supralabial.

Snout scales: SnS—Number of scales between left and right nares and touching rostral.

Subcaudal scales: Subcaud—Size of median subcaudal scales relative to adjacent caudal scales.

Supralabials: **Suplab**—Number of enlarged scales bordering the mouth from the rostral to below the posterior border of eye.

Total pores: TotPore—Total number of femoral and precloacal pores.

Fourth finger lamellae (scansors): **4FingLm**—Nuimber of 4th digit lamellae; usually lamellae extend from distal tip of digit to the base of the digit at its intersection with palm. Count includes the distalmost, unpaired lamellae of digital pad.

Fourth finger lamellae divided: **4FingDv**—Number of paired or divided 4th finger lamellae.

Fourth toe lamellae (scansors): 4ToeLm—As for 4FingLm.

Fourth toe lamellae divided: **4ToeDv**—Number of paired or divided 4th toe lamellae.

B. Specimens Examined

Samples are arranged roughly from north to south and east to west, and identified by the locality name used in the text. Some samples are composites. Precise locality data are available from the electronic databases of the California Academy of Sciences' (CAS) and the Smithsonian Institution-National Museum of Natural History's (USNM) webpages.

CHINA: Yunnan *Hemidactylus aquilonius*. Liuku – CAS 207461–462, 207464, 207466, 215039, 215041–042, 215045–048, 228103–104, 228107–109.

MYANMAR: KACHIN [Kachin State] Hemidactylus aquilonius. Putao – CAS 221204–205, 221208, USNM 564840; Machanbaw - 230218; Pidaung Wildlife Sanctuary - CAS 230368, 230371-374; He Pu village - CAS 232810-811, 232882, 232884, 233000, 233019. SAGAING [Sagaing Divis.] Hemidactylus aquilonius. Alaungdaw Kathapa Natl. Park, in or vicinity of - CAS 206649, 215444, 215519, 215759, 215777, USNM 564841-842; Chatthin W.S. - USNM 520552-056, 537425-426; Pale - CAS 215434, 215437; Sweekawngan village - CAS 232243-244. MANDALAY [Mandalay Divis] Hemidactylus aquilonius. Kyidaunggan - CAS 206504; Tha Pyaew village - 208455-456, 208458, 208460; Popa Mountain Park, in or vicinity of -213956, 215827, 231322; Min-Gon-Taung Wildlife Sanctuary, in or vicinity of -215945, 216029, 216068, 231394, 231454; Shwe-U-Daung Wildlife Wildlife Sanctuary, in or vicinity of - CAS 216133, 216345 [Shan State]; Pyin-Oo-Lwin, vicinity of - USNM 564845-849. Shin-Ma-Taung [Magway Divis.] Hemidactylus thayene. Shin-Ma-Taung Wildlife Sanctuary, in or vicinity of - CAS 215841, 215843-844, 215846, 215848, USNM 564833-834. SHWE-SETTAW [Magway Divis.] Hemidactylus thayene. Shwe-Settaw Wildlife Sanctuary, in or vicinity of - CAS 213598-599, 213603, 213619, 213779, 213782-783, 213835, 213838, 213840, 213845, 213860-861, 213876-878, 213882, USNM 564821-823, 564825-832. YANGON [Yangon Divis.] Hemidactylus thayene. Hlawga Wildlife Park – CAS 213320, 213333, 213428, 230426.

CHINA: Hong Kong Hemidactylus bowringii. MCZ R172987, R172989, R172991, R172994–995, R172999–3000, R173003, R173005, R173011.