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TWO NEW CRYPTIC SPECIES OF *TAKYDROMUS* (SQUAMATA: LACERTIDAE) FROM TAIWAN

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ABSTRACT: Two new grass lizard species, previously confused with *Takydromus formosanus*, were identified in Taiwan using mitochondrial DNA sequences. In the present study, 40 morphological characters and their taxonomic significances were assessed using principal components analysis and discriminant analysis. The three species can be distinguished by morphology of body sizes, dorsal and caudal scales, and most importantly, by male coloration during the breeding seasons. The present study increases the total number of *Takydromus* to 19 species, of which 10 are insular endemics, with six only occurring in Taiwan.

Key words: Allopatric speciation; Biogeography; Courtship; Cryptic species; Sexual dichromatism; Sexual dimorphism

THE EAST ASIAN grass lizard genus *Takydromus* Daudin, 1802 (Reptilia: Lacertidae) is widely distributed in the Oriental and eastern Palaearctic regions, with 17 species currently recognized (Arnold, 1997; Chou et al., 2001). With their specialized slender body shapes and extraordinarily long tails (e.g., tail length usually exceeding 380% of snout–vent length (SVL) in *T. sexlineatus*, and nearly 420% of SVL in *T. sauteri*), most *Takydromus* species inhabit grasslands, while others prefer dense scrub or forest edge (Ziegler and Bischoff, 1999; Ziegler et al., 1998). Among the regions of their distribution, the East Asian islands, including Japan, Ryukyu, and Taiwan, harbor the highest diversity of *Takydromus*. Nine of the 17 present species are distributed to this region, while eight species are endemic to these islands. This distributional pattern has led to extensive studies of their systematics and biogeography using morphological characters (Arnold, 1997; Chou et al., 2001) and molecular markers (Lin et al., 2002; Ota et al., 2002).

Lack of the ability to disperse over a long distance may have played a major role in allopatric speciation of these lizards among the islands (Lin, 2003; Lin et al., 2002). A recent study using molecular markers indicated that populations previously identified as *Takydromus formosanus*, an endemic species distributed throughout the lowland regions of Taiwan, are highly differentiated and do not form a monophyletic clade (Lin, 2003; Lin et al., 2002). These studies were initiated by the observation that adult males collected from different geographical regions on the island exhibited distinct color patterns during breeding seasons. Analyses of the mitochondrial DNA sequence data of over 2000 base pairs suggested the existence of three allopatric phylogroups respectively distributed to the northern, eastern, and western parts of Taiwan. These clades show high sequence divergences ranging from 8% to 12% in p-distance. Phylogenetic relationships among these lineages (Fig. 1, modified from Lin, 2003) along with microsatellite genotyping (Wang, 2006) show the existence of two cryptic species based on the following evidence: (1) the three regional populations do not share a most recent common ancestor (Fig. 1); (2) inter-regional sequence divergences of mitochondrial sequence are much higher than intra-regional polymorphisms (>8% versus <1.5%, in p-distance); (3) divergence of mitochondrial sequences among these clades has exceeded that among some other *Takydromus* species (e.g., the three members of the *Takydromus stejnegeri* species group, with interspecific divergence under 5%); (4) prominent genetic differentiation in microsatellite markers (Wang, 2006); and (5) secondary sexual characters differ in mature males (personal observation). Obviously, the taxonomic status of these clades requires a detailed revision. Except for those proposed by Arnold (1989; 1997), more detailed characters are required to distinguish among these lizards.

In the present study, morphological characters of the three regional clades were

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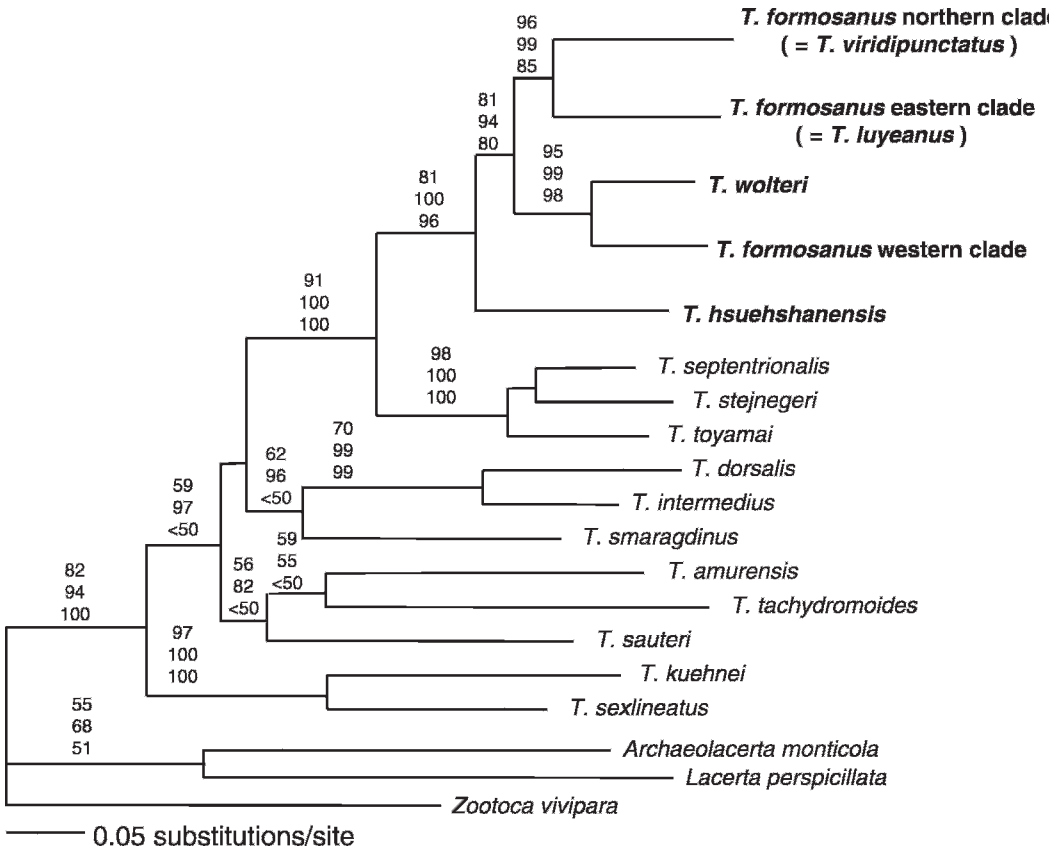

FIG. 1.—Phylogeny of the *Takydromus* populations that were previously identified as *Takydromus formosanus* showing a paraphyly and high genetic differentiation among the three regional clades. This phylogeny was reconstructed based on 1491-bp mitochondrial sequences using maximum likelihood criteria. The three values above each branch represent bootstrap support using maximum likelihood, maximum parsimony, and neighbor joining criteria. Modified from Lin (2003).

measured and compared. The type material of *T. formosanus*, collected in 1894 and now deposited in the British Natural History Museum (Boulenger, 1894), was examined and compared with the specimens recently collected to confirm the taxonomic identity of *T. formosanus*. Principal components analysis and discriminant analysis revealed distinct differences among these regional lineages and represented that the western population should be addressed as the "real" *Takydromus formosanus*. Herein, we describe the northern and the eastern populations as two new species.

MATERIALS AND METHODS

Specimens assigned to *Takydromus formosanus* were first grouped into three regional clades according to both molecular phylogenetic groupings and collection sites (Fig. 2), which are always in congruence (Lin, 2003). Mitochondrial sequences of all the specimens measured in this study were obtained and analysed by Lin (2003). Coloration of each individual was observed and photographed in life. Characters were investigated after the specimens were fixed in 70% ethanol. Only mature individuals were included in this study, with 65, 43, and 28 specimens from the northern, eastern, and western clades, respectively. Various thresholds of maturation were assigned according to the size of the smallest gravid female or the smallest male showing courtship coloration in each clade.

Forty-one morphometric characters were obtained from each individual, including 15

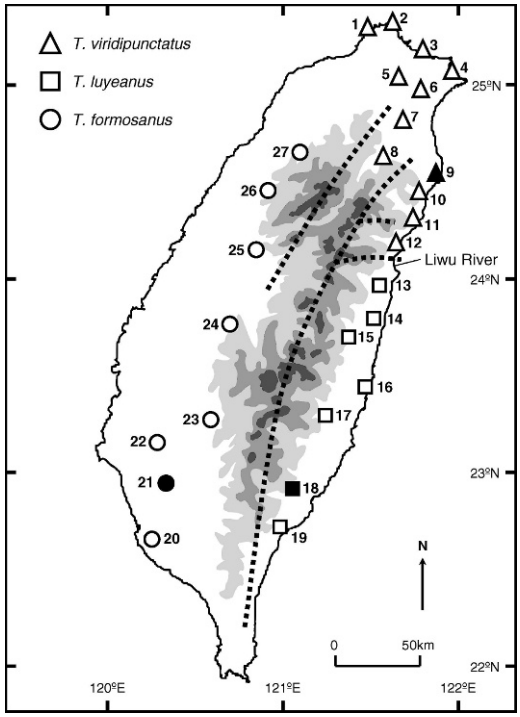

FIG. 2.—Collection sites of *Takydromus viridipunctatus* (triangles), *T. luyeanus* (rectangles), and *T. formosanus* (circles). The closed symbols in the map refer to the type locality of each species. Sample locations are listed as follows: (1) Sanzhi; (2) Wanli; (3) Keelung; (4) Shuangxi; (5) Wuli; (6) Pinglin; (7) Fushan; (8) Qilan; (9) Suao; (10) Dongao; (11) Nanao; (12) Heping; (13) Hualien City; (14) Shoufong; (15) Wanrong; (16) Jingpu; (17) Yuli; (18) Luye; (19) Taidong City; (20) Kaohsiung; (21) Xinhua; (22) Madou; (23) Guanziling; (24) Xitou; (25) Dongshi; (26) Taian; (27) Nanzhuang.

measurements (in length), 24 meristic characters (in number), and 2 qualitative traits (courtship coloration). Measurements were taken with dial calipers to the nearest 0.1 mm, including: snout–vent length (SVL, from tip of snout to anterior margin of vent); tail length (TL, from posterior margin of vent to tail tip, measured only from specimens with complete and original tails); head length (HL, from tip of snout to anterior margin of ear opening); head width (HW, measured at the broadest point); head height (HH, measured at the highest point); skull length (SKL, from tip of snout to posterior margin of occipital); snout–eye length (SEL, from tip of snout to anterior margin of eye); mouth length (ML); snout–arm length (SAL, from tip of snout to anterior margin of forelimb); arm-leg length (ALL, from middle of the forelimb to middle of hind leg); humerus length (HML); radius-ulna length (RUL); femur length (FML); tibia-fibula length (TFL); and longest toe length (LTL, length of fourth toe on hind limb). All measurements were taken from the left side of the lizard. Statistical analysis of various characters among three species was performed using one way ANOVA and Tukey test. Comparisons of body size between sexes of the same species were carried out by *t*-test (Zar, 1999).

Definition of scales followed those of Arnold (1989, 1997) unless otherwise noted. The 24 meristic characters include: chin-shields (CS); femoral pores (FP); supralabials (SL); infralabials (IL); supraocular (SO); supraciliary (SC); supratemporals (ST); anterior dorsal scale rows (ADS, distinctly enlarged and keeled scales on anterior dorsum, counted transversely at position of forelimbs); posterior dorsal scale rows (PDS, counted transversely at the position of hind limbs); dorsal scale numbers (DSN, counted longitudinally from posterior margin of occipital to posterior margin of hind limbs); ventral rows (VR, counted transversely at midbody); ventral scale numbers (VN, counted longitudinally from the posterior margin of collars to the anterior margin of preanal scales, took average from the middle two rows); paraventrals (PVT, enlarged and keeled scales above ventrals, could be counted transversely from both sides); caudal scales (CDS, counted around the tail at the position of the 11th to 15th scale to avoid the difference between males and females); and subdigital lamellae on fingers (SDF1 to SDF5) and toes (SDT1 to SDT5). We took an average of these meristic characters from both sides of the body except for ADS, PDS, VR and CDS. Comparisons of meristic characters among species were carried out by Kruskal-Wallis test (Zar, 1999).

The last two characters evaluated in this study are the color of lateral surface and the color spots on this area. According to our recent observations (Y. R. Chen and S.-M. Lin, unpublished data), we suspected that these spots can be an indicator of maturation in males.

In the original description by Boulenger (1894), *T. formosanus* was described based on "several specimens" without indicating the sample size. We located five specimens that might represent the syntypes in the Natural History Museum, London. The first specimen, an adult male collected by P. A. Holst in January 1894 from "Taiwanfoo, Central Formosa", is much larger in size than the others and preserved individually. The other four specimens, collected in November 1894, are immature individuals and were preserved together. To assign the type specimen to one of the three groups, the same set of characters as above were evaluated from the first specimen.

Principal components analysis (PCA) and discriminant analysis (DA) were carried out using Statistica (StatSoft, Inc.) and S-PLUS 2000 (Lucent Tech., Inc.), respectively. Only characters representing significant interspecific differences were included in the analyses. Although all measurements showed significant differences between the western and the other two clades, they were all highly correlated to SVL. Hence, only SVL, along with 19 meristic characters (see Table 1) and 2 qualitative traits, were included in these analyses. Analyses were conducted separately for the two sexes.

Results

SVL, HL, and the 24 meristic characters of the three regional clades are listed in Table 1. All 15 measurements (only SVL and HL are shown in the table) and 19 among the 24 meristic characters demonstrated interspecific significance. The western clade has a smallest body size in all measurements, while the northern clade were largest.

Sexual dimorphism was observed in the northern and the eastern clades (Table 2), but not in the western one. Male individuals of the northern clade have numerous tiny green spots on their lateral surfaces with a pale-brown background, while that of the eastern clade have yellow spots on a blackish or dark-brown background. In contrast, spots on the lateral surface were absent in females of both clades, as well as both sexes from the western clade. However, the lateral surfaces of females of the northern and the eastern clades are pale-brown, while that of the western clade (both sexes) are red-brown. The western clade has a significantly larger snout–vent length in females, while the northern and the eastern clades have significantly larger head length (Table 2).

The PCA ordination plots clearly shows morphometric differences among the three regional clades in males, but fail to distinguish between the northern and the eastern clades in females (Fig. 3). The first two principal components accounted for 46.70% of variation in males and 47.43% in females. However, females could be further distinguished by the discriminant analysis (Fig. 4). Separation of the western clade from the others are contributed by their smaller SVL, lack of lateral spots, and higher scale numbers in supratemporals (ST), caudal scales (CDS), subdigital lamellae (SDF and SDT). Separation between the northern and eastern clades are contributed by supraciliary (SC), supratemporals (ST), dorsal scale numbers (DSN), and differences in their lateral colors (for males). In both analyses, the type specimen of *T. formosanus* is allocated to the western clade. These evidences indicate that the name of *T. formosanus* should be applied to the western clade, while the northern and eastern clades should be treated as new species.

Discussion

Two newly discovered cryptic species, named as *T. viridipunctatus* (the northern clade) and *T. luyeanus* (the eastern clade), were misidentified as *T. formosanus* in the past several decades. One of the issues that kept them undiscovered is possibly because numbers of chin shields and femoral pores was the major diagnostic characters for this genus. These three species do not show variation in these characters; they each have three pairs of chin shields and two pairs of femoral pores (Table 3). Although chin shields and femoral pores are sufficient for distinguishing among other species of *Takydromus* occurring in Taiwan and adjacent regions, these characters are not sensitive enough to provide a diagnosis among the *T. formosanus* species group. Most pictures noted as "*T. formosanus*" in literature were

TABLE 1.—Measurements (SVL and HL only) and meristic characters of *T. formosanus* (the western clade), *T. viridipunctatus* (the northern clade), and *T. luyeanus* (the eastern clade) represented by mean ± SD. Comparisons among species were carried out by one way ANOVA and Tukey test. See text for description of characters.

Characters	*T. formosanus* (n = 28)	*T. viridipunctatus* (n = 65)	*T. luyeanus* (n = 43)
SVL(mm)**	42.42 ± 4.17^{c} (37.2–52.6)	51.32 ± 3.14^{a} (44.5–59.5)	48.73 ± 2.65^{b} (42.3–54.2)
HL(mm)**	9.76 ± 0.67^{c} (8.9–11.2)	11.51 ± 0.97^{a} (9.8–13.9)	11.06 ± 0.86^{b} (9.6–12.5)
CS	3.00 ± 0.00 (3)	3.02 ± 0.09 (3; occasionally 4)	3.01 ± 0.07 (3; 4 in one case)
FP	2.00 ± 0.00 (2)	2.10 ± 0.28 (2; occasionally 3)	2.14 ± 0.18 (2; occasionally 3)
SL*	6.04 ± 0.27^{a} (5–7; usually 6)	5.85 ± 0.38^{b} (5–7; usually 6)	6.01 ± 0.27^{ab} (5–7; usually 6)
IL	5.09 ± 0.33 (4–6; usually 5)	5.05 ± 0.17 (4–6; usually 5)	5.08 ± 0.21 (4–6; usually 5)
SO	4.02 ± 0.09 (4; 5 in one case)	3.95 ± 0.24 (3–5; usually 4)	4.00 ± 0.11 (3–5; usually 4)
SC**	4.37 ± 0.45^{a} (4–5; 3 in one case)	4.02 ± 0.51^{b} (3–6; usually 4)	4.41 ± 0.56^{a} (3–6; usually 4)
ST**	4.59 ± 0.66^{a} (4–6)	2.57 ± 0.65^{c} (2–3; occasionally 4)	3.13 ± 0.55^{b} (2–4)
ADS**	7.93 ± 0.26^{b} (8; 7 in two cases)	8.38 ± 0.65^{a} (8–10; usually 8)	8.09 ± 0.42^{b} (7–10; usually 8)
PDS**	7.26 ± 0.44^{a} (7–8)	6.97 ± 0.47^{b} (6–8; usually 7)	6.62 ± 0.53^{c} (6–7; 8 in one case)
DSN**	46.78 ± 1.71^{a} (44–50)	45.63 ± 2.20^{b} (43–51)	40.62 ± 1.56^{c} (37–43)
VR	8.00 ± 0.00 (8)	8.00 ± 0.00 (8)	8.00 ± 0.00 (8)
VN**	31.44 ± 1.20^{ab} (29–34)	30.71 ± 1.31^{b} (28–33)	32.18 ± 1.39^{a} (29–35)
PVT**	3.19 ± 0.37^{b} (3–4)	3.14 ± 0.35^{b} (3–4)	3.66 ± 0.45^{a} (3–4)
CDS**	15.93 ± 0.38^{a} (16; 14 in 1 case)	14.00 ± 0.00^{c} (14)	14.33 ± 0.71^{b} (14; 15 in 2 and 16 in 4 cases)
SDF1**	8.22 ± 0.42^{a} (8–9)	7.32 ± 0.59^{b} (6–8)	7.40 ± 0.50^{b} (7–8)
SDF2**	12.00 ± 0.54^{a} (11–13)	11.58 ± 0.68^{b} (10–13)	11.42 ± 0.75^{b} (10–13)
SDF3**	17.56 ± 0.69^{a} (16–18)	16.75 ± 1.10^{b} (15–19)	16.60 ± 0.89^{b} (15–18)
SDF4**	21.37 ± 0.96^{a} (19–23)	20.84 ± 1.14^{b} (18–23)	20.36 ± 1.23^{b} (18–22)
SDF5**	12.07 ± 0.47^{a} (11–13)	10.88 ± 0.60^{b} (9–12)	11.13 ± 0.59^{b} (10–12)
SDT1**	8.81 ± 0.57^{a} (8–10)	8.23 ± 0.61^{b} (7–9)	8.60 ± 0.62^{a} (7–10)
SDT2**	14.15 ± 0.85^{a} (12–16)	13.29 ± 0.79^{b} (12–15)	13.20 ± 0.99^{b} (12–17)
SDT3**	20.22 ± 1.29^{a} (16–22)	19.40 ± 1.25^{b} (17–22)	19.36 ± 1.21^{b} (17–22)
SDT4**	27.33 ± 1.33^{a} (26–30)	26.12 ± 1.58^{b} (23–30)	26.22 ± 1.54^{b} (23–31)
SDT5**	16.41 ± 1.03^{a} (15–19)	14.86 ± 0.88^{c} (14–17)	15.49 ± 1.04^{b} (14–18)

*$P < 0.05$; **$P < 0.01$

TABLE 2.—Comparison between males and females of *T. formosanus*, *T. viridipunctatus*, and *T. luyeanus*. Statistical significance was calculated by *t*-test. SVL = snout–vent length; HL = head length.

		SVL (mm)		HL (mm)		HL/SVL (%)	
T. formosanus	♂	40.56 ± 3.19	**$P = 0.0262$**	9.69 ± 0.81	$P = 0.5618$	23.89 ± 0.61	**$P = 0.0025$**
	♀	44.27 ± 4.89		9.84 ± 0.57		22.37 ± 1.45	
T. viridipunctatus	♂	51.54 ± 2.78	$P = 0.5551$	12.35 ± 0.75	**$P < 0.0001$**	23.95 ± 0.82	**$P < 0.0001$**
	♀	51.02 ± 3.61		10.69 ± 0.58		20.99 ± 0.85	
T. luyeanus	♂	49.30 ± 2.60	$P = 0.3297$	12.22 ± 0.73	**$P < 0.0001$**	24.78 ± 0.78	**$P < 0.0001$**
	♀	48.50 ± 2.86		10.45 ± 0.43		21.60 ± 1.14	

taken near Taipei City and are actually *T. viridipunctatus*.

Differences among species in coloration of males in breeding seasons suggest differentiation in their courtship strategies. Another clue for such a difference comes from their body sizes and HL/SVL ratio. *Takydromus formosanus*, the only species among the three without sexual dichromatism, has females with larger body sizes than males ($P < 0.05$, Table 2). In contrast, *T. viridipunctatus* and *T. luyeanus*, which exhibit prominent sexual dichromatism, have males and females with similar body sizes but differ in their head lengths and HL/SVL ratios ($P < 0.05$, Table 2). These observations strengthen the validity of these newly discovered species, not only in the view point of the "phylogenetic species concept" (e.g., monophyly, genetic specialty, and diagnostic characters), but also in the view point of "biological species concept" (reproductive isolation). Experiments in sexual selection and courtship behavior have been initiated in our laboratory to answer some of these questions.

Arnold (1997) reviewed the entire genus of *Takydromus*. Excluding the uncertain species *T. haughtonianus* Jerdon, 1870 (known from the single type specimen and representing overlapping characters of *T. sexlineatus*), 16 species were recognized. Discovery of *T. hani* (Chou et al., 2001) from Vietnam brought the number of species in this genus to 17, while our study increases that number to 19. It is noticeable that 10 of these species are island-endemic, and most of them are distributed in restricted areas. According to our current knowledge, coexistence of different *Takydromus* species has never been observed in any other East Asian island (Arnold, 1997; Lin et al., 2002; Ota et al., 2002). Most *Takydromus* species are adapted to similar niches, with interspecific competition possibly being the major reason for the rarity of sympatric distributions in this genus (Lin et al., 2002; Ota et al., 2002). With seven species, including six endemics, Taiwan represents the highest species diversity of *Takydromus* in the world.

Lin et al., (2002) and Ota el al. (2002) investigated the molecular phylogeny and biogeography of *Takydromus* on East Asian islands, and both studies suggested that their diversification was possibly due to the highly complex topography and paleogeological events on these islands. Mountains on Taiwan Island may have played an important role as natural barriers for these species. In the case of the *Takydromus formosanus* species group, the Central Mountain Range (positioned northeast to southwest) separates *T. luyeanus* from the others, while the Miaoli Plateau further separates *T. viridipunctatus* from *T. formosanus*. *Takydromus hsuehshanensis* is restricted to high mountain regions with elevations over 2000 m, completely isolated from the other closely related species.

The boundary between neighboring species is in need of further investigations. Artificial deforestation should facilitate the dispersal and colonization of these grass-inhabiting species and subsequently obscure their original barriers, in result of negative effects on conservation of these endemic species. Recently, we have greatly enlarged our sample sizes and delimitate these specimens using both morphological and genetic markers. In the case of *T. viridipunctatus* and *T. luyeanus*, we have traced the species boundary to a narrow range of less than 5 km (near the Liwu

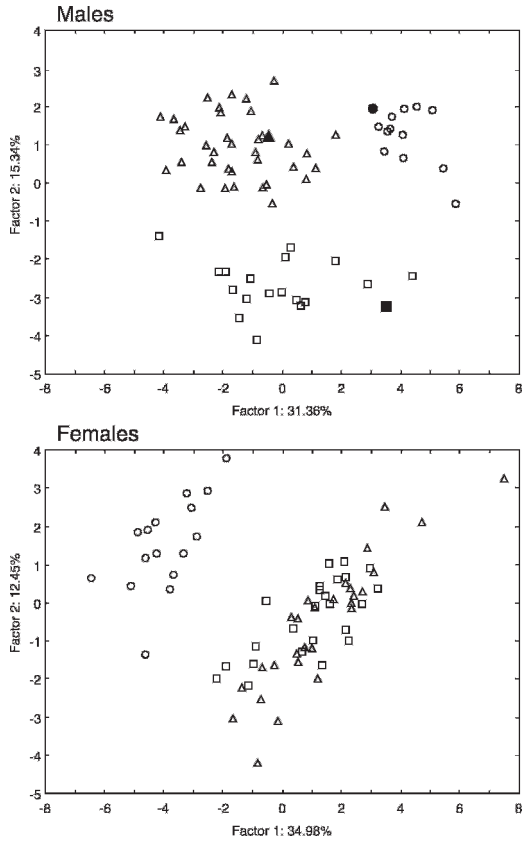

FIG. 3.—Principle compents analysis (PCA) of *Takydromus formosanus* (circles), *T. viridipunctatus* (triangles), and *T. luyeanus* (rectangles). The closed symbols indicate the type specimen for each species.

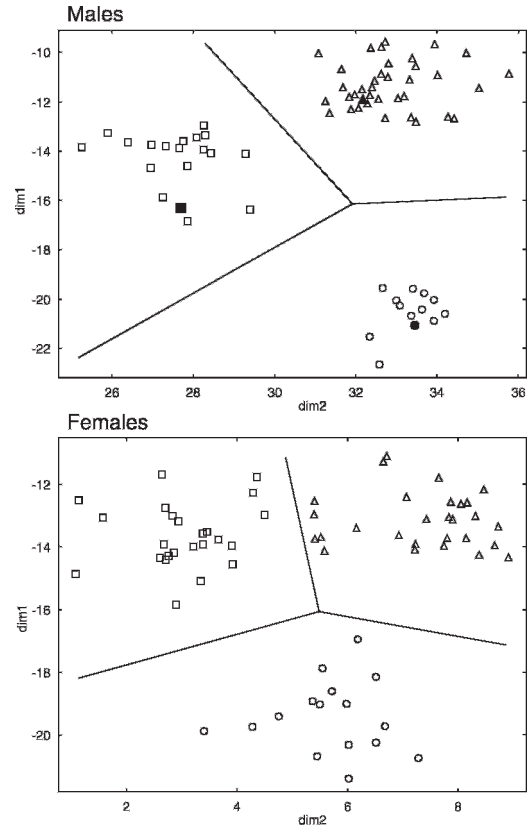

FIG. 4.—Discriminant analysis (DA) of *Takydromus formosanus* (circles), *T. viridipunctatus* (triangles), and *T. luyeanus* (rectangles). The closed symbols indicate the type specimen for each species.

River, see Fig. 2). An evolutionary study focusing on their contact zones is our major approach in the future.

SPECIES ACCOUNTS

Takydromus **viridipunctatus** *sp. nov.*

Takydromus formosanus auct. non. Boulenger, 1894; Chen, 1956 (in part): 337; Wang and Wang, 1956 (in part): 39; Chen, 1969 (in part): 96; Chen and Yu, 1984 (in part): 102; Lin and Cheng, 1990 (in part): 80–82, Fig. 82, ♂ (not *T. stejnegeri*); Lue et al. 1987 (in part): 72–74, Fig. 72–73, ♂, Fig. 74, ♀; Lue, 1990 (in part): 45, Fig. 45, ♂; Zhao and Adler, 1993 (in part): 206; Arnold, 1997 (in part): 273; Lue et al. 1999 (in part): 122–123, Fig. 122 (upper), ♂, Fig. 123, ♂; Zhao et al. 1999 (in part): 260–261; Shang, 2001 (in part): 87–89, Figs. 87, ♂ (upper) and juvenile (lower), Figs. 88, ♂ (upper) and ♀ (lower); Lin et al. 2002 (in part); Ota et al. 2002 (in part); Schlüter, 2003 (in part): 54–55, Fig. 54–55, ♂.

Holotype.—NMNS 4431, an adult male (Figs. 5, 7) from Su-ao, Yilan County, Taiwan (24° 35′ 23.4″ N, 121° 51′ 37.5″ E; see Fig. 2). Captured when perching on high grasslands (*Miscanthus sinensis*) near the coastline at an elevation of 10 m. Collected at night on 21 June 2003 by Yu-Jun Hong, How-Ying Hsu, Yi-Fen Chen, and Si-Min Lin. Deposited in Natural Museum of Natural Science, Taichung, Taiwan.

Paratypes.—Thirteen adult males and 11 adult females. Collected from Su-ao (BMNH 2008.266♂; NMNS 4432-02♂, 4432-03♂, 4432-04♂; NTNUB 241501♂, 241502♂), Dong-ao (USNM 565984♂, 565985♀; NMNS

TABLE 3.—Comparison among the seven *Takydromus* species in Taiwan.

	Chin shields	Femoral pores	Ventrals	Longitudinal Dorsal number	Caudal scales	Lateral spots in males	Distribution in the world	Population status
T. formosanus	3	2	Keeled	44–47	16	Absent	Endemic to western Taiwan	Very common
T. viridipunctatus	3	2	Keeled	43–51	14	Lemon green	Endemic to northern Taiwan and Guashan Islet	Very common
T. luyeanus	3	2	Keeled	37–43	14	White or yellow	Endemic to eastern Taiwan and Ludao Islet	Very common
T. hsuehshanensis	3	2	Smooth	38–46	14	Green	Endemic to high mountains in Taiwan	Locally common
T. stejnegeri	3	1	Keeled	42–48	14–16	Absent	Endemic to western and northern Taiwan, and Penghu Archipelago	Very common
T. sauteri	4	1	Keeled	54–58	10	Absent	Endemic to eastern Taiwan, and Lanyu Islet	Common in Lanyu, but rare in Taiwan
T. kuehnei	4	3–5	Smooth	44–48*	14	Light yellow	South-eastern China, Taiwan (*T. k. kuehnei*) and Vietnam (*T. k. vietnamensis*)	Widely spread but uncommon

* Longitudinal dorsal number of *T. kuehnei* was based on a fewer sample size. More than 20 individuals were observed in the other 6 species.

4432-05♂, 4432-09♀), and Nan-ao (BMNH 2008.267♀; NMNS 4432-10♀; NTNUB 241503♂, 241504♂, 241509♀, 241510♀) by Yu-Jun Hung and Si-Min Lin. Collected from Sanzhi by Yu-Jen Liang, Ying-Rong Chen and Si-Min Lin (NMNS 4432-01♂, 4432-06♀; NTNUB 241507♀, 241508♀). Collected from Jinshan by Ying-Rong Chen, Kun-Yan Chung, and Si-Min Lin (NMNS 4432-07♀, 4432-08♀). Collected from Wanli (NTNUB 241505♂) and Pingxi (NTNUB 241506♂) by Si-Min Lin. All individuals were collected from the habitat of *Miscanthus* grasslands. Separately deposited in the Natural History Museum, London (the BMNH series, 1 male and 1 female); National Museum of Natural History, Washington DC (the USNM series, 1 male and 1 female); Natural Museum of Natural Science, Taiwan (the NMNS series, 5 males and 5 females); and National Taiwan Normal University (the NTNUB series, 6 males and 4 females).

Referred specimens.—Males: FORN3801 from Sanzhi; FORN2621, 2622, 2623, 2624, 2625, 2626 from Keelung; FORN1001 from Shuangxi; FORN1625, 1627, 1628, 1629 from Wulai; FORN0406, 0408, 0410, 0413, 0415 from Qilan; FORN3507, 3518, 3531, 3532 from Su-ao; and FORN0203, 0215, 0216, 3705 from Nanao. Females: FORN3802, 3803, 3804 from Sanzhi; FORN2631, 2632, 2633, 2634 from Keelung; FORN1517, 1518 from Fushan; FORN0412 from Qilan; FORN3606 from Dong-ao; FORN 0204, 0206, 3706, 3707, 3708, 3709, 3712, 3713 from Nanao; and FORN0104 from Heping.

Diagnosis.—Number of chin shields and femoral pores are commonly applied as the most important characters distinguishing among the *Takydromus* species in Taiwan and adjacent regions. Only 4 among the 19 currently recognized species in this genus exhibit "3 pairs of chin shields" and "2 pairs of femoral pores": *T. hsuehshanensis*, *T. formosanus*, *T. viridipunctatus*, and *T. luyeanus* (Table 3). Conjunction of these two characters helps to separate these four species from the others.

Takydromus viridipunctatus can be distinguished from *T. hsuehshanensis* by its keeled ventrals. *Takydromus hsuehshanensis* is the only one among the four that has smooth ventrals. *Takydromus hsuehshanensis* has a comparatively robust body shape, stronger

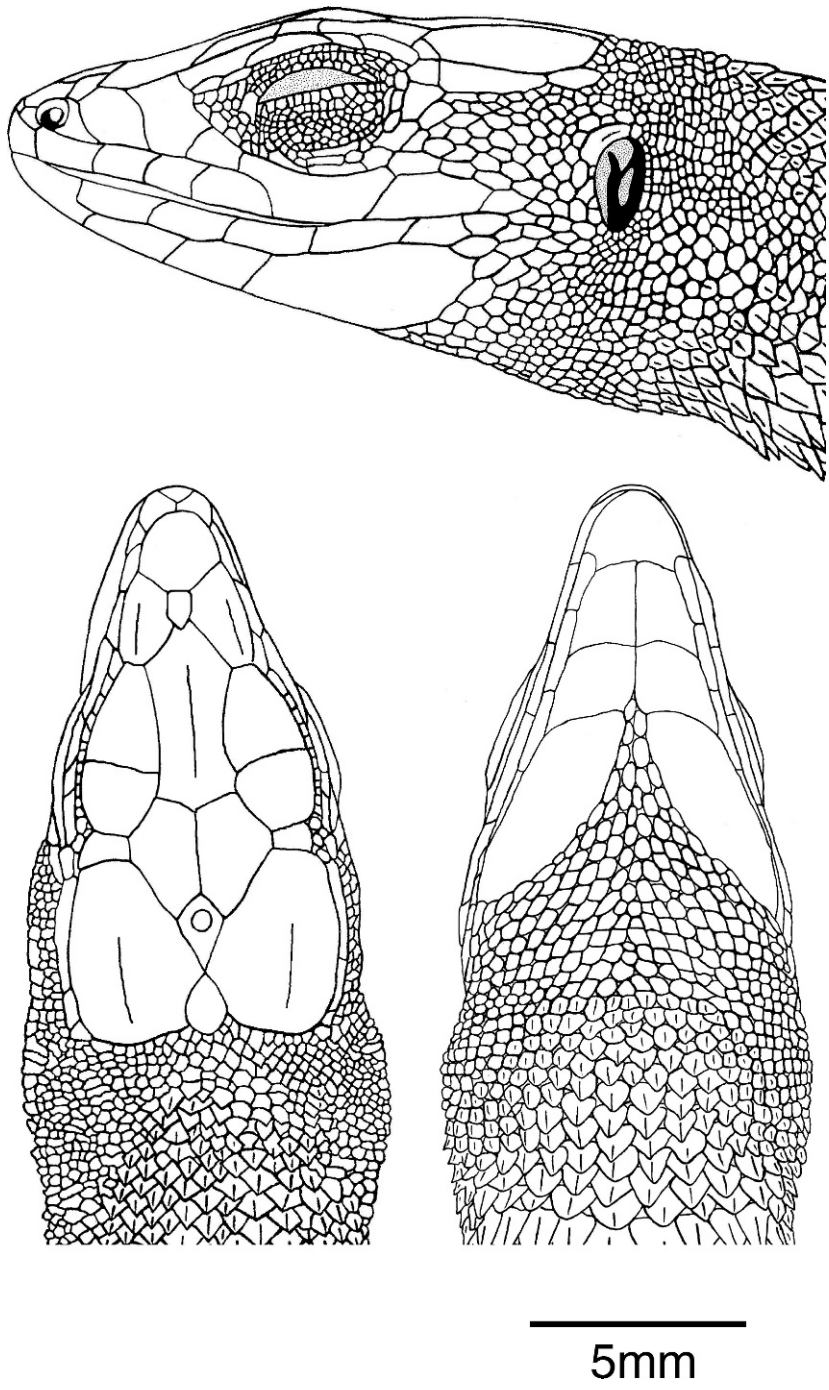

FIG. 5.—Head of the holotype of *Takydromus viridipunctatus* (NMNS 4431) in lateral (upper), dorsal (lower-left), and ventral (lower-right) views.

FIG. 6.—(A) *Takydromus viridipunctatus*, holotype, NMNS 4431, adult male, 51.3 mm SVL; (B) *T. viridipunctatus*, paratype, CCULS 1517, adult female, 49.2 mm SVL; (C) *T. luyeanus*, holotype, NMNS 4433, adult male, 50.6 mm SVL; (D) *T. luyeanus*, paratype, NTNUB 241508, adult female, 47.2 mm SVL; compared to (E) *T. formosanus*, CCULS 2217, adult male, 39.1 mm SVL; and (F) *T. formosanus*, CCULS 1702, adult female, 48.6 mm SVL.

limbs and toes, a shorter tail without curling ability, and poor ability to climb on vegetation (Huang, 1998; and K.-Y. Lue and S.-M. Lin, personal observation).

Takydromus viridipunctatus can be distinguished from *T. formosanus* by fewer caudal scale rows at the position of the 11th to 15th scales (14 versus 16 rows), fewer supratemporals (2 or 3 versus >4), fewer subdigital lamellae in the fingers and toes, and a larger and more robust body shape (see Table 1). About 70% of mature *T. viridipunctatus* reached an SVL of over 50 mm (mean ± SD = 51.32 ± 3.14 mm), but no *T. formosanus* reached this size (42.80 ± 4.55 mm). In addition, adults of *T. viridipunctatus* exhibit noticeable sexual dimorphism (Fig. 6). Males of *T. viridipunctatus* exhibit shiny light-green

spots along the lateral surface during breeding seasons, sometimes covering the entire lateral surface of the trunk. In contrast, coloration of *T. formosanus* is brown year round, with no sexual dichromatism (Fig. 6).

Takydromus viridipunctatus can be distinguished from *T. luyeanus* by having more dorsal scales counted in longitudinal direction (45.58 ± 2.23 versus 40.62 ± 1.56). Mature males of *T. viridipunctatus* exhibit light-green spots with a light-brown background, whereas *T. luyeanus* has a black lateral background decorated with white or light-yellow spots. Adults of *T. viridipunctatus* usually have a slightly larger body size (SVL = 51.32 ± 3.14 mm versus 48.86 ± 2.74 mm).

Takydromus viridipunctatus is sometimes found sympatrically distributed with *T. stejnegeri* and *T. kuehnei* in northern Taiwan. It can be distinguished from *T. stejnegeri* by a difference in number of femoral pores in each side (2 versus 1). It can be distinguished from *T. kuehnei* by fewer femoral pores (2 versus 3–5 pairs) and fewer chin shields (3 versus 4 pairs).

Description of the Takydromus viridipunctatus *holotype*.—Measurements (in mm): SVL 51.9, HL 12.2, HW 7.0, HH 6.3, TL 120.25. Rostral separated from frontonasal by supranasals; nostril surrounded by supranasal, postnasal, and anteriormost supralabial; supralabials six and infralabials five at each side; supraoculars four at each side, the anteriormost and the posteriormost ones much smaller than others; supraciliaries four at each side, relative lengths 2 > 1 > 4 > 3; anteriormost supraciliary in contact with anteriormost supraocular, posterior three supraciliaries separated from posterior supraoculars by supraciliary granules; supraciliary granules 14 on left, 12 on right; postnasal one, followed by two loreals at each side, anterior loreal smaller than posterior one; three prefrontals separating frontal from frontonasal, the middle one much smaller than surrounding scales; frontal hexagonal, weakly keeled; frontoparietals two and connected; parietals two, slightly keeled, separated by interparietal and occipital; supratemporals two at each side, the first one nearly twice as long as the second; temporal scales imbricate, slightly keeled, slightly larger than scales posterior to ear opining; three pairs of chin shields, anteriormost two pairs in contact medially; collars distinct, in 11 rows; dorsal scales on body enlarged, imbricate, strongly keeled and obtusely pointed, extending anteriorly beyond forelimbs on to neck, in nine rows at position of forelimbs and seven rows at hind limbs, the central row much smaller and not continuous; 48 and 46 scales counted longitudinally from occipital to the posterior margin of hind limb on middle-left and middle-right rows, respectively; lateral body scales small and relatively uniform in size, granular, arranged in disorder, roughly 7–9 rows on each side at midbody; ventrals slightly mucronate, strongly keeled, obtusely pointed, in eight longitudinal rows, thirty-one scales counted longitudinally from collars to preanal on middlemost two rows; paraventrals in three rows on left and four rows on right side, strongly keeled, the first row (adjacent to the ventrals) about the same size as the ventrals, the others gradually diminishing in size; preanal single, enlarged, with two distinct longitudinal keels, and with a pair of keeled scales of similar length but one-third width beside; two femoral pores on each side; scales on anterior and dorsal surfaces of forelimbs enlarged, keeled, rhomboid, and imbricate; scales on posterior and ventral surfaces of arms small and granular; scales on ventral surface of forearms smooth, with three enlarged rows; two rows of large scales on anterior surfaces of thighs, strongly keeled, rhomboid, and imbricate; three rows of large scales on ventral surfaces of thighs, slightly keeled, diminishing in size posteriorly; four rows of enlarged scales on anterior and ventral surfaces of legs, the largest row smooth and hexagonal, 150% to 200% wider than the neighboring rows, the other rows keeled and rhimboid; relative lengths of appressed fingers IV > III > II = V > I; subdigital lamellae eight (left) – eight (right), 12-12, 18-18, 22-21, 12-11 on fingers I, II, III, IV, and V, respectively; relative lengths of appressed toes IV > III > V > II > 1; subdigital lamellae nine (left) – nine (right), 14-14, 20-21, 27-27, 15-15 on fingers I, II, III, IV, and V, respectively; tail long (232% of SVL), posterior 80.7 mm regenerated; covered with strongly keeled scales, in 18 rows at base,

decreased to 14 rows and remained stable from the 5th scale.

Color in life.—Pupil golden to golden bronze; dorsal surfaces of head, body, and tail brown; ventral surfaces of head, body, and tail white to pale brown; upper arm, thigh, and proximal portions of forearm and shank brown; distal portions of forearm and shank pale brown or pale orange; digits dark brown. In mature males, two thick white stripes extend posteriorly. The first begins from the supraocular, extend through the outer-most row of dorsals and upper edge of hind limb, and ending at the posterior part of hind limb. The second begins at the supralabials, through lower part of ear opening and upper edge of fore limbs, and end at anterior part of the hind limbs. In females, these two stripes became pale brown; the anterior half of the second stripe sometimes green or greenish yellow. A thin black stripe, closely beside the upper edge of the second white stripe, extending posteriorly from nasal to anterior edge of the forelimb, interrupted by eye and ear. The lateral area between the two stripes brown; decorated with light green spots in mature males during breeding seasons, which sometimes cover the entire lateral surface. Juveniles lack stripes and decorations on lateral surfaces.

Color in ethanol.—Green spots in life faded to pale blue or bluish white; other colors similar to those in life.

Variation.—Meristic and morphometric data of *T. viridipunctatus* are shown in Table 1 and concluded in Table 3. Dorsal scales counted in longitudinal direction range between 43 and 51. Number of caudal scales is consistently 14. Number of femoral pores is usually 2, occasionally 3.

Distribution and ecology.—*Takydromus viridipunctatus* is only known from the northeastern part of Taiwan, including Taipei City, Taipei County, Yilan County, and the northern margin of Hualien County (Fig. 2). This species is found in a variety of environments, including grasslands, farms, gardens, shrubs, and edge of forests, from coastline to an elevation of about 1000 m (Yang-Ming Mountain). They spend the daytime in a variety of different environments, but spend most of the night perching on grasses, especially *Miscanthus* spp., the most abundant grass species in subtropical Taiwan. Inhabiting moderately to highly disturbed environments, this species can be treated as an indicator of deforestation and human activity. Population density was very high so that up to 300 individuals could be captured by 6 collectors within a 500 m transect in a single summer night.

In some places, this species is sympatrically distributed with *T. stejnegeri* and *T. kuehnei*. However, *T. stejnegeri* seems to prefer more open habitat, and demonstrates a better tolerance to human activities. *Takydromus kuehnei* exclusively inhabits the edge of forests and spends most of their time on shrubs and trees.

Clutch size two, sometimes three (about 10% ratio). Gravid females are found during May to August. At least two clutches are produced during late spring to early summer, and more clutches are possibly produced if in good nutritional conditions.

Etymology.—This specific name refers to the "green spotted" (*viridi* + *punctatus*) lateral surfaces of mature males during the breeding seasons.

Takydromus **luyeanus** *sp. nov.*

Takydromus formosanus auct. non. Boulenger, 1894: 462; Chen, 1956 (in part): 337; Wang and Wang, 1956 (in part): 39; Chen, 1969 (in part): 96; Chen and Yu, 1984 (in part): 102; Lin and Cheng, 1990 (in part): 80–82; Lue et al. 1987 (in part): 72–74; Lue, 1990 (in part): 45; Zhao and Adler, 1993 (in part): 206; Arnold, 1997 (in part): 273; Lue et al. 1999 (in part): 122–123; Zhao et al. 1999 (in part): 260–261; Shang, 2001 (in part): 87–89, Figs. 89, ♂ (uppermost); Lin et al. 2002 (in part); Ota et al. 2002 (in part); Schlüter, 2003 (in part).

Holotype.—NMNS 4433, an adult male (Figs. 6, 7) from Luye, Taidong County, Taiwan (22° 53′ 47.0″ N, 121° 05′ 19.0″ E; see Fig. 2). Perching on high grasslands (*Miscanthus sinensis*) on the bank of Luye Stream, the branch of Beinan River, at an elevation of 180 m. Collected at night on 13 July 2004 by Chun-Wen Chang and Si-Min Lin. Deposited in Natural Museum of Natural Science, Taichung, Taiwan.

Paratypes.—Eleven adult males and 13 adult females. Collected from Luye (USNM 565983♀, NTNUB 241511♂) and Taidong City (BMNH 2008.268♂, 2008.269♀; USNM 565982♂; NMNS 4434-04♂, 4434-05♂, 4434-09♀, 4434-10♀; NTNUB 241513♂, 241517♀, 241518♀, 241519♀, 241520♀) by Chun-Wen Chang and Si-Min Lin. Collected from Hualien City by Ying-Rong Chen, Hsin-Yun Chao and Si-Min Lin (NMNS 4434-01♂, 4434-02♂, 4434-03♂, 4434-06♀). Collected from Wanrong by Chao-Jun Wang, Ying-Rong Chen, and Si-Min Lin (NMNS 4434-07♀, 4434-08♀; NTNUB 241514♂, 241516♀). Collected from Shoufeng by Si-Min Lin (NTNUB 241512♂, 241515♀). All individuals were collected from the habitat of *Miscanthus* grasslands. Separately deposited in the Natural History Museum, London (the BMNH series, 1 male and 1 female); National Museum of Natural History, Washington DC (the USNM series, 1 male and 1 female); Natural Museum of Natural Science, Taiwan (the NMNS series, 5 males and 5 females); and National Taiwan Normal University (the NTNUB series, 4 males and 6 females).

Referred specimens.—Males: FORE4004, 4012 from Luye; FORE3301, 3303 from Shoufeng; FORE2001, 2003, 2004, 2006 from Yuli; FORE2101, 2102, 2103, 2113 from Jingpu; and FORE3426 from Taidong City. Females: FORE0708, 3201, 3202, 3203 from Hualien City; FORE 1918 from Wanrong; FORE2002, 2005, 2007 from Yuli; FORE2104, 2105, 2106, 2108, 2109, 2111 from Jingpu; and FORE3402, 3419, 3420, 3423 from Taidong City.

Diagnosis.—As mentioned in the diagnosis of *T. viridipunctatus*, only 4 among the 19 currently recognized species in *Takydromus* exhibit the characters of "3 pairs of chin shields" and "2 pairs of femoral pores" (Table 3). Conjunction of these two characters helps to separate these four species from the others. Similar to *T. viridipunctatus*, *T. luyeanus* can be distinguished from *T. hsuehshanensis* by its keeled ventrals. The body shape of *T. luyeanus* is smaller and more slender compared to *T. hsuehshanensis*, which has stronger limbs and toes, a shorter tail without curling ability, and lacks the ability to climb on vegetation.

Takydromus luyeanus can be distinguished from *T. formosanus* and *T. viridipunctatus* by fewer dorsal scales counted in the longitudinal direction (mean ± SD = 40.62 ± 1.56). This character usually exceeds 43 in *T. viridipunctatus* (45.58 ± 2.23) and 44 in *T. formosanus* (46.79 ± 1.68) but seldom exceeds 42 in *T. luyeanus*. *Takydromus luyeanus* can be further distinguished from *T. formosanus* by having fewer caudal scales (14 rows, occasionally 15 or 16), fewer supratemporals (3 or 4 versus >4), and larger and more robust body shapes. Similar to *T. viridipunctatus*, *T. luyeanus* adults also exhibit noticeable sexual dimorphism. Male *T. luyeanus* exhibit white or light-yellow spots on a black background along the lateral surfaces during breeding seasons (Fig. 6). Color of these spots provides a further diagnosis between male *T. luyeanus* and *T. viridipunctatus*: the latter exhibit greenish spots on a brownish background on their lateral surfaces.

Takydromus luyeanus is sometimes sympatrically distributed with *T. sauteri* and *T. kuehnei* in eastern Taiwan. It may be distinguished from both of these species by a difference in number of femoral pores (2 pairs in *T. luyeanus*, 1 pair in *T. sauteri*, and 3–5 pairs in *T. kuehnei*) and number of chin shields (3 pairs in *T. luyeanus*, versus 4 pairs in the others).

Description of Takydromus luyeanus *holotype*.—Measurements (in mm): SVL 49.4, HL 11.4, HW 6.6, HH 5.6, TL 160.4. Rostral separated from frontonasal by supranasals; nostril surrounded by supranasal, postnasal, and anteriormost supralabial; supralabials six and infralabials five on each side; supraoculars four on each side, the anteriormost and the posteriormost ones much smaller than others; supraciliaries three on each side, the second slightly larger, the first and the third roughly in equal size; anteriormost supraciliary in contact with anteriormost supraocular, posterior two supraciliaries separated from posterior supraoculars by supraciliary granules; supraciliary granules 16 on left, 15 on right; postnasal one, followed by two loreals on each side, anterior loreal smaller than posterior one; prefrontals two, separating frontal from frontonasal; frontal hexagonal, weakly keeled; frontoparietals two and connected; parietals

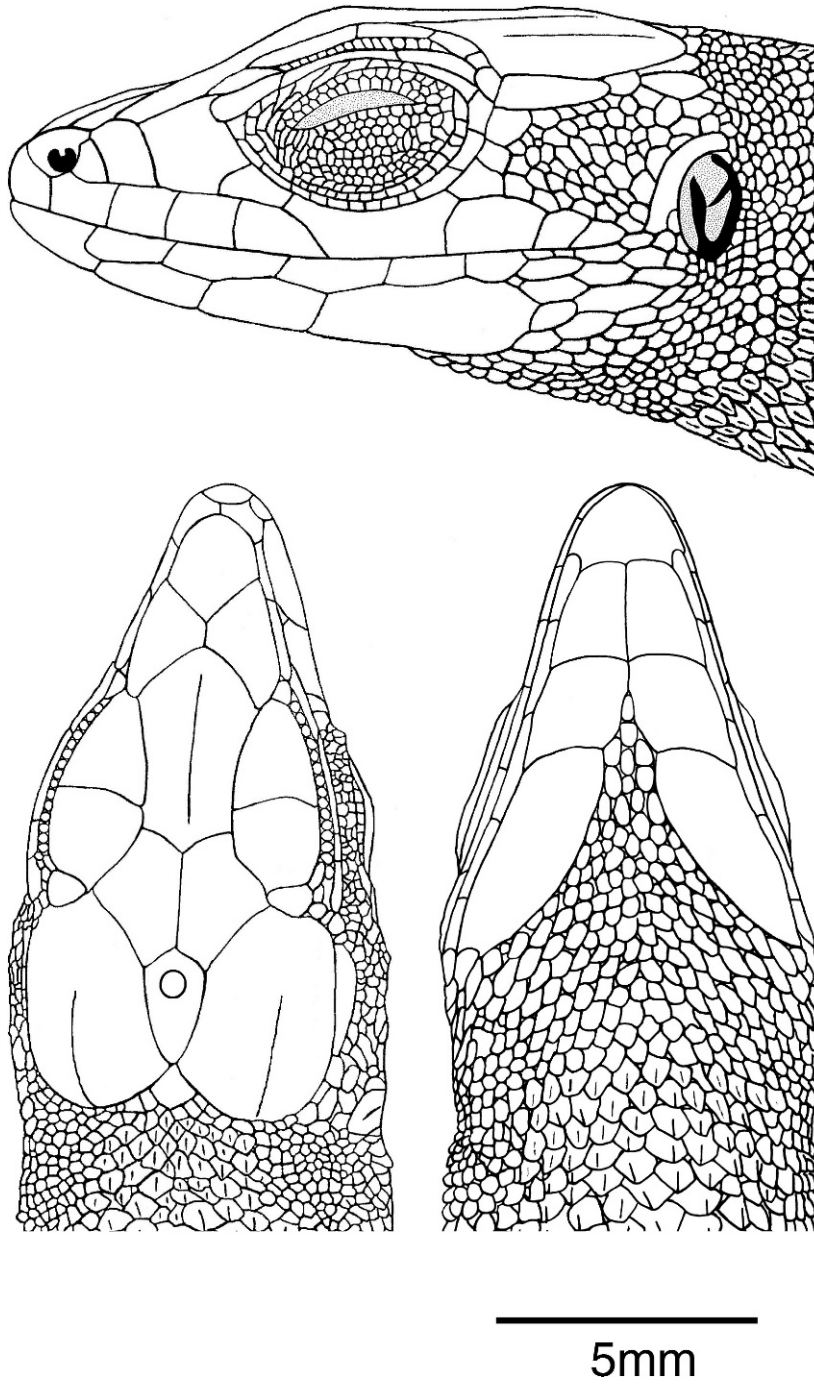

FIG. 7.—Head of the holotype of *Takydromus luyeanus* (NMNS 4433) in lateral (upper), dorsal (lower-left), and ventral (lower-right) views.

two, slightly keeled, completely separated by interparietal and occipital; supratemporals two on each side, the first one nearly four times as long as the second; temporal scales imbricate, slightly keeled, slightly larger than scales posterior to ear opining; three pairs of chin shields, anteriormost pair entirely in contact medially, second pair connected anteriorly and separated posteriorly by wedge of small scales; collars distinct, in 13 rows; dorsal scales on body enlarged, imbricate, strongly keeled and obtusely pointed, extending anteriorly beyond forelimbs on to neck, in eight rows at position of forelimbs and six rows at hind limbs, thirty-nine scales counted longitudinally from occipital to the posterior margin of hind limb on middlemost two rows; lateral body scales small and relatively uniform in size, granular, arranged in disorder, roughly 5–6 rows on each side at midbody; ventrals slightly mucronate, strongly keeled, obtusely pointed, in eight longitudinal rows, 32 scales counted longitudinally from collars to preanal on middlemost two rows; paraventrals in three rows on each side, strongly keeled, the first row (adjacent to the ventrals) about the same size as the ventrals, the second and third rows gradually diminishing in size; preanal single, enlarged, with two distinct longitudinal keels, and with a pair of keeled scales of similar length but one-fourth to one-third width beside; two femoral pores on each side; scales on anterior and dorsal surfaces of forelimbs enlarged, keeled, rhomboid, and imbricate; scales on posterior and ventral surfaces of arms small and granular; scales on ventral surface of forearms smooth, with three enlarged rows; two rows of large scales on anterior surfaces of thighs, strongly keeled, rhomboid, and imbricate; three rows of large scales on ventral surfaces of thighs, slightly keeled, diminishing in size posteriorly; four rows of enlarged scales on anterior and ventral surfaces of legs, the second row smooth and hexagonal, 200%–250% wider than neighboring rows, the other three rows keeled and rhimboid; relative lengths of appressed fingers IV > III > II = V > I; subdigital lamellae eight (left) – eight (right), 13-13, 19-18, 22-22, 13-12 on fingers I, II, III, IV, and V, respectively; relative lengths of appressed toes IV > III > V > II > 1; subdigital lamellae nine (left) – nine (right), 15-15, 22-22, 28-29, 17-17 on fingers I, II, III, IV, and V, respectively; tail extremely long (325% of SVL), covered with strongly keeled scales, in 18 rows at base, decreased to 14 rows and remained stable from the 7th scale.

Color in life.—Pupil golden to golden bronze; dorsal surfaces of head, body, and tail brown; ventral surfaces of head, body, and tail white to pale brown; upper arm, thigh, and proximal portions of forearm and shank brown; distal portions of forearm and shank pale brown or pale orange; digits dark brown. In mature males, two thick white stripes extending posteriorly. The first begins at the supraocular, extends through the outer-most row of dorsals and the upper edge of hind limb, and ends at the posterior part of the hind limb. The second begins at the supralabials, extends through the lower part of ear opening and upper edge of fore limbs, and ends at anterior part of the hind limbs. In females, these two stripes fade to pale brown; the anterior half of the second stripe is sometimes green. A thin black stripe, closely beside the upper edge of the second white stripe, extends posteriorly from the nasal to anterior edge of the forelimb, interrupted by eye and ear. The lateral area between the two stripes is brown in females, black in males; decorated with white or yellow spots in mature males during breeding seasons. Juveniles lack of the stripes and decorations at lateral surfaces.

Color in ethanol.—Yellow spots in life faded to white; other colors similar to those in life.

Variation.—Meristic and morphometric data of *T. luyeanus* are presented in Table 1 and concluded in Table 3. Dorsal scales counted in longitudinal direction range between 37 and 43. Number of caudal scales is usually 14, occasionally 15 or 16. Number of femoral pores is usually 2, occasionally 3.

Distribution and ecology.—*Takydromus luyeanus* is only known from eastern Taiwan, including Hualian and Taidong County. Similar to *T. viridipunctatus*, this species is found in a variety of different environments, including grasslands, farms, gardens, shrubs, and edge of forests, from the eastern coastline to foothill (<200 m). Population density could be quite high; up to 150 individuals could be

captured at a single summer night by six collectors within a 2 ha. area. This species is sympatrically distributed with *T. sauteri* and *T. kuehnei*, but the latter two species are much rarer in these sympatric areas.

Clutch size two, occasionally three (less than 5% ratio). Gravid females are found during April to August. At least two clutches are produced during late spring to early summer, and more clutches are possibly produced if in good nutritional conditions.

Etymology.—The specific name has multiple meanings. First, it refers to the place "Luye", in eastern Taiwan, where the type specimen was collected. The name of this place in Chinese means "the field where the Sika Deer wandered", indicating the typical habitat of this species. The writing of these words in Chinese is coincidently identical to the name of the famous Japanese naturalist and anthropologist Tadao Kano (1906–1945), who dedicated most of his life to Taiwan and made remarkable contributions in biogeography.

Key to the species of Takydromus *occurring in Taiwan, Japan, Ryukyus, and adjacent islands*

1A.	Dorsal scales small, not in obvious longitudinal rows	*T. dorsalis*
1B.	Dorsal scales large, in longitudinal rows	2
2A.	Femoral pores three to five pairs	3
2B.	Femoral pores one or two pairs	4
3A.	Ventrals in six rows	*T. keuhnei*
3B.	Ventrals in eight rows	*T. amurensis*
4A.	Femoral pores one pair	5
4B.	Femoral pores two pairs	8
5A.	Ventrals in six rows	6
5B.	Ventrals in eight rows	7
6A.	Chin shields three pairs	*T. smaragdinus*
6B.	Chin shields four pairs	*T. sauteri*
7A.	Dorsal surfaces of head and body brown or brownish tan, with ventrolateral white lines	*T. stejnegeri*
7B.	Dorsal surfaces of head and body brilliant green in life, light blue or bluish gray in preservative; ventrolateral white line on head or body absent	*T. toyamai*
8A.	Ventrals smooth	9
8B.	Ventrals keeled	10
9A.	Chin shields three pairs	*T. hsuehshanensis*
9B.	Chin shields four pairs	*T. tachydromordes*
10A.	Dorsal scales (counted in longitudinal rows) less than 42, with white of light yellow spots on lateral side in mature males	*T. luyeanus*
10B.	Dorsal scales (counted in longitudinal rows) more than 43	11
11A.	Caudal scales (counted from 11th to 15th) in 14 rows; lateral green spots present in mature males; snout–vent length in adults usually more than 48 mm	*T. viridipunctatus*
11B.	Caudal scales (counted from 11th to 15th) in 16 rows; lateral spots absent in both sexes; snout–vent length in adults usually less than 47 mm	*T. formosanus*

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Appendix I

Specimens Examined

Takydromus formosanus: Males: FORW1901, 1902, 1903, 1904, 1905 from Madou, Tainan County; FORW2205, 2215, 2217, 2218 from Xinhua, Tainan County; FORW2301 from Guanziling, Tainan County; FORW2802, 2803 from Nanzhuang, Miaoli County. Females: FORW1901, 1906, 1907, 1908 from Madou, Tainan County; FORW2203, 2216, 2219, 2220 from Xinhua, Tainan County; FORW2304 from Guanziling, Tainan County; FORW1307 from Dongshi, Taichung County; FORW1702, 1703, 1705 from Kaohsiung City; FORW2701, 2702 from Taian, Miaoli County; FORW2804 from Nanzhuang, Miaoli County.