Taxonomic Status of the Taiwanese Populations of *Rhabdophis tigrinus* (Squamata: Colubridae): Morphological and Karyological Assessment

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Abstract: Taxonomic treatment of the Taiwanese populations of *Rhabdophis tigrinus* has been controversial. Some authors adopt a subspecific name, *R. t. formosanus*, whereas others negate taxonomic subdivision of *R. tigrinus*. We compared external characters and karyotype between the Taiwanese and other populations. Results indicate that the former has a unique W chromosome, which is metacentric and distinctly smaller than the Z chromosome. The Taiwanese populations also differ from others, except for populations of Kyushu, Japan, in having more subcaudals (80± in males, 77± in females). From the Kyushu populations, Taiwanese *R. tigrinus* is distinct in having 15 or more lateral dark blotches between the neck and the 50th ventral (14± in the former). All these characters, as well as deduced East Asian paleogeography, strongly suggest that the Taiwanese populations have been constituting an independent evolutionary unit by themselves since their entry into this island from the southeastern continent. Thus, we consider that they deserve recognition as a distinct taxon and tentatively retain them at the subspecific status as *R. t. formosanus*.

Key words: *Rhabdophis tigrinus formosanus*; Taiwan; Morphological variation; Karyotype; Taxonomy

The natricine snake *Rhabdophis tigrinus* is widely distributed in the main islands of Japan (exclusive of Hokkaido), the Korean Peninsula, southeastern Russia, continental China exclusive of the western and extremely southern parts, and Taiwan (Nakamura and Ueno, 1963; Paik and Yang, 1986; Zhao and Adler, 1993). Based on three specimens from the montane region of Taiwan, Maki (1931) described *R. t. formosanus* (originally as *Natrix tigrina formosana*). He argued that this subspecies is distinguishable from the other subspecies (*R. t. tigrinus* and *R. t. lateralis*) in having more subcaudals [85–88 in *formosanus*, vs 66–85 and 50–72 (or 73) in nominotypical subspecies and *lateralis*, respectively] (Maki, 1931).

Imaiizumi (1957), while demonstrating extensive geographic variations in ventral and subcaudal counts of *R. tigrinus* from the main islands of Japan and the eastern continent, gave the range of subcaudal counts for six males from Kyushu as 72–86. He assumed a clinal increase of subcaudals, as well as of ventrals, in the Japanese populations.

Ota and Mori (1985), in a report on the fourth specimen of *R. t. formosanus*, compared the subcaudal count between this subspecies and *R. t. tigrinus* from Yakushima (an island representing the southwestern end of the range of the latter in Japan), and confirmed a slight overlap in variation of this character between the Taiwanese and Japanese populations. Based on the direct observations of specimens (for the Taiwanese and Yakushima populations) and literature descriptions [i.e., Goris (1971), for other populations in Japan], they suspected that *R. t. formosanus* could be more clearly distinguished from *R. t. tigrinus* by the number of dark blotch rows on the dorsum (i.e., five rows in *R. t. formosanus*, vs. three and four rows in Yakushima and other Japanese populations, respectively).

However, based on detailed examinations of samples from eastern Honshu, mid-western Honshu, and Kyushu of Japan, Toriba (1992) argued for the prevalence of the five blotch row condition also in the Japanese populations. On the basis of photographs given in Ota and Mori (1985), he further surmised that the four blotch row condition in the anterior body observed in the Kyushu and eastern Honshu samples also occurs in the Taiwanese populations as well. Thus, Toriba (1993) negated the validity of the subspecies *formosanus*. Other recent authors,
TABLE 1. Morphological variation (x ± SD, followed by ranges in parentheses) in *Rhabdophis tigrinus* from Taiwan. See text for character abbreviations.

| Characters          | Males                         | Females                        | Intersexual differences |
|---------------------|-------------------------------|--------------------------------|-------------------------|
| Adult SVL (in mm)   | 566.7 ± 55.1 (455–668) (N = 20) | 633.2 ± 126.0 (521–854) (N = 9) | NS* (F = 4.02, DF = 1, 27) |
| Immature SVL (in mm)| 390.2 ± 46.8 (355–483) (N = 6) | 356.2 ± 97.2 (227–485) (N = 5) | NS* (F = 0.58, DF = 1, 9) |
| TL/SVL              | 0.352 ± 0.021 (0.312–0.391) (N = 22) | 0.311 ± 0.022 (0.285–0.367) (N = 11) | p < 0.001** (F = 26.98, DF = 1, 30) |
| VT                  | 164.0 ± 2.2 (159–169) (N = 26) | 164.9 ± 1.7 (162–167) (N = 14) | NS* (F = 1.63, DF = 1, 38) |
| SC                  | 85.0 ± 2.5 (80–90) (N = 22) | 80.1 ± 3.6 (77–88) (N = 11) | p < 0.001* (F = 21.64, DF = 1, 31) |
| VT + SC             | 248.9 ± 3.8 (243–259) (N = 22) | 244.5 ± 4.3 (239–253) (N = 11) | p < 0.01* (F = 9.23, DF = 1, 31) |
| BBWL                | 60.6 ± 3.4 (52–67) (N = 24) | 60.9 ± 3.4 (55–67) (N = 12) | NS* (F = 0.08, DF = 1, 34) |
| BB50                | 16.4 ± 1.4 (15–20) (N = 24) | 17.1 ± 1.4 (15–20) (N = 12) | NS* (F = 1.88, DF = 1, 34) |

*: ANOVA.

**: TL (log-transformed) compared by ANCOVA with SVL (log-transformed) as the covariate; no significant difference in slope (F = 4.12; DF = 1, 29).

however, have continued to apply this sub-specific name to the Taiwanese populations (e.g., Lin, 1996; Lue et al., 1989; Ota, 1997; Zhao and Adler, 1993).

Recent progress of herpetological surveys in Taiwan revealed that *R. tigrinus* is not necessarily rare in some middle to high altitude areas of this island (Lue et al., 1989), as had previously been considered (Ota and Mori, 1985). However, no attempts have been made to conduct further, more reliable evaluation of the taxonomic status of the Taiwanese populations.

We recently collected a good series of *R. tigrinus* from the north-central montane region of Taiwan. This has brought us an opportunity to analyze variations between Taiwanese populations and non-Taiwanese conspecifics.

**MATERIALS AND METHODS**

A total of 40 specimens of *R. tigrinus* from Taiwan, including the holotype and the paratype of *R. t. formosanus* and the specimen reported by Ota and Mori (1985), were examined. Of these, 34 were recently collected from Ssuyuan-Yakou (alt. 1900 m) in the north-central part of the island (see Appendix for further details). Sex and maturity of each specimen were determined on the basis of gonadal observations following Ota and Iwanaga (1997).

For each specimen, morphological characters were examined after preservation in 10% formalin or 70% ethanol. Snout-vent length (SVL) and tail length (TL) were measured to the nearest 1 mm, with the latter being only for specimens with undamaged tail tips. The number of ventral scutes (VT) was counted following Ota and Mori's (1951) definition. The number of subcaudal scale pairs (SC) was counted for tails having undamaged tips.

The number of dark blotches was counted transversely in the anterior (TBA), middle (TBM), and posterior portions of the body (TBP) at points, respectively, defined as 15%, 50%, and 85% ventral scale lengths sensu Ota et al. (1997). Lateral dark blotches were also counted on the right side from the neck to cloaca (BBWL) and to the 50th ventral (BB50).

In addition, one male and three females from Ssuyuan-Yakou (Appendix) were karyotyped following the method of Ota and Iwanaga (1997). The karyotype was determined for each individual on the basis of no less than five well-spread metaphase cells and described using the terminology of Levan et al. (1964), as modified by Green and Sessions (1991).

Forty-nine specimens of *R. t. tigrinus* from Shikoku and Kyushu, southwestern Japan, were also examined for morphological comparisons (Appendix). Comparative data for other populations were taken from the literature (see below). With respect to quantitative tail characters such as SC, citation of literature data may lead to an underestimation of the inherent population conditions as a result of inclusion of
FIG. 1. Female karyotype of Rhabdophis tigrinus from Ssuyuan-Yakou, Taiwan (KUZ 34428). Autosomal pairs are arranged and numbered in order of size reduction. Note that the W chromosome is metacentric and distinctly smaller than the Z chromosome. Thick bar equals 10 μm.

RESULTS

TBA was four in 28 specimens, five in nine specimens and six in one specimen. In the remaining two specimens, the dark blotches at 15% ventral scale length position formed a continuous band and thus could not be counted separately. Frequency of such a conversion of transverse blotch rows into continuous bands tended to be higher posteriorly, and TBM and TBP were, respectively, five in 36 and 30 specimens, and were not determined in the remaining four and 10 specimens. Variations in other quantitative characters are summarized in Table 1. In the Taiwanese sample, TL in relation to SVL, SC, and VT + SC were significantly greater in males than in females, whereas no significant intersexual differences were recognized in adult SVL, immature SVL, VT, BBWL, or BB50.

Values for meristic lepidoses in Shikoku and Kyushu samples were, respectively, within ranges of corresponding characters in Western Honshu and Kyushu samples reported by other authors (Imaizumi, 1957; Ota and Mori, 1985). Values for BBWL and BB50 ranged from 48-56 and 13-16 in the Shikoku sample, and 45-54 and 7-14 in the Kyushu sample, respectively.

Both male and female karyotypes of the Taiwanese sample consisted of 16 macro- and 24 microchromosomes (Fig. 1). In the female karyotype, two macrochromosomes, both metacentric, formed a pair apparently heteromorphic in size. The larger of these, close to the autosomal pair 4 in size and distinctly larger than pair 5, looked identical with components of one homologous pair in the male karyotype. On the other hand, the smaller one, nearly as large as pair 5, was unique to the female karyotype. We thus consider the former and the latter as Z and W sex chromosomes, respectively.

Distinct size gaps were evident between pairs 1 and 2, pairs 4 and 5, pairs 5 and 6, and pairs 7 and 8 of autosomes. Of the seven pairs of autosomal macrochromosomes, pairs 1-3 and 5 were metacentric, whereas pairs 4, 6, and 7 were telocentric. All microchromosomes (pairs 8-19) appeared telocentric, and the fundamental number was thus calculated as 50.

DISCUSSION

It is known that some non-Taiwanese populations of R. tigrinus show variations in the centromeric position and relative size of W sex chromosome. Toriba (1987), for instance, reported that the W chromosome in samples from eastern Japan was subtelocentric, whereas in samples from western Japan and Korea, the W chromosome was telocentric like that in samples from northeastern continental China and eastern Russian [Panshi (Jilin) and Chaoyang (Liaoning): Diao et al., 1985; Primorsky Kray: Toriba, unpublished observation]. These W chromosomes seem to be as large as, or slightly larger than their counterpart Z chromosomes.
(Diao et al., 1985; Toriba, 1987 [Fig. 1]). Toriba (1992) further mentioned that both karyomorphs occur in mid-western Honshu, but did not examine their exact sympathy or gene flows between them. On the other hand, W chromosomes in populations from Taiyuan (Shanxi), Dazheng, and Leishan (Guizhou) in central-eastern continental China are submetacentric and distinctly larger than Z chromosomes (Ma, 1986; Wang et al., 1993; Xu et al., 1991). The karyotype of the Taiwanese populations of *R. tigrinus*, while showing good agreement with those of the non-Taiwanese conspecific populations in the diploid number (40) and autosomal arrangement, is unique in having a metacentric W chromosome which is distinctly smaller than the Z chromosome.

The results of observations of TBA, TBM, and TBP supported Toriba's (1992) claim against the validity of the transverse number of dark blotches on body as a discriminant character for the Taiwanese populations of *R. tigrinus*. Nevertheless, these populations are still morphologically distinct from conspecific continental populations in having more subcaudals [80–90 in males (N = 22) and 77–88 in females (N = 11: Table 1), vs. 48–73 in males (N = 296) and 32–67 in females (N = 461) from the continental China (Chen, 1991; FTUDB, 1974; Huang, 1990; Ji, 1987; Pope, 1935; Wang, 1991; Wen, 1987; Wu et al., 1985; Zhao and Huang, 1982), 59–79 in males (N = 164) and 45–71 in females (N = 150) from Korea (Paik and Yang, 1986), and 60–64 in males (N = 4) and 47–61 in females (N = 5) from eastern Russia (Emelianov, 1929). This character also discriminates the Taiwanese populations from populations of Honshu and Shikoku, Japan [57–79 in males (N = 44) and 56–76 in females (N = 96: Imaizumi, 1957; this study)]. However, ranges of subcaudal counts partially overlap between the former and the Kyushu populations [72–86 in males (N = 29) and 67–84 in females (N = 46: Imaizumi, 1957; Ota and Mori, 1985; this study)], as was already pointed out by Ota and Mori (1985).

From the Kyushu populations, the Taiwanese populations are apparently distinct in having longitudinally narrower dark blotches on the anterior body. This is reflected well by BB50, which ranges from 15–20 in the Taiwanese populations (N = 36: Table 1), but is 7–14 in the Kyushu populations (N = 52: Toriba, 1992; this study).

Imaizumi (1957) surveyed geographic variations in the ventral and subcaudal numbers of the Japanese *R. tigrinus*, and recognized a gross southwestward increase in both characters. This may suggest that the relatively large subcaudal counts in the Taiwanese populations, though partially overlapping with those of the Kyushu populations, represent an extreme state of such a clinal variation. Even so, however, it is almost certain that the Taiwanese and Japanese populations were independently derived from continental populations and that the large subcaudal count in the former has evolved from a much smaller number [represented by the continental populations: see above] after their isolation in Taiwan, because Taiwan and the main islands of Japan, while having been connected separately with the continent a few times, have had no direct landbridge connections at least since the early Pleistocene (Ota, 1991, 1998; Hikida and Ota, 1997).

On the other hand, Toriba (1992) demonstrated a clinal southwestward decrease of BB50 in the Japanese populations of *R. tigrinus*. Our results obviously indicate that the Taiwanese populations do not follow this pattern at all.

All these evidences strongly suggest that the Taiwanese populations constitute a distinct evolutionary unit by themselves. This, as well as their diagnosability from the remaining conspecific populations by a combination of characters (80 ≤ SC in males, 77 ≤ SC in females, and 15 ≤ BB50 in both sexes), lends substantial support for recognition of the Taiwanese populations as a distinct taxon. Whether species or subspecies category is appropriate for them should be a matter of further debate (see Frost and Hillis [1990] and associated discussion for relevant general issues). We prefer taking a conservative stance at present to use the subspecific name, *Rhabdophis tigrinus formosanus* (Maki, 1931).

On the other hand, we have found no characters that collectively discriminate the continental populations from the Japanese populations. We thus consider *R. t. lateralis* (Berthold, 1859), a name which has been frequently used for the former (e.g., Wang et al., 1993; Zhao and Adler, 1993), as invalid, and regard all non-Taiwanese populations as the nominotypical subspecies, *R. t. tigrinus* (Boie, 1826).

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APPENDIX

Material examined.—Institutional acronyms used below are: JSI, Japan Snake Institute; KUZ, Department of Zoology, Graduate School of Science, Kyoto University; NSMT, National Science Museum, Tokyo; OMNH, Osaka Museum of Natural History; TM, Taiwan Museum; and URM, Museum Attached to the University of the Ryukyus. Asterisks denote the specimens karyotyped.

Rhabdophis tigrinus formosanus. Tayuling, Hualien Pref. (alt. 2500 m) (N=1): KUZ 3296; Ssuyuan-Yakou, Taichung Pref. (alt. 1900 m) (N=34): KUZ 34408-409, 34427*-428*, 34437-438, 34449-455, 34462*-463*, 34464, 47706-722, OMNH R4073; Hsitou, Nantou Pref. (alt. 1200 m) (N=1): KUZ 47705; Patungkuan, Nantou Pref. (alt. 3000 m) (N=1): NSMT H02967 (holotype); Hsuehshan, Taichung Pref. (alt. 2700 m) (N=1): NSMT H02968 (paratype); Wuling Farm, Taichung Pref. (alt. 1800 m) (N=2): TM RS0255, RS0284.

R. t. tigrinus. Sanuki, Shikoku, Japan (N=1): NSMT 3017; Kochi Pref., Shikoku, Japan (N=1): one uncatalogued URM specimen; Kumamachi, Ehime Pref., Shikoku, Japan (N=1): NSMT 3605; Fukuoka, Fukuoka Pref., Kyushu, Japan (N=2): two uncatalogued URM specimens; Takada, Oita Pref., Kyushu, Japan (N=2): KUZ 21597-598; Amakusa, Kumamoto Pref., Kyushu, Japan (N=2): KUZ 5013, 5016; Nakadorijima, Nagasaki Pref., Kyushu, Japan (N=1): KUZ 28030; Tanegashima, Kagoshima Pref., Kyushu, Japan (N=3): KUZ 32242-244; Kagoshima, Kagoshima Pref., Kyushu, Japan (N=1): one uncatalogued URM specimen; Yakushima, Kagoshima Pref., Kyushu, Japan (N=29): 28 uncatalogued KUZ specimens, one URM uncatalogued specimen; Kyushu, six uncatalogued JSI specimens.