

Unmasking *Rana okinavana* Boettger, 1895 from the Ryukyus, Japan (Amphibia: Anura: Ranidae)

Masafumi Matsui*

Graduate School of Human and Environmental Studies, Kyoto University,
Yoshida Nihonmatsu-cho, Sakyo-ku, Kyoto,
606-8501 JAPAN

Examination of the lectotype and a paralectotype of *Rana okinavana* Boettger, 1895 revealed that the species is not a brown frog of the subgenus *Rana*, occurring in the middle group of the Ryukyu Archipelago, but is identical with a frog of the subgenus *Nidirana* from the southern group of the Archipelago and Taiwan, now called *R. psaltes* Kuramoto, 1985. The type locality of *R. okinavana* given in the original description, Okinawa of the middle Ryukyus, is highly doubtful and should be somewhere in the Yaeyama Islands of the southern Ryukyus. The name *R. psaltes* is relegated to a subjective junior synonym of *R. okinavana* Boettger, 1895, while the brown frog of the subgenus *Rana* from the northern Ryukyus requires a replacement name.

Key words: brown frog, *Nidirana*, Okinawa Island, synonym, taxonomy, Yaeyama Islands

INTRODUCTION

The Ryukyu Archipelago is geographically split into northern (Osumi and Tokara Is.), middle (Amami and Okinawa Is.), and southern (Miyako and Yaeyama Is.) groups (Ota, 1998), and each of these island groups exhibits its own high endemism in biota. The amphibian fauna of the archipelago has been well studied (e.g., Inger, 1947; Kuramoto, 1979; Toyama, 2003), but there still remain taxonomic problems in several taxa. One example is a brown frog of the genus and subgenus *Rana* endemic to the middle group. This frog is not a rare species and has been studied widely in these 60 years under the name of *R. okinavana* Boettger, 1895.

Boettger (1895a) described *R. okinavana* on the basis of three females (but see below) from “Liukiu-Inseln, angeblich von Okinawa in der mittleren Gruppe” (the Ryukyu Islands, allegedly from Okinawa in the middle group). Of these three specimens Boettger (1895b) listed, two are in the Senckenberg Museum, Frankfurt am Main (SMF) and the remaining one is said to be in the Bremen Museum (Stejneger, 1907). The catalogue number of the specimens in SMF, No. 1072, 1 shown in Stejneger (1907), seems to have been given shortly after Boettger’s (1895a) original description. Much later, Mertens (1967) designated the specimen with his catalogue number 1047, 3a in SMF to be the lectotype (SMF 5830), noting it to be a male.

Stejneger (1907: 102) examined the two specimens in SMF, translated the original German description and measurement table into English, and added short notes. Since then, nobody has examined the types in SMF except for Mertens (1967). Van Denburgh (1912) reported that he

failed to collect *R. okinavana* from Okinawa (=Okinawajima I.), but that he could obtain 25 specimens from Ishigaki shima (=Ishigakijima I. in the southern group) that are referable to *R. okinavana*. This frog, however, has never been recorded from the southern Ryukyus by subsequent regional surveys (e.g., Okada, 1931). Boulenger (1920) stated that he had access only to the descriptions, which he summarized, and erroneously cited Boettger’s original remarks that the species is allied to “*R. labialis*”.

Meanwhile, the occurrence of a brown frog of the subgenus *Rana* (Dubois, 1992), superficially similar to *R. japonica* of the main islands of Japan, was known from Okinawajima I. of the middle group (Stejneger, 1907). In contrast to *R. okinavana* from the southern group, this brown frog has been reported by several authors from the middle group (e.g., Okada, 1931) and has experienced a complex taxonomic history (Shibata and Matsui, 1985). Inger (1947) combined the frogs from both the middle and southern Ryukyus and applied the name *R. okinavana* to them, although he examined only *R. okinavana* reported by Van Denburgh (1912) and did not study the brown frog of the middle group. Almost all subsequent researchers of the Ryukyus (e.g., Nakamura and Uéno, 1963; Maeda and Matsui, 1989, 1999) followed Inger’s (1947) view and used the name of *R. okinavana* for the brown frog from the middle group without any doubt.

As noted above, *R. okinavana* has not been reported from the southern group since Van Denburgh (1912), but another frog, *R. psaltes* Kuramoto, 1985, was found there much later (Kuramoto, 1973; Otsu, 1975). *Rana psaltes* is superficially similar to the brown frog of the middle Ryukyus in having moderate body size and brown dorsum. However, it is not a member of the subgenus *Rana*, but is the type species of *Nidirana* (Dubois, 1992; Maeda and Matsui, 1999).

In 1999, I had the chance to examine the lectotype and

* Corresponding author. Phone: +81-75-753-6846;
Fax : +81-75-753-6846;
E-mail: fumi@zoo.zool.kyoto-u.ac.jp

a paralectotype of *R. okinavana* stored in SMF. My examination revealed that the types are completely different from the brown frog of the middle Ryukyus, now widely referred to "*R. okinavana*" (e.g., Nakamura and Uéno, 1963; Maeda and Matsui, 1989). Instead, they surely represent a member of the subgenus *Nidirana* (Dubois, 1992; Chou, 1999). The sole member of this subgenus known from the Ryukyus is *R. psaltes* Kuramoto, 1985, and I confirmed that it is conspecific with *R. okinavana*.

MATERIALS AND METHODS

I examined two type specimens of *R. okinavana*, SMF 5830 (lectotype) and 5831 (paralectotype). Both of these were formerly reported as 1072, 1 (Stejneger, 1907), but Mertens (1967) noted the lectotype as his 1047, 3. I found two small labels, one indicating 1072, 1a and another 1047, 3a, in the jar of SMF 5830. For comparisons, I examined the type series of *R. psaltes* from the southern Ryukyus [OMNH (Osaka Museum of Natural History) 10835=hotype; 8026–8030, 10836–10840=paratypes; all from Iriomotejima I. of the Yaeyama Islands] and specimens of the brown frog now widely called "*R. okinavana*" from the middle Ryukyus (KUHE=Graduate School of Human and Environmental Studies, Kyoto University 28141–28161 from Okinawajima I. of the Okinawa Islands).

Body measurements were taken mostly following Matsui (1984): Snout-vent length (SVL); head length (HL); head width (HW); snout length (SL); eye length (EL); tympanum diameter (TD); internarial distance (IND); interorbital distance (IOD); upper eyelid width (UEW); forelimb length (FLL); hindlimb length (HLL); tibia length (TL); foot length (FL); inner metatarsal tubercle length (IMTL); first toe length (1TL). All measurements were made to the nearest 0.05 mm with dial calipers.

RESULTS

Notes on types of *R. okinavana*

Both the two type specimens were in good condition (Fig. 1A, B, D, E, I), and the following original description by Boettger (1895b: 266; translated with slight modification by Stejneger, 1907: 102) proved to well illustrate them: "In general similar to *R. lateralis* Boulenger, but with shorter snout and more robust. Vomerine teeth in two rounded bundles beginning on a line with the posterior border of the choanae and separated from them as well as from each other by equal intervals. Head moderately large; snout short, anteriorly slightly pointed, and somewhat produced, as long as the diameter of the eye. Nostrils equidistant from tip of snout and eye. Canthus rostralis angular, loreal region slightly depressed longitudinally; interorbital space scarcely broader than the upper eyelid; tympanum very distinct, 3/4 the size of the eye. Fingers moderately long, first longer than second; toes 3/5 webbed and in addition with narrow dermal margins to the last phalanx; tips of digits truncate but without distinct disks; subarticular tubercles well developed; inner metatarsal tubercle oval, prominent, but less than half the length of the inner toe; no outer metatarsal tubercle. The adpressed hind leg reaches between anterior border of eye and nostril. Skin on back and underside rather smooth, on the sides with large flat warts; a narrow, high, strongly swollen dorso-lateral glandular fold; a second fold beginning beneath the eye and ending above the shoulder in two round or oval glandular aggregations. Upper side gray, frequently with a fine, somewhat lighter median dorsal line; a black wedge-shaped spot from nostril through eye extending

over the temporal region; a blackish line bordering the upper lip and separated from the freno-temporal spot by a pure white band which ends on the glandular protuberances above the insertion of the arm. Tympanum brown. Dorso-lateral fold externally edged with black, the sides being often entirely blackish; posterior extremities with dark cross bands; posterior aspect of femur whitish yellow with black spots and marblings. Underside whitish yellow, spotted and dotted all over very densely with blackish brown, on the underside of the head being mostly uniform blackish gray".

Boettger (1895b: 267) noted that all the three syntypes are females, and Stejneger (1907) also noted the two specimens in SMF he examined as females. However, Mertens (1967) reported the lectotype to be a male, as noted above. Although I did not dissect the specimens, I reached a conclusion different from these previous authors, as shown below. The largest specimen in the measurement table of Boettger (1895b) assuredly represents the lectotype (SMF 5830: Fig. 1A, D), but it is not clear which of the remaining two specimens is the paralectotype (SMF 5831: Fig. 1B, E, I). From the body size, I tentatively assign the smallest one in Boettger's (1895b) table to the paralectotype. The following is the comparison of measurements (in mm) made for the lectotype and paralectotype in this study (Table 1) and those given by Boettger (1895b), respectively: SVL=47.2 and 41.6 vs. 46 and 40, HL=17.7 and 15.2 vs. 17 and 16, HW=16.2 and 14.0 vs. 16 and 15, TD=4.1 and 3.8 vs. 4 and 3.5, FLL=26.3 and 24.0 vs. 25 and 22.5, HLL=76.3 and 66.2 vs. 76 and 67, and TL=22.9 and 19.9 vs. 23.5 and 20.5. Thus, the two measurements agreed fairly well, in spite of the probably different methods used and possible shrinkage from over 100 years of preservation.

The following additional information on the types of *R. okinavana* will aid in defining this species: Canthus rostralis is blunt, but fairly distinct. Lores are nearly vertical and slightly concave. Snout is slightly longer than the upper eyelid, and is shorter than the distance of anterior corners of upper eyelids. Pineal spot is visible slightly posterior to the line connecting anterior borders of upper eyelids. Each of the vomerine teeth series bears four teeth.

The first finger is longer than the fourth. Tips of fingers are swollen but lack the circummarginal groove. Tips of toes are also swollen, each with a circummarginal groove on second to fourth. Webbing formula is I2–2II2–3⁺III2–3⁺IV3–2V, with narrow dermal fringes to the last phalanx on all toes. A tarsal ridge is present, and a skin ridge fringes the fifth toe along its outer margin. In contrast to the original description, tibio-tarsal articulation reaches to the level of center of eye when hindlimb is carried forward along the body. Heels barely touch when hindlimbs are flexed perpendicular to the body axis.

The hindlimb is dorsally covered with several longitudinal tubercles, and those on tibia tend to form ridges. Most importantly, the paralectotype has a flat skin gland on the flank from the base of the forelimb to midway between axilla and groin (Fig. 1I; suprabrachial gland of Dubois, 1992), although the gland is much smaller and weaker in the lectotype. The paralectotype lacks distinct nuptial pads, but has small vocal openings inside of jaw commissures, though they are very difficult to locate. I could not find the openings in the lectotype. Thus, I judge the lectotype to be a female and

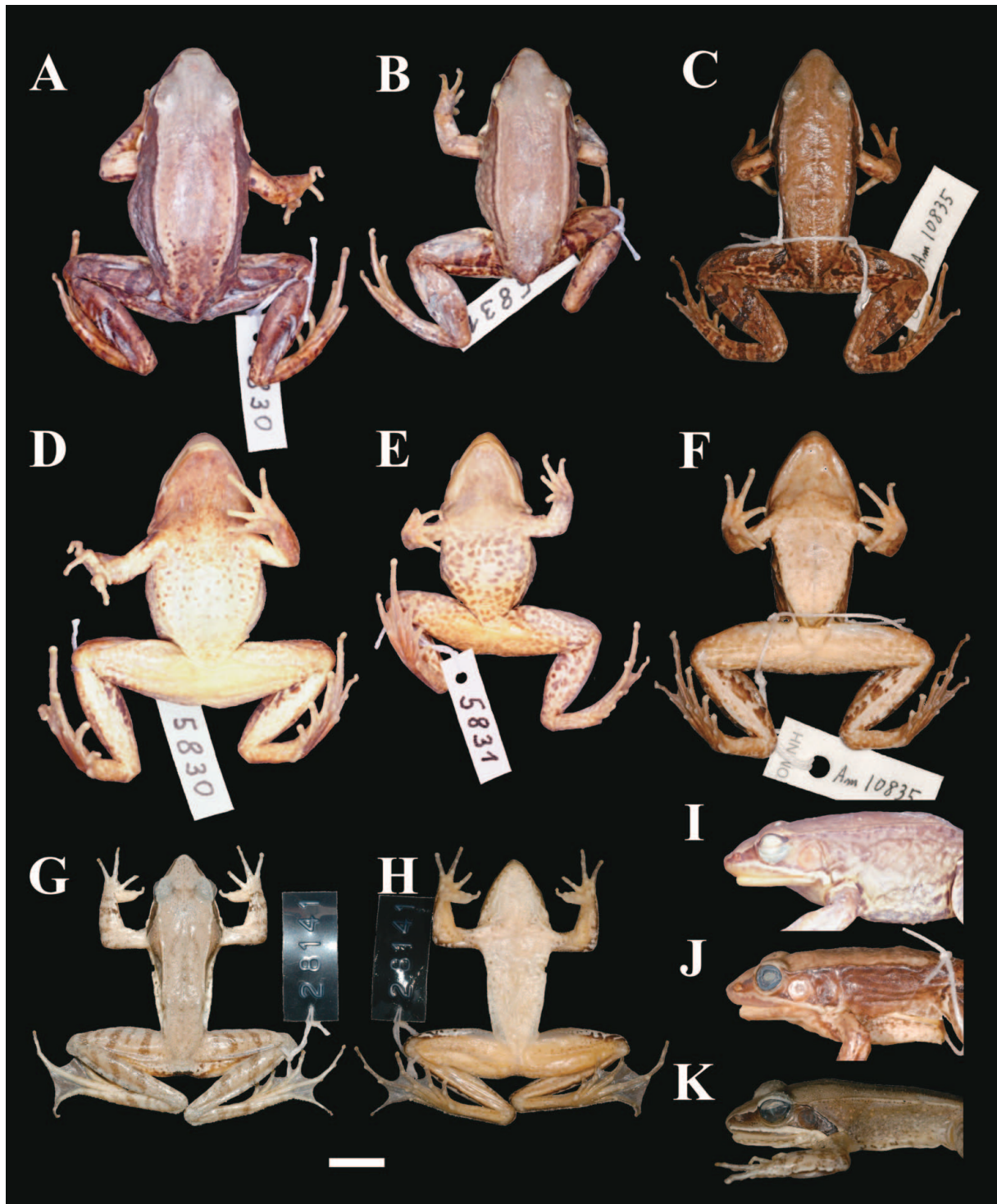


Fig. 1. Dorsal (A–C, G), ventral (D–F, H), and lateral (I–K) views of *R. okinavana* (A, D=lectotype, B, E, I=paratype), *R. psaltes* (C, F, J=holotype), and the brown frog from Okinawa (G, H, K). Scale bar for A–H=10 mm. I–K not to the scale.

the paratype to be a male. Dark bands on the hindlimb are narrowly edged with light color. The light-colored mid-dorsal stripe is nearly absent in the paratype.

Comparisons with type series of *R. psaltes*

Almost all characteristics of the types of *R. okinavana*

listed above agreed with those of *R. psaltes* examined, and there were only slight morphometric differences. Two female paratypes of *R. psaltes* were morphologically very similar to the lectotype of *R. okinavana*. The body size of the female *R. psaltes* (42.4–42.6 mm) was smaller than the size of *R. okinavana* (47.2 mm), but only a few of the morphometric

Table 1. Measurements (mean±1SD, in mm followed by ranges in parenthesis) of 14 characters in *Rana okinavana*, *R. psaltes*, and the brown frog from Okinawa. See Materials and Methods for museum and character abbreviations.

	<i>R. okinavana</i>		<i>R. psaltes</i>			Brown frog from Okinawa	
	SMF 5830	SMF 5831	OMNH 10835	OMNH	OMNH	KUHE	KUHE
	Lectotype Female	Paralectotype Male	Holotype Male	Paratypes 8 Males	Paratypes 2 Females	19 Males	2 Females
SVL	47.2	41.6	41.9	41.0 (39.5–42.8)	42.5 (42.4–42.6)	36.5 (32.7–39.4)	48.7 (47.5–49.9)
HL	17.7	15.2	16.2	14.0 (15.0–16.8)	16.0 (16.0–16.0)	13.6 (11.9–15.0)	17.7 (17.5–17.9)
HW	16.2	14.0	15.0	14.3 (13.4–15.2)	15.1 (14.9–15.2)	12.0 (10.7–13.1)	15.9 (15.8–15.9)
SL	7.3	6.7	6.7	6.6 (6.2–7.0)	6.8 (6.7–6.8)	5.5 (5.0–6.1)	7.4 (7.1–7.6)
EL	5.9	4.9	6.2	5.0 (4.8–5.2)	5.4 (5.2–5.6)	5.1 (4.5–5.7)	6.6 (6.2–7.0)
TD	4.1	3.8	4.2	3.9 (3.6–4.2)	3.9 (3.7–4.1)	3.1 (2.7–3.6)	3.7 (3.3–4.2)
IND	5.6	4.9	4.9	4.8 (4.4–5.2)	4.9 (4.8–4.9)	3.2 (2.8–3.5)	4.2 (4.0–4.3)
IOD	4.6	4.2	4.3	4.0 (3.7–4.3)	4.1 (4.0–4.2)	2.9 (2.7–3.3)	3.8 (3.7–3.9)
UEW	4.0	3.5	3.6	3.7 (3.2–4.0)	3.6 (3.5–3.7)	3.1 (2.6–3.5)	4.1 (4.0–4.1)
FLL	26.3	24.0	25.3	25.0 (24.1–26.4)	25.7 (25.2–26.2)	24.0 (21.0–26.3)	31.1 (30.6–31.5)
HLL	76.3	66.2	70.8	71.0 (68.6–73.2)	75.8 (75.8–75.8)	69.4 (61.2–77.2)	93.4 (91.6–95.5)
TL	22.9	19.9	21.8	21.3 (20.6–22.3)	23.2 (23.1–23.2)	21.9 (18.9–24.2)	30.3 (29.8–30.8)
FL	23.3	20.5	23.5	23.1 (21.5–24.0)	24.2 (23.9–24.5)	21.1 (18.8–23.1)	27.5 (27.1–27.8)
IMTL	2.6	2.2	2.5	2.6 (2.4–2.8)	2.5 (2.3–2.6)	1.6 (1.3–2.1)	1.9 (1.6–2.2)

values relative to SVL differed between the two species, although the small sample size prohibited statistical comparisons. Compared with *R. okinavana*, *R. psaltes* had larger forelimb (59.2–61.8% vs. 55.7% in *R. okinavana*), hindlimb (178.0–178.8% vs. 161.7%), tibia (54.2–54.7% vs. 48.5%), and foot (56.4–57.5% vs. 49.4%).

The male holotype (Fig. 1C, F, J) and eight male paratypes of *R. psaltes* were also very similar to the paralectotype of *R. okinavana*. The range of body size of male *R. psaltes* (39.5–42.8 mm) included the size of *R. okinavana* (41.6 mm), and they tended to differ only in a few dimensions relative to SVL; *R. psaltes* had larger eye (14.0–16.1% vs. 13.2% in *R. okinavana*), hindlimb (166.8–180.3% vs. 159.1%), foot (52.2–58.8% vs. 49.3%), and inner metatarsal tubercle (5.8–6.6% vs. 5.3%) than *R. okinavana*. These results indicate that *R. psaltes* and *R. okinavana* differ only in the relative size of the hindlimb and foot when both sexes are considered.

Although Kuramoto (1985) reported the absence of vocal sacs in *R. psaltes*, males of the type series proved to have vocal openings, as does the paralectotype of *R. okinavana*. Likewise, males of *R. psaltes* do not have distinct nuptial pads, but they do have small nuptial asperities on the median surface of the first finger.

Comparisons with the brown frog from the middle Ryukyus

Two females of the brown frog now called "*R. okinavana*" from Okinawajima I. examined were morphologically fairly different from the lectotype of *R. okinavana*. Body size of the female brown frogs (47.5–49.9 mm) did not much differ from that of *R. okinavana* (47.2 mm). However, dimensions relative to SVL tended to differ markedly between the two species. Compared with *R. okinavana*, the brown frog had larger eye (13.1–14.0% vs. 12.5% in *R. okinavana*), forelimb (63.1–64.4% vs. 55.7%), hindlimb (190.8–192.8% vs. 161.7%), tibia (61.7–62.7% vs. 48.5%), and foot (55.7–57.1% vs. 49.4%), and smaller tympanum (6.8–8.3% vs. 8.7%), internarial (8.4–8.6% vs. 11.9%), interorbital (7.7–7.8% vs. 9.7%), and inner metatarsal tubercle (3.4–4.3% vs. 5.5%).

The males of the two species also differed. Nineteen male brown frogs were smaller (SVL=32.7–39.4 mm vs. 41.6 mm in *R. okinavana*) and had relatively larger eye (13.2–14.9% vs. 11.8%), forelimb (63.7–67.4% vs. 57.7%), hindlimb (182.0–200.5% vs. 159.1%), tibia (57.4–63.7% vs. 47.8%), and foot (55.4–60.6% vs. 49.3%), and smaller internarial (7.7–9.2% vs. 11.8%) and interorbital (7.2–8.6% vs. 10.1%) than the *R. okinavana* paralectotype. Thus, in both sexes, the brown frog has larger eye, forelimb, hindlimb,

tibia, and foot, and smaller internarial and interorbital, all relative to SVL, than *R. okinavana*.

The brown frog (Fig. 1G, H, K) has a much more slender body, unlike the robust body of *R. okinavana* and *R. psaltes*. The dorsum of the brown frog is scattered with small asperities, and even in individuals with a nearly smooth dorsum, weak asperities are found on the upper eyelid. These asperities are never found in *R. okinavana* and *R. psaltes*. In addition, the brown frog has a chevron ridge medial to the shoulder (Fig. 1G), like other frogs of the subgenus *Rana*, but this ridge is absent in *R. okinavana* and *R. psaltes*. The brown frog also differs from *R. okinavana* and *R. psaltes* in the absence of distinct longitudinal rows of tubercles on the hindlimb. In the brown frog, the dorsolateral fold slightly diverges outward posterodorsal to the tympanum to form a weak supratympanic fold, but the dorsolateral fold is straight and does not flare out in *R. okinavana* and *R. psaltes*. A marked difference is the absence in the brown frog of a suprabrachial gland, which characterizes *R. okinavana* and *R. psaltes*.

The snout of the brown frog is more pointed and lower in height than in *R. okinavana* and *R. psaltes* (Fig. 1 J–K). The fourth finger is longer than the first in the brown frog, but the situation is reversed in *R. okinavana* and *R. psaltes*. In the brown frog, the inner metacarpal tubercle is much less developed than in *R. okinavana*. The toe tip of the brown frog approaches forming a disc, but is smaller and less developed than in *R. okinavana*. In contrast, toe webbing is more developed in the brown frog than in *R. okinavana* and *R. psaltes*, with the first to third toes fully webbed to the distal or second articulation. The brown frog has longer hindlimbs than *R. okinavana* and *R. psaltes*, with the tibio-tarsal articulation reaching between eye and nostril or to the snout tip, and heels that are greatly overlapping. The male brown frog has a large nuptial pad, unlike male *R. okinavana* and *R. psaltes*. The body color is also different; the light-colored mid-dorsal stripe, the dark marking below the dorsolateral fold, and dark ventral marblings, especially large ones on the posteroventral side of the tibia, are absent, but the tympanum is masked black in the brown frog, unlike *R. okinavana* and *R. psaltes*.

DISCUSSION

From the present examination of the types, it is evident that *R. okinavana* is quite different from the brown frog now widely called under that name (e.g., Inger, 1947; Nakamura and Uéno, 1963; Maeda and Matsui, 1999), but is nearly identical with *R. psaltes* (Kuramoto, 1985). Confusion of *R. okinavana* with the brown frog from the middle Ryukyus seems to stem from the surveys of only the literature and not of the types, as well as from the lack of actual comparisons of specimens from both the middle and southern Ryukyus. *Rana okinavana*, the brown frog, and *R. psaltes* are superficially similar in that they are moderate in size and have a brown dorsum. However, possession of a suprabrachial gland clearly separates *R. okinavana* and *R. psaltes* from the brown frog from the middle Ryukyus. Probably because all the previous authors (Stejneger, 1907; Van Denburgh, 1912; Boulenger, 1920; Inger, 1947) failed to notice this structure, which was stated in the original description, although vaguely (“on the sides with large flat warts”: Boettger, 1895a,b), and is actually present in the male *R. okina-*

vana, the species was confused with the brown frog of the middle Ryukyus by the later authors.

The type locality of *R. okinavana*, “the Ryukyu Islands, so called Okinawa in the middle group” (Boettger, 1895a, b), is most probably erroneous. Boettger obtained specimens of *R. okinavana* together with *Rana eiffingeri* Boettger 1895 [= *Chirixalus eiffingeri* Boettger (1895)] from a Japanese collector through Mr. B. Schmacker, then in Shanghai. Boettger (1895a, b) reported the type locality of the latter rhacophorid as Ohosima (=Amamioshima I.) or more probably Okinawa (=Okinawajima I.), the middle Ryukyus. However, as far as we know, *C. eiffingeri* occurs only in the Yaeyama Islands (Ishigakijima I. and Iriomotejima I.) of the southern Ryukyus and Taiwan, and not in the middle Ryukyus (Maeda and Matsui, 1989). Therefore, the type localities of the two frogs described by Boettger (1895a, b) are both highly doubtful.

Rana okinavana, with a unique character of suprabrachial gland, is considered a member of the section *Babina* (Dubois, 1992; elevated to a genus distinct from *Rana* by Frost *et al.*, 2006), and more specifically, the subgenus *Nidirana* because of the presence of distinct dorsolateral fold (Chou, 1999). The only member of *Nidirana* now known from Japan is *R. psaltes*. It was not long ago that the presence of a member of *Nidirana* was ascertained in the Yaeyama Islands of the southern Ryukyus. Since the report of Van Denburgh (1912), no intensive research was made in the Yaeyama Islands, and no one secured specimens of *Rana* with a moderate body size until the first half of the 1970s, when two authors independently reported a *Rana* species from the Yaeyama Islands (Kuramoto, 1973; Otsu, 1975). Both of these authors identified the species as *R. adenopleura* Boulenger, 1909, originally described from Taiwan. Matsui and Utsunomiya (1983) reported marked differences in call characteristics between the populations of *R. adenopleura* from the Yaeyama Islands and Taiwan, and suggested their independent taxonomic status. Finally, Kuramoto (1985) described the species from the Yaeyama Islands as *R. psaltes*.

It is very difficult to differentiate *R. psaltes* from *R. okinavana*, as shown above, and it seems unlikely that more than one species occurs on small islands of the Yaeyama Islands (i.e., Ishigakijima I. and Iriomotejima I.) in the southern Ryukyus. Thus, it is most probable that *R. okinavana* Boettger, 1895 is identical with, and a subjective senior synonym of, *R. psaltes* Kuramoto, 1985. Slight morphometric differences between the types of *R. okinavana* and *R. psaltes*, especially in lengths related to the hindlimb, may include allometric and geographic variation. This may possibly be the case, if the syntypes of *R. okinavana* were collected from Ishigakijima I. in contrast to those of *R. psaltes* that were from Iriomotejima I., because some morphometric and genetic variation between the two islands has been reported for another ranid, *Rana (Odorrana) utsunomiyaorum* (Matsui, 1994; Matsui *et al.*, 2005). Because *R. psaltes* is now known to occur also in Taiwan (Chou, 1994), the name for the Taiwanese population should be also changed.

As a result of this study, the brown frog now referred to “*R. okinavana*” from the middle Ryukyus proves to be distinct from true *R. okinavana* and needs a formal description, which is now underway.

ACKNOWLEDGMENTS

I thank Günther Köhler of the Forschungsinstitut und Naturmuseum Senckenberg and Kiyotaka Hatooka of the Osaka Museum of Natural History for allowing me to examine type specimens under their care; Annemarie Ohler of the Museum national d'Histoire naturelle, Paris for helping to access specimens; Atsushi Tominaga of Kyoto University for preparing the fig.; and Kanto Nishikawa and Akira Mori of Kyoto University for help in obtaining literature. This study was supported by a grant under The Monbusho International Scientific Research Program (Field Research, No. 10041166).

REFERENCES

- Boettger O (1895a) Neue Frösche und Schlangen von den Liukiu-Inseln. Ber Thätig Offenbacher Ver Naturk 33/36: 101–117
- Boettger O (1895b) Neue Frösche und Schlangen von den Liukiu-Inseln. Zool Anz 18: 266–270
- Boulenger GA (1920) A monograph of the South Asian, Papuan, Melanesian, and Australian frogs of the genus *Rana*. Rec Ind Mus 20: 1–126
- Chou W-H (1994) Geographic distribution. *Rana psaltes*. Herpetol Rev 25: 75
- Chou W-H (1999) A new frog of the genus *Rana* (Anura: Ranidae) from China. Herpetologica 55: 389–400
- Dubois A (1992) Notes sur la classification des Ranidae (Amphibiens Anoures). Bull Mens Soc Linn Lyon 61: 305–352
- Frost DR, Grant T, Faivovich JN, Bain RH, Haas A, Haddad CFB, De Sá RO, Channing A, Wilkinson M, Donnellan SC, Raxworthy CJ, Campbell JA, Blotto BL, Moler P, Drewes RC, Nussbaum RA, Lynch JD, Green DM, Wheeler WC (2006) The amphibian tree of life. Bull Amer Mus Nat Hist 297: 1–370
- Inger RF (1947) Preliminary survey of the amphibians of the Riukiu Islands. Fieldiana: Zool 32: 295–352
- Kuramoto M (1973) The amphibians of Iriomote of the Ryukyu Islands: ecological and zoogeographical notes. Bull Fukuoka Univ Educ Pt 3 22: 139–151
- Kuramoto M (1979) Distribution and isolation in the anurans of the Ryukyu Islands. Jpn J Herpetol 8: 8–21
- Kuramoto M (1985) A new frog (genus *Rana*) from the Yaeyama group of the Ryukyu Islands. Herpetologica 41: 150–158
- Maeda N, Matsui M (1989) Frogs and Toads of Japan. Bun-ichi Sogo Shuppan, Tokyo
- Maeda N, Matsui M (1999) Frogs and Toads of Japan, Revised Edition. Bun-ichi Sogo Shuppan, Tokyo
- Matsui M (1984) Morphometric variation analyses and revision of the Japanese toads (Genus *Bufo*, Bufonidae). Contrib Biol Lab Kyoto Univ 26: 209–428
- Matsui M (1994) A taxonomic study of the *Rana narina* complex, with description of three new species. Zool J Linn Soc 111: 385–415
- Matsui M, Utsunomiya T (1983) Mating call characteristics of the frogs of the subgenus *Babina* with reference to their relationship with *Rana adenopleura*. J Herpetol 17: 32–37
- Matsui M, Shimada T, Ota H, Tanaka-Ueno T (2005) Multiple invasions of the Ryukyu Archipelago by Oriental frogs of the subgenus *Odorrana* with phylogenetic reassessment of the related subgenera of the genus *Rana*. Mol Phylogenet Evol 37: 733–742
- Mertens R (1967) Die herpetologische Sekition des Nature-Museums und Forschungs-Institutes Senckenberg im Frankfurt a. M. nebst einem Verzeichnis ihrer Typen. Senckenb Biol 48 A:1–106
- Nakamura K, Uéno SI (1963) Japanese Reptiles and Amphibians in Colour. Hoikusha, Osaka
- Okada Y (1931) The Tailless Batrachians of the Japanese Empire. Imperial Agricultural Experimental Station of Tokyo, Tokyo
- Ota H (1998) Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu Archipelago, Japan, with special reference to their paleogeographic implications. Res Popul Ecol 40: 189–204
- Otsu T (1975) Amphibia of Okinawa Islands. Bull Yamagata Univ Nat Sci 18: 545–552
- Shibata Y, Matsui M (1985) Taxonomic notes on some Japanese amphibians I. Problems concerning *Rana macropus* Boulenger, 1886. Bull Osaka Mus Nat Hist 38: 1–4
- Stejneger L (1907) Herpetology of Japan and adjacent territory. Bull US Natl Mus 58: 1–577
- Toyama M (2003) Amphibians. In “The Flora and Fauna of Inland Waters in the Ryukyu Islands” Ed by M Nishida, S Shokita, Tokai University Press, Tokyo, pp 499–509
- Van Denburgh J (1912) Concerning certain species of reptiles and amphibians from China, Japan, the Loo-Choo Islands, and Formosa. Proc Calif Acad Sci IV 3: 187–257

(Received September 5, 2006 / Accepted October 3, 2006)