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Call Structures of the Rhacophorid Frogs from Taiwan

By

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(With 13 Text-figures)

INTRODUCTION

Calls are species-specific attributes of vocalizing animals and carry much information on various aspects of animal behavior. The most important role of anuran calls is to attract the conspecific females toward the vocalizing males as reported by many authors (LITTLEJOHN and MICHAUD, 1959; LITTLEJOHN, 1960, 1961; LITTLEJOHN and LOFTUS-HILLS, 1968; OLDHAM and GERHARDT, 1975; GAMBS and LITTLEJOHN, 1979; KRUSE, 1981). To avoid confusion in the acoustic signal, each species in the same habitat should have a unique call with respect to temporal and frequency features of the sounds. The species-specific nature of anuran calls has been used as the basis for discriminating closely related species (JOHNSON, 1959; LITTLEJOHN and OLDHAM, 1968; DUBOIS, 1975; FROST and BAGNARA, 1976; KURAMOTO, 1980a) and for determining species relationships (BLAIR, 1958, 1960; MECHAM, 1971; NELSON, 1973; KURAMOTO, 1980a).

In previous studies, the author has clarified the acoustic features of Japanese frogs (KURAMOTO, 1975, 1977, 1980a, b). In contrast, few acoustic studies have been performed on Taiwanese frogs (KURAMOTO and UTSUNOMIYA, 1981) and on Asiatic frogs outside of Japan and Taiwan (HEYER, 1971). The anuran fauna of Taiwan includes the relatives to the frogs of Japan, especially to those of the Ryukyu Islands, and acoustic studies on Taiwanese frogs will shed light on the phylogenetic relationships of the frogs distributed there.

In the present study the author deals with call structures of six Taiwanese rhacophorid frogs. All of the Japanese rhacophorid frogs have call structures that are composed of a series of short pulses, mostly with clear harmonic bands (KURAMOTO, 1975). Whether the same general trend is found for Taiwanese rhacophorids and whether there are variations between conspecific populations of Taiwan and the Ryukyu Islands are examined. Finally, the possible course of acoustic divergence in the family Rhacophoridae is postulated in connection with classification and ecology of this group of frogs.

MATERIALS AND METHODS

Calls of *Rhacophorus taipeianus* LIANG and WANG, *R. moltrechti* BOULENGER, *Polypedates leucomystax* (Kuhl), *Buergeria robusta* (Boulenger), *B. japonica* (Hallowell) and *Chirixalus eiffingeri* (Boettger) were recorded in 1977, 1978, 1981 and 1982 at one or more localities shown in Fig. 1. The generic names follow Liem (1970), and the term rhacophorid is used here to indicate the frogs belonging to the family Rhacophoridae, not to the genus *Rhacophorus*. Temperature records were taken in the vicinity of the calling males. The calls analyzed were recorded in the field except the calls of *B. robusta* which were recorded in the laboratory. Tape recorders used were TC–1015, TC–1051 and TCM–100 (SONY).

Sonagrams were prepared with Digital Sona-Graph$^{\text{TM}}$ 7800 (KAY). For the analysis of short calls and a part of long calls, standard (2.56 sec) sonagrams with 300 Hz or 45 Hz band-width filter were used. The whole structure of long calls and of the series of calls were analyzed based on 5.12 or 10.24 sec sonagrams with 150 Hz and 75 Hz band-width filter, respectively, and on time waveform display. Expanded time waveforms were depicted to visualize the nature of pulses.

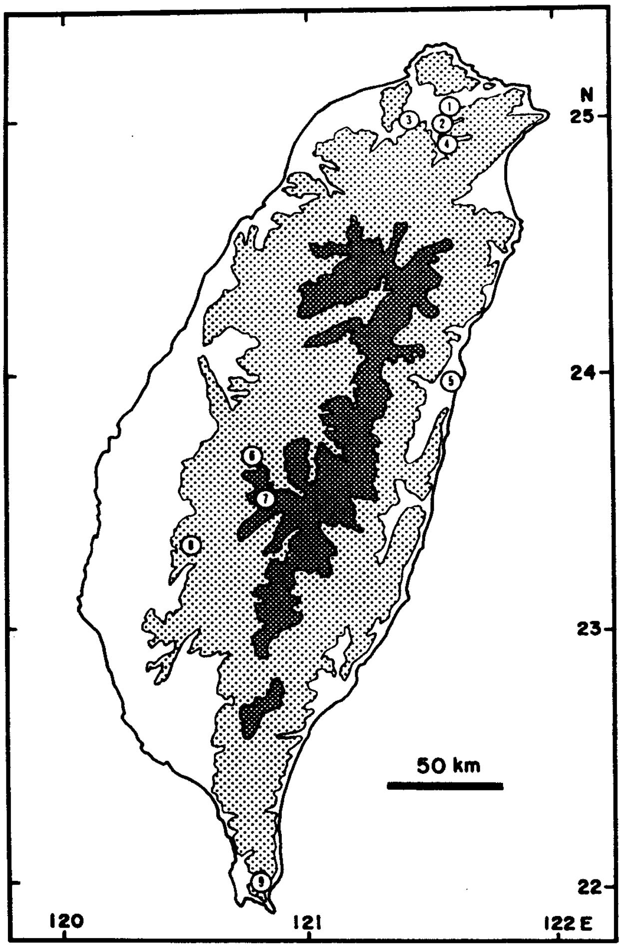

Fig. 1. Map of Taiwan showing the localities where the calls of frogs were recorded. 1, Nankang (Nangang). 2, Mucha (Muzha). 3, Shulin. 4, Kuishanli (Guishanli). 5, Hualien (Hualian). 6, Shitou (Xitou). 7, Alishan. 8, Kuantzuling (Guanziling). 9, Manchou (Manzhou). Contour lines indicate the elevation of 200 and 2000 m above sea level.

When a call is composed of several groups of pulses, each group is termed here note, and when there are two kinds of notes which differ in pulse repetition rate and/or frequency characteristics, a note or a group of similar notes is termed phase. Main acoustic parameters measured are: duration of the calls, phases, notes and pulses; number of notes and pulses; pulse repetition rate (number of pulse per sec); frequency range; fundamental frequency; and harmonic bands. Parameters such as time intervals between calls, notes or pulses, and the degree of frequency modulation are given where they are pertinent in characterizing the calls.

Since the ecology of Taiwanese frogs has been poorly known (LUE and CHEN, 1982), a brief description on the distribution, habitat, breeding site, breeding season, form of egg mass and calling site of the male are given based largely on the author's own field observation.

OBSERVATION

I. Rhacophorus taipeianus

R. taipeianus occurs in the hilly or low mountainous regions of northern Taiwan. It breeds from December to February and the males call from muddy depressions under piles of rice straw or among grasses near water. Foamy egg masses are deposited in these depressions, often half-buried in the soil. The calls were

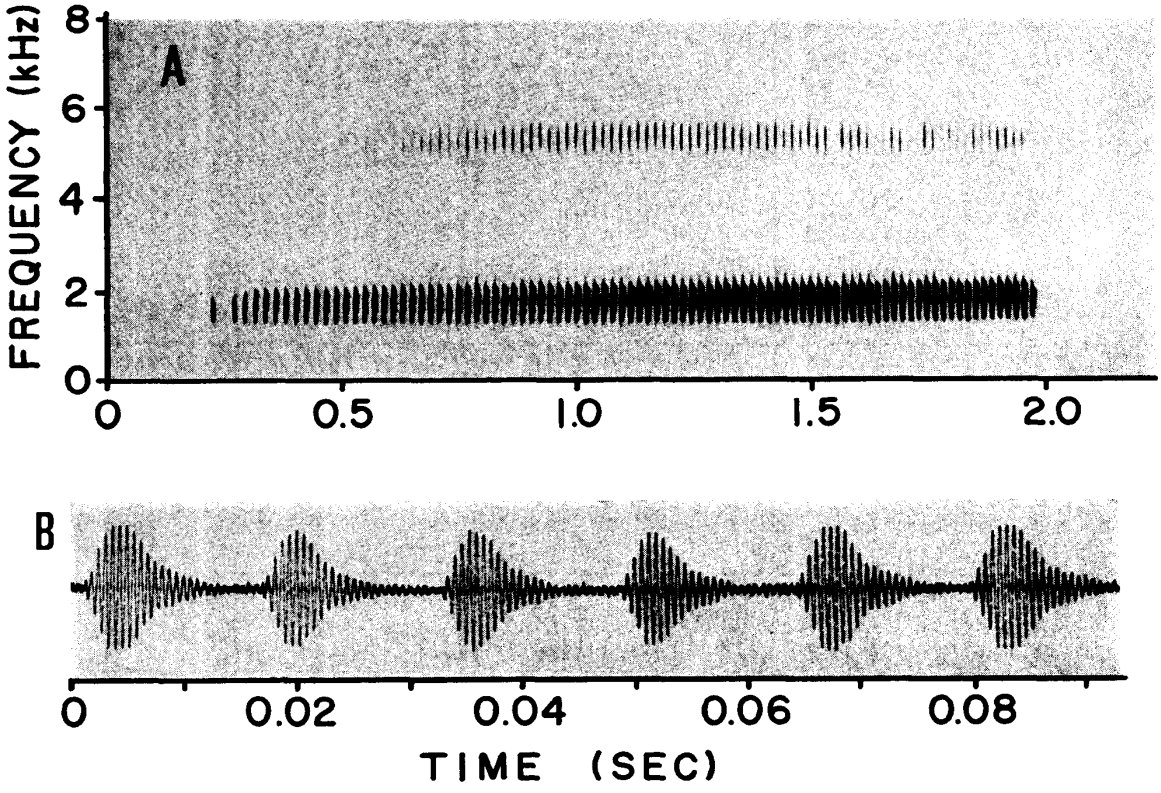

Fig. 2. A: Single-note call of *R. taipeianus* recorded at Nankang (14°C, 300 Hz filter). B: Waveforms of pulses in a call of *R. taipeianus* recorded at Shulin (17°C). Ordinate represents amplitude.

recorded at Mucha on 26 February 1977 (21°C), at Shulin on 27 February 1977 (17°C) and at Nankang on 30 December 1981 (17°C) and 5 January 1982 (14°C).

The calls of *R. taipeianus* were long series of many pulses which had relatively narrow frequency ranges (Fig. 2A). Fundamental frequencies of the calls recorded at Nankang were at 1.74 kHz (14°C) and 1.70 kHz (17°C), and weak harmonic bands appeared at about 3.5 and 5.3 kHz (14°C) and at 3.4 and 5.0 kHz (17°C). Each pulse showed regular symmetrical waveform with rather rapid rise time (Fig. 2B).

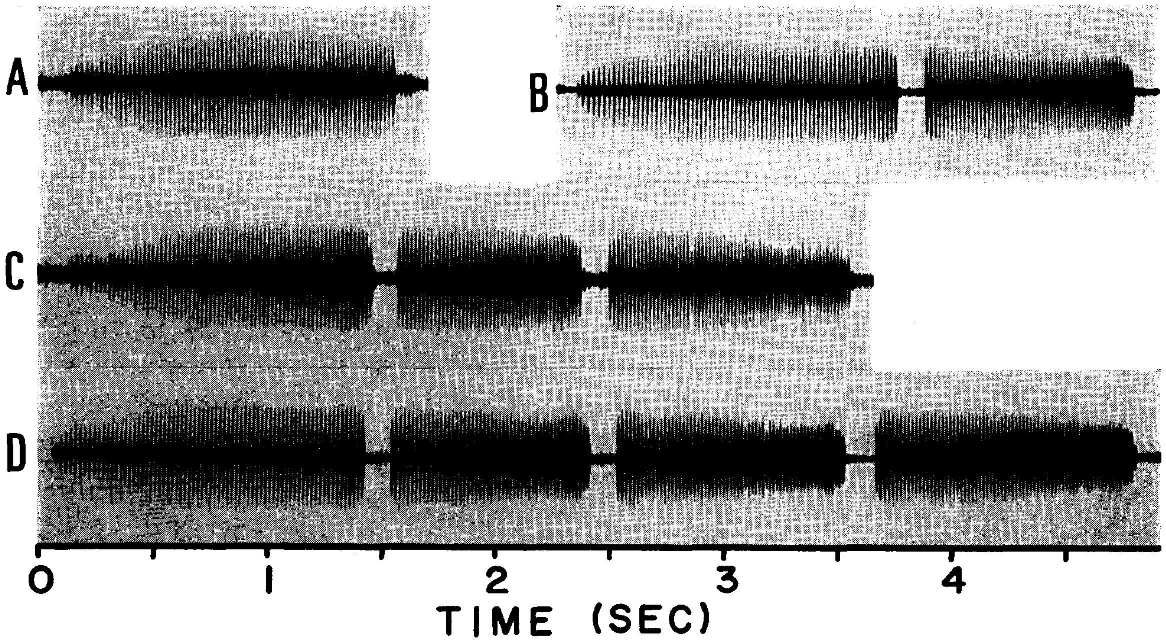

Fig. 3. Time waveforms of single- (A), 2- (B), 3- (C), and 4-note call (D) of *R. taipeianus* recorded at Nankang (14°C). Each vertical line shows a single pulse.

TABLE 1

Duration and pulse repetition rate in different call types of *R. taipeianus* (x̄±SE)

Locality Temp	Call type	N	Call duration (10⁻² sec)	Note duration (10⁻² sec)				Pulse repetition rate (Pulse/sec)			
				1st note	2nd note	3rd note	4th note	1st note	2nd note	3rd note	4th note
Nankang 14°C	1-note	8	160± 8	160±8	—	—	—	52±0.2	—	—	—
	2-note	8	286±16	154±6	120±10	—	—	52±1.2	57±1.6	—	—
	3-note	8	342± 6	128±6	85± 1	107±2	—	54±0.4	61±0.8	63±0.4	—
	4-note	1	473	135	87	100	115	53	60	63	62
Shulin 17°C	1-note	8	154± 4	154±4	—	—	—	62±0.3	—	—	—
	2-note	4	257± 6	139±5	105± 5	—	—	63±0.3	66±0.4	—	—
	3-note	2	363	138	90	109	—	62	66	67	—
Nankang 17°C	1-note	8	148± 3	148±3	—	—	—	68±1.0	—	—	—
	2-note	8	240± 4	128±3	101± 2	—	—	66±1.4	71±1.0	—	—
	3-note	8	326± 7	114±3	83± 4	107±2	—	62±0.9	69±1.2	72±0.8	—
	4-note	8	410± 5	109±1	69± 2	89±2	110±1	61±0.6	66±0.6	72±0.9	72±0.4
Mucha 21°C	1-note	7	136± 5	136±5	—	—	—	66±0.6	—	—	—
	2-note	6	235± 9	122±6	101± 4	—	—	67±0.4	69±0.5	—	—

In addition to the calls consisting of a single note, there were many calls which involved two, three or four notes (Fig. 3). Several acoustic parameters of the four call types are compared in Table 1. Total duration of a call extended as the note increased but not in proportional manner, because the duration of the note reduced with the number of notes. In 2-note calls the first note was always longer than the second; in 3-note calls the first note was generally longer than the third and the third invariably longer than the second; in 4-note calls the first and fourth note were nearly the same in length, the third note was shorter than the first and fourth, and the second note was the shortest (Table 1). The time interval between two successive notes was 0.11–0.12 sec in all kinds of multi-note calls. Pulse repetition rate in each note became higher toward the end note (Table 1). With increasing temperature, the call and note duration decreased and pulse repetition rate rose.

The author observed that 1-note calls were usually emitted at the beginning of vocalization of individual males, while multi-note calls were predominant at high level of vocal activity. Similarly, multi-note calls were recorded more abundantly in the midst of the breeding season; near the end of the breeding season (February) multi-note calls were very few.

An actively calling male observed at Nankang (17°C) emitted 10–19 calls per minute. Mean interval between two successive calls was 2.32 sec and sometimes it was as short as 0.54 sec.

II. Rhacophorus moltrechti

R. moltrechti occurs in the mountainous regions of central and south Taiwan and breeds from February to June. The male calls from hollows in soil or under stone, but in a few occasions at rainy nights it calls while exposing himself on the ground. Foamy egg masses are usually completely buried in the soil near water and partly exposed on the ground in only a few cases. The calls were recorded at Shitou on 26 and 27 February 1982 (12°C) and at Alishan on 13 June 1982 (13°C).

The calls of *R. moltrechti* were long trills which sometimes lasted over 5 sec. It consisted of many pulses that formed several notes. As readily recognized in the sonagram (Fig. 4A), the call was divided into two distinct phases. One phase constituting the first half was composed of slowly repeating pulses and the other phase constituting the latter half was composed of rapidly repeating pulses that had a somewhat lower frequency level. The two phases are referred here to as slow phase and fast phase, respectively.

Table 2 lists the acoustic parameters of the two phases. Generally the slow phase was longer than the fast phase, although there were extensive variations. The first note in the slow phase was significantly longer and had lower pulse repetition rate than the other note in the slow phase. Pulses in the fast phase were repeated more than twice as fast as those in the slow phase.

Fundamental frequency of the slow phase was at about 1.2 kHz with clear harmonic bands. The intensity of the bands gradually reduced toward the higher

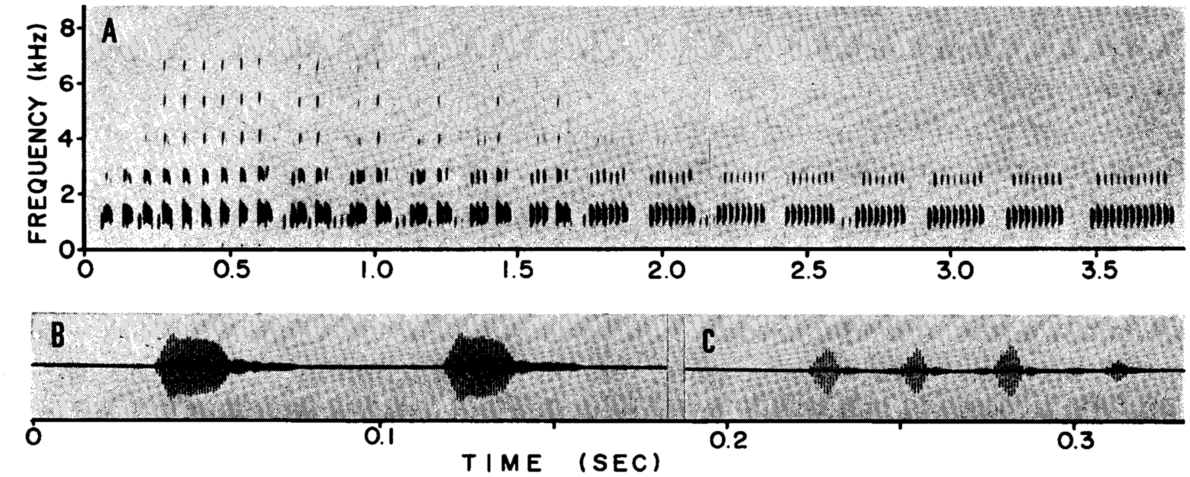

Fig. 4. A: Call of *R. moltrechti* recorded at Alishan (13°C, 300 Hz filter). B and C: Waveforms of pulses in the slow (B) and fast phase (C) of a call of *R. moltrechti* recorded at Shitou (12°C).

TABLE 2

Duration and pulse repetition rate of the calls of *R. moltrechti* ($\overline{x} \pm SE$, range in parenthesis)

Locality Temp	N	Call duration (10^{-2} sec)	Phase duration* (10^{-2} sec)	No. note	Note duration (10^{-2} sec)		Pulse repetition rate		Frequency (kHz)	
					1st note	2nd note	1st note	Last note	Funda-mental	2nd harmonics
Shitou 12°C	15	378±34 (198–658)	(S) 208±13 (137–288)	2.9±0.2 (2–4)	119±6 (86–168)	38±5 (22–77)	12±0.2 (11–13)	12±0.2 (11–14)	1.22±0.01 (1.2–1.3)	2.46±0.02 (2.3–2.5)
			(F) 156±31 (24–220)	3.4±0.6 (1–9)	21±3 (4–41)	39±3 (16–61)	35±0.5 (32–39)	34±0.3 (33–36)	1.13±0.01 (1.1–1.2)	2.31±0.04 (2.3–2.4)
Alishan 13°C	15	389±17 (270-504)	(S) 226±11 (162–282)	6.1±0.3 (4–8)	83±5 (60–108)	25±2 (16–36)	17±0.7 (14–20)	26±1.8 (19–39)	1.19±0.02 (1.1–1.3)	2.37±0.06 (2.0–2.6)
			(F) 157±15 (68–310)	5.3±0.5 (2–10)	22±2 (14–29)	23±2 (14–31)	48±1.1 (38–53)	46±0.6 (42–49)	1.13±0.03 (1.1–1.3)	2.27±0.06 (2.0–2.6)

* S, Slow phase F, Fast phase

frequencies. The fast phase had a mean fundamental frequency of 1.13 kHz with harmonic bands at about 2.3 and 3.4 kHz. The third harmonic band was very weak and the harmonic bands above the third were scarcely discernible. Each frequency band showed moderate frequency modulation.

The pulses in the two phases differed remarkably as revealed in the expanded waveform (Fig. 4B and C). The pulse in the slow phase was longer than that in the fast phase. In the slow phase, the maximum amplitude peak of a pulse was attained shortly after onset of the pulse, and a high amplitude level was retained for about 0.01 sec after the peak. The main wave was followed by a weak wave of nearly the same duration. In the fast phase, the maximum amplitude peak was situated at about 2/3 of the main wave length and the weak waves were not so closely associated with the main wave as in the slow phase.

Duration of the calls recorded at Shitou and Alishan did not differ significantly, but the calls of Shitou had fewer notes, longer note duration and lower pulse repetition rate than the calls of Alishan (Table 2). Since the temperature of the two localities differed only slightly, these differences may be ascribed to the acoustic divergence between the two populations.

An actively vocalizing male recorded in Alishan emitted 5–9 calls per minute. Time intervals between two successive calls were 3–8 sec.

III. Polypedates leucomystax

This species is the most widespread rhacophorid frog and its range covers a vast area of Southeast Asia. In Taiwan, it occurs everywhere in the forested lowlands and low mountains. Differing from above two species, male *P. leucomystax* calls mostly from the shrubs and rarely calls from the ground. Egg laying occurs from May to July and the foamy egg masses are deposited among various vegetations near the still water. The author recorded the calls of *P. leucomystax* at three localities; Hualien on 26 May 1978 (25°C), Manchou on 14 June 1982 (27°C) and Kuishanli on 18 and 26 June 1982 (25°C).

The calls of *P. leucomystax* consisted of sharp pulses. Some calls had only a single pulse, while others have two, three, four or more pulses (Fig. 5A). Each pulse covered a wide spectrum of frequencies up to 8 kHz and neither definite fundamental frequency nor harmonic bands were recognized. The main frequency range was between 0.5 and 3.3 kHz. The waveform of the pulse was irregular (Fig. 5B).

From the author's field observation it was concluded that the males emitted multi-pulse calls in a high activity level of vocalization. At the beginning of calling after sunset, the males emitted calls mostly composed of a single pulse and the frequency of multi-pulse calls increased with time. Usually a male

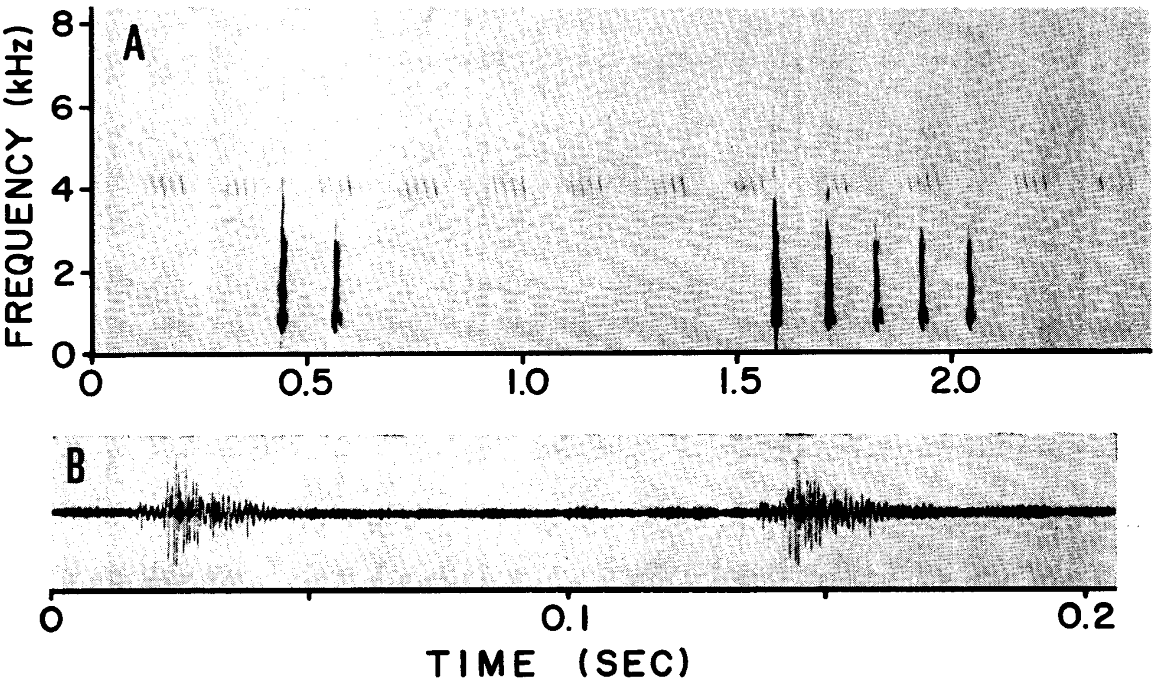

Fig. 5. A: Two successive calls of *P. leucomystax* recorded at Manchou (27°C, 300 Hz filter). The calls consist of two and five pulses. Background noises at 3–5 kHz are the calls of insects. B: Waveforms of two pulses in a call of *P. leucomystax* recorded at Manchou (27°C).

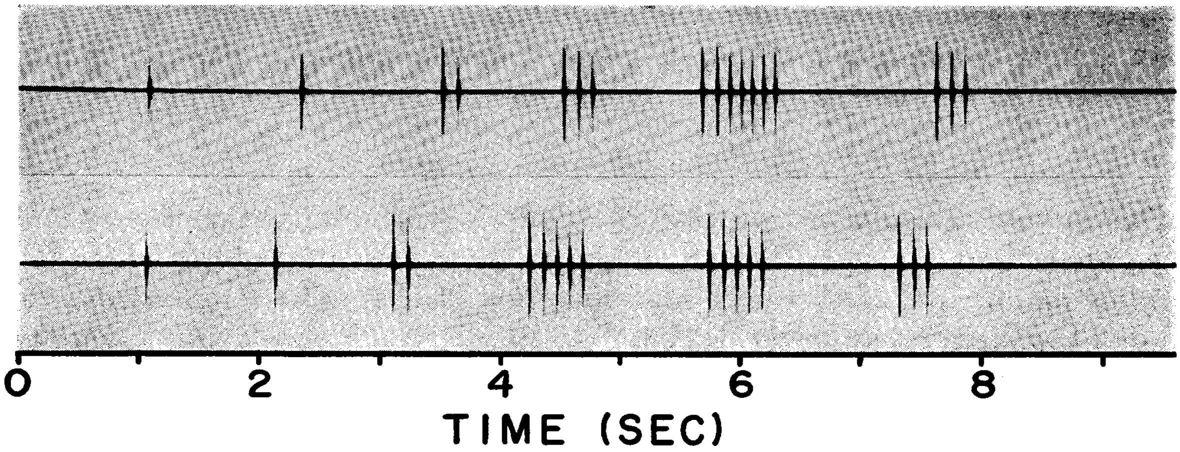

Fig. 6. Two series of calls emitted by a single male of *P. leucomystax* recorded at Manchou (27°C). Time waveform display.

TABLE 3

Duration, pulse interval and pulse repetition rate in the multi-pulse calls of *P. leucomystax* ($\bar{x} \pm SE$)

Locality Temp	Call type	N	Call duration (10^{-2} sec)	Pulse interval (10^{-2} sec)				Pulse repetition rate
				1st–2nd	2nd–3rd	3rd–4th	4th–5th	
Hualien 25°C	2-pulse	8	16.8±0.3	15.5±0.3	—	—	—	6.2±0.1
	3-pulse	5	33.3±1.0	16.6±0.8	15.3±0.9	—	—	6.2±0.2
	4-pulse	5	51.4±0.9	17.8±0.5	16.4±0.4	16.1±0.2	—	6.0±0.1
	5-pulse	2	62.8	16.3	15.5	15.0	14.8	6.5
Kuishanli 25°C	2-pulse	8	20.1±0.8	17.4±0.8	—	—	—	5.9±0.3
	3-pulse	9	33.5±1.4	16.8±0.6	14.4±0.8	—	—	6.7±0.3
	4-pulse	9	46.3±0.6	17.2±0.1	12.9±0.2	13.7±0.4	—	6.9±0.1
	5-pulse	5	58.1±1.6	16.3±0.6	12.2±0.4	12.7±0.3	14.6±0.5	7.3±0.2
Manchou 27°C	2-pulse	10	15.3±0.2	13.0±0.1	—	—	—	7.6±0.1
	3-pulse	10	26.5±0.3	12.7±0.1	11.7±0.3	—	—	8.5±0.1
	4-pulse	5	37.8±0.3	12.9±0.1	11.3±0.1	11.6±0.2	—	8.6±0.1
	5-pulse	4	45.4±1.8	12.8±0.1	11.0±0.1	10.9±0.1	11.6±0.4	9.3±0.4

started a series of calls with several single-pulse calls (Fig. 6), but the series evoked in the high vocal activity level contained few single-pulse calls. The intervals between two successive calls varied from 0.86 to 1.76 sec with a mean of 1.13±0.04 sec (N=28). Multi-pulse calls of *P. leucomystax* are probably predominant in the midst of the breeding season, as the multi-note calls of *R. taipeianus*.

Pulse intervals in multi-pulse calls did not vary greatly within each of three populations examined, but the first interval (between 1st and 2nd pulse) was always longer than the other intervals (Table 3). The last interval in the calls with more than 3 pulses tended to be longer than the preceding intervals except for the first interval. Mean pulse repetition rate was 6.25 pulse/sec in Hualien, 6.71 pulse/sec in Kuishanli and 8.50 pulse/sec in Manchou. Differences in the pulse interval and pulse repetition rate of the three populations may be partly due to acoustic divergence.

IV. Buergeria robusta

B. robusta, together with *B. buergeri* of Japan proper, is unique among rhacophorid frogs in its stream habitat. It occurs along streams in the low mountainous regions and breeds from March to May. Differing from the above three species, the eggs are not laid in a terrestrial foam nest but laid on the sandy or gravelly bottom of the stream, often under stones. The males call from the stones and rocks in the streams. To avoid extensive background noise of the running water, the author recorded the calls of *B. robusta* in the laboratory using

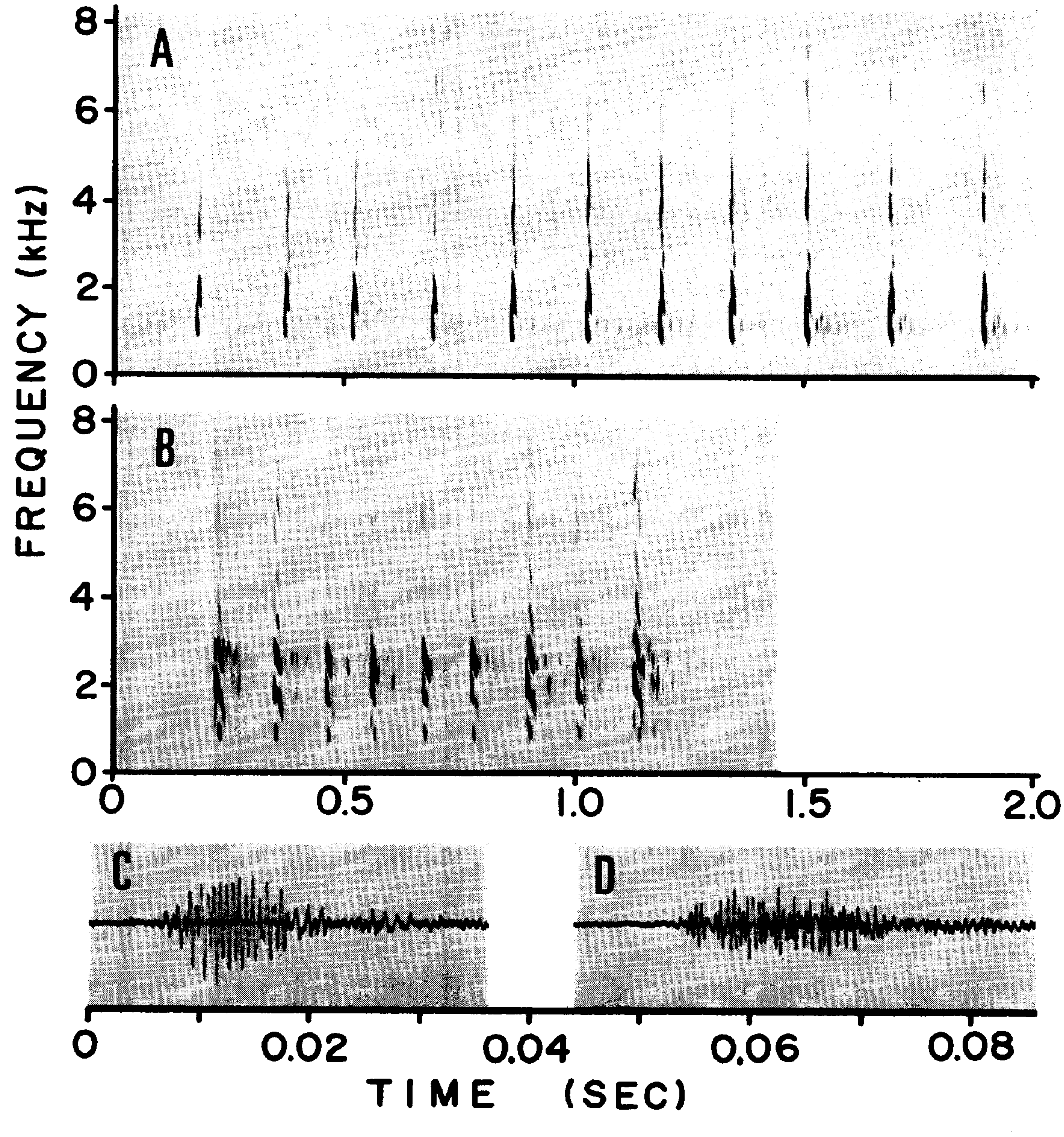

Fig. 7. A: Normal call of *B. robusta* collected at Hualien and recorded in the laboratory (25°C, 300 Hz filter). B: Rapid call of *B. robusta* from Hualien recorded in the laboratory (28°C, 300 Hz filter). Noise following each pulse is due to sound reflection. C and D: Waveform of a pulse in a normal (C) and in a rapid call (D).

specimens collected at Hualien on 28 May 1978. Recordings were made on 28 May (28°C) and 5 June 1978 (25°C).

The calls of *B. robusta* consisted of short pulses as those of *P. leucomystax* (Fig. 7A), but the calls of the former were much longer and contained more pulses and the pulses were repeated more slowly than the calls of the latter (Table 4). The pulse contained a wide range of frequencies as in *P. leucomystax*, but differed from the latter in the presence of weak harmonic bands, although each band had a broad band-width. Two dominant frequency bands centered around 1.1–1.2 kHz and 1.8–1.9 kHz. The pulse was more sharply defined than in *P. leucomystax*. Waveform (Fig. 7C) was more regular than that of *P. leucomystax*, and this, together with harmonic nature of the sound, made the tone of calls more musical than the calls of *P. leucomystax*.

Many calls with a higher pulse repetition rate were recorded at 25°C and 28°C (Fig. 7B). These rapid calls probably had a rivalry or aggressive role because the males emitted these calls when two individuals were in close proximity in a vial. Wide variations in acoustic parameters of rapid calls probably reflected the various degree of interaction between two or more males involved. Usually the rapid calls given by two or more males partly overlapped with each other. In Table 4, several acoustic parameters of rapid calls are compared with those of normal calls described above. The rapid call retained the harmonic nature, but it had slightly longer and less sharply defined pulses than the normal call. Waveform of the pulse was irregular compared with that of the normal call (Fig. 7D).

TABLE 4

Duration and pulse repetition rate of the calls of *B. robusta* collected at Hualien and recorded in the laboratory ($\bar{x} \pm$SE, range in parenthesis)

Temperature	Call type	N	Call duration (10^{-2} sec)	No. pulse	Pulse repetition rate
25°C	Normal	13	152.2± 9.7	9.4±0.5	5.7±0.1
			(100–196)	(7–12)	(4.9– 6.2)
	Rapid	4	151.8±42.2	13.8±2.7	8.9±0.8
			(85–276)	(8–21)	(7.2–11.2)
28°C	Rapid	13	107.7±12.3	11.9±1.2	10.7±0.4
			(63–188)	(7–20)	(8.9–13.0)

Two dominant frequency bands of rapid calls centered around 1.8 and 2.5 kHz. These values were significantly higher than the values of normal calls but did not differ between rapid calls recorded at 25° and 28°C.

V. Buergeria japonica

This small, ground-dwelling rhacophorid frog occurs in Taiwan and the Ryukyu Islands. In Taiwan it lives in small ditches and rice fields in the hilly or low mountainous regions. The breeding season is from March to June or probably to mid-summer. The eggs are laid in shallow water in loosely connected, thin gelatinous layer. Usually the eggs sink to the bottom after a few hours of oviposition. The males call from the edge of water or in the shallow, slowly flowing water. The calls of *B. japonica* were recorded at Hualien on 26 May 1978 (25°C), at Kuantzuling on 23 March 1982 (20°C) and at Kuishanli on 18 and 26 June 1982 (25°C).

The calls of *B. japonica* were composed of many pulses and the structure varied remarkably within a population and between populations. Tentatively, they were classified into three call types; short trills, long trills and whistles. These three types were distinct from each other and no intermediate call type was recorded. The long trills and whistles seemed to be evoked at a high vocal activity.

The short trills of Kuishanli were significantly longer than those of Kuantzuling and Hualien (Table 5, Fig. 8A). In the last portion of the short trills, there were one or more pulse groups which differed from the main phase in both frequency and temporal features. The pulse group (note) was composed mostly of 3 pulses which were repeated more rapidly than the pulses of the main phase. Dominant

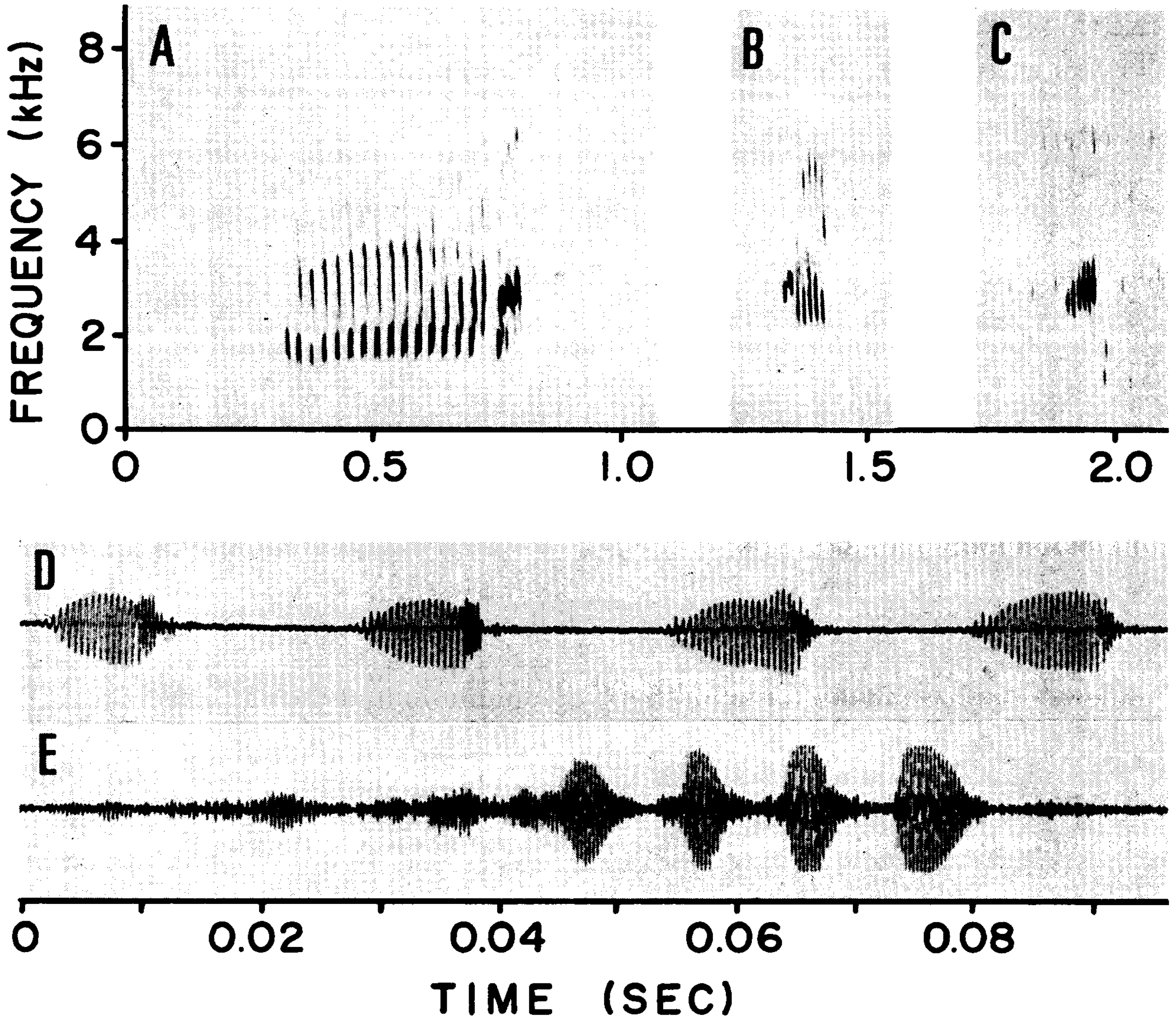

Fig. 8. A, B and C: Short trills of *B. japonica* recorded at Kuishanli (A, 25°C), Kuantzuling (B, 20°C) and Hualien (C, 25°C). 300 Hz filter. D and E: Waveforms of short trills recorded at Kuishanli (D) and Hualien (E).

TABLE 5

Duration and pulse repetition rate of the short trills of *B. japonica*
($\bar{x} \pm$SE, range in parenthesis)

Locality Temp	N	Call duration (10 $^{-2}$sec)	No. pulse	Pulse repetition rate*	Last note	
					Duration	No. pulse
Kuishanli 28°C	46	48.3±3.1 (20–116)	17.5±1.0 (8–43)	34.9±0.6 (28– 41)	4.7±0.1 (4–6)	3.0±0.1 (2–4)
Kuantzuling 20°C	8	12.3±0.5 (10– 15)	10.4±0.4 (9–12)	89.2±3.2 (82–100)	— —	— —
Hualien 25°C	15	8.8±0.3 (7– 11)	7.8±0.5 (4–10)	90.9±4.2 (71–110)	— —	— —

* Excluding pulse rate in the last note

frequency of the main phase was low, being about 1.8 kHz. In the last part of the main phase, a second dominant band appeared which had a final frequency level as high as that of the last phase, about 3 kHz. Of 46 calls analyzed, 10 had 2 pulse groups and two had 4 and 9 pulse groups in the last phase. The pulse in both phases showed frequency modulation.

The short trills recorded at Kuantzuling and Hualien (Fig. 8B and C) differed

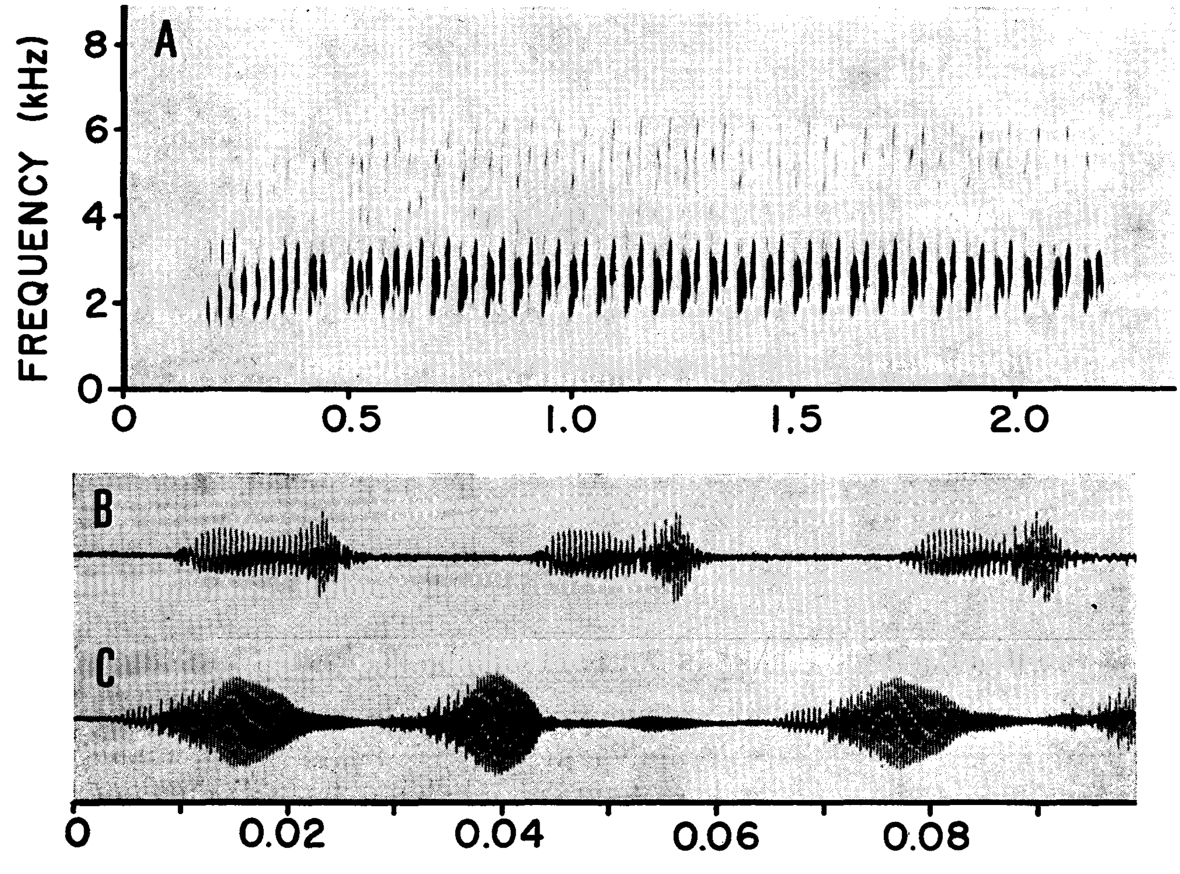

Fig. 9. A: Long trill of *B. japonica* recorded at Kuishanli (25°C, 300 Hz filter). B and C: Waveforms of the pulses from the first phase (B) and main phase (C).

remarkably from the short trills of Kuishanli in acoustic structure, but were similar to each other in their short duration, high pulse repetition rate and high dominant frequency. They resembled the last phase of the short trill of Kuishanli except that the pulse did not form 3-pulse notes. The short trills of Kuantzuling and Hualien differed from those of Kuishanli also in their waveforms (Fig. 8D and E).

The long trill recorded at Kuishanli was not a simple extension of the short trills (Fig. 9A). It consisted of two phases which differed in duration and pulse characteristics (Table 6). The two phases are referred to here as first phase and main phase. The acoustic structure of the first phase was essentially identical with that of the short trill. It accompanied the last note characterizing the short trills of Kuishanli. The main phase was long, about 4/5 of the whole duration of long trill, and was composed of alternatively repeating, two kinds of pulses which differed in frequency characteristics. The pulse that had lower dominant frequency showed frequency modulation. Waveform of the pulses involved in the first phase differed from that in the main phase (Fig. 9B and C), but resembled the pulses in the short trill. This call was not recorded at Kuantzuling and Hualien. In some calls, the frequency of the main phase decreased toward the end of a call.

The long trill recorded at Hualien had quite a different acoustic structure from that described above. It consisted of similar notes each containing about 6 pulses (Fig. 10). Apparently this call was composed of rapidly repeating short

TABLE 6

Acoustic parameters of the long trill of *B. japonica* from Kuishanli ($\bar{x} \pm$ SE, range in parenthesis)

Temp	N	Call duration (10^{-2} sec)	No. pulse	First phase		Main phase		
				Duration (10^{-2} sec)	Pulse rate	Pulse rate	Frequency (lower pulse)	Frequency (upper pulse)
25°C	8	213.7±20.8 (140–282)	70.6±6.9 (47–94)	35.6±6.6 (18–67)	39.7±2.1 (30.2–48.3)	32.1±0.3 (31.0–33.6)	2.99±0.09 (2.7–3.4)	3.13±0.09 (2.8–3.5)

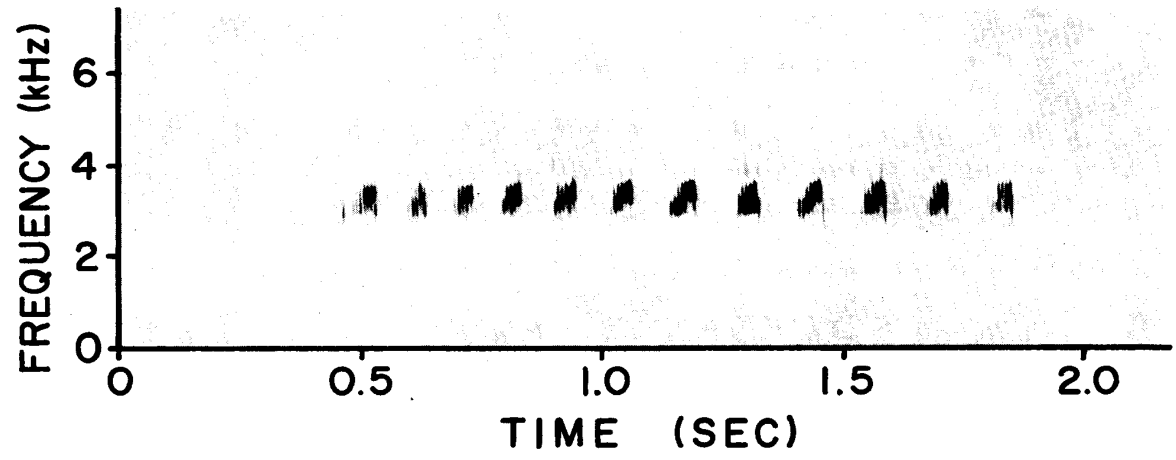

Fig. 10. Long trill of *B. japonica* recorded at Hualien (25°C, 300 Hz filter).

TABLE 7

Acoustic parameters of the long trill of *B. japonica* from Hualien
(x̄±SE, range in parenthesis)

Temp	N	Call duration (10^{-2} sec)	No. note	Note duration (10^{-2} sec)	Pulse repetition rate	Fundamental frequency (kHz)
25°C	6	77.3±19.9 (21–139)	8.3±1.7 (3–12)	8.2±2.1 (5–18)	120.4±2.4 (111–127)	3.09±0.04 (3.0–3.2)

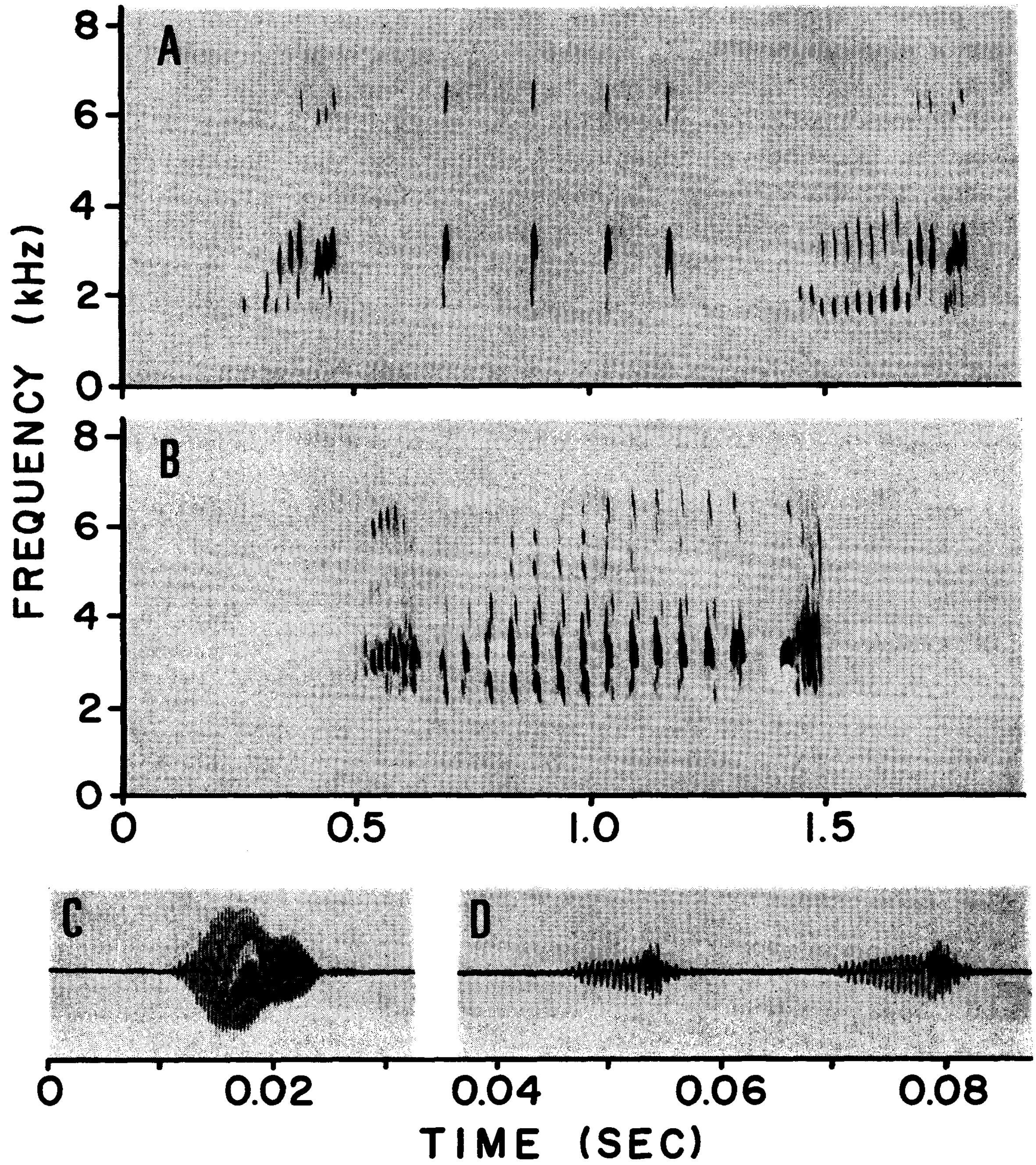

Fig. 11. A and B: Whistles of *B. japonica* recorded at Kuishanli (A, 25°C) and Kuantzuling (B, 20°C). 300 Hz filter. C and D: Waveforms of several pulses from middle phase (C) and early part of the last phase (D) of a whistle recorded at Kuishanli.

trills, viewed from both pulse repetition rate and dominant frequency (Table 7). The author could not record this type of call at Kuishanli and Kuantzuling.

The whistles recorded at Kuishanli were composed of three phases; first, middle and last phase (Fig. 11A). The first and last phase were short and had a fast pulse repetition rate (Table 8). Although the structures of these phases were essentially identical with that of the short trill, the author treated them as two parts of a whistle because the whistle always accompanied them, that is, the middle phase alone was never evoked. The last phase was longer and showed more typical structure of the short trill than the first phase.

The middle phase that characterized the whistle was longer than the other two phases and often lasted over 1 sec. The length of this phase depended on the number of pulses included. The fundamental frequency of the pulse was at about 3 kHz, and the pulse showed frequency modulation. The pulses of the middle phase and those of the first or last phase differed in their waveforms (Fig. 11C and D). The waveforms of the first and last phase resembled those of the short trill.

TABLE 8

Duration and pulse repetition rate of the whistle of *B. japonica*

($\bar{x}\pm$SE, range in parenthesis)

Locality Temp	N	Call duration (10^{-2} sec)	First phase*		Middle phase*		Last phase*	
			Duration (10^{-2} sec)	Pulse rate	Duration (10^{-2} sec)	Pulse rate	Duration (10^{-2} sec)	Pulse rate
Kuishanli 25°C	17	160.4±9.9 (95–243)	18.5±1.5 (6–29)	41.0±1.6 (32–53)	54.9±5.5 (28–113)	5.6±0.3 (4.2–8.8)	43.4±4.5 (15–100)	34.7±1.2** (28–44)
Kuantzuling 20°C	8	110.2±8.4 (78–146)	14.0±1.3 (8–19)	74.0±3.5 (63–84)	72.7±7.4 (41–102)	19.9±0.2 (18.9–20.4)	8.3±1.0 (4.5–14)	93.2±2.6 (89–100)
Hualien 25°C	5	82.8±4.9 (67–94)	7.7±0.6 (6–10)	100.5±0.5 (100–102)	43.9±6.1 (25–62)	25.9±1.4 (20.6–28.0)	3.4±0.2 (3–4)	102.5±3.2 (91–107)

* From the first to last pulse, excluding interval time

** Excluding the last note which had mean pulse repetition rate of 61.8±1.7

The whistles recorded at Kuantzuling (Fig. 11B) and Hualien were similar to each other. Corresponding to the short duration and fast pulse repetition rate of the short trills of the two populations, the first and last phase were shorter and consisted of more rapidly repeating pulses than those of the whistles recorded at Kuishanli. The last phase was very short in Kuantzuling and Hualien. Pulses in the middle phase were also repeated rapidly in these populations. The time intervals between the first and middle phase and between the middle and last phase were 0.24 sec in the calls of Kuishanli, while they were 0.04–0.09 sec in the calls of Kuantzuling and Hualien.

VI. *Chirixalus eiffingeri*

This small arboreal frog with dark brown coloration occurs in Taiwan and Yaeyama group of the Ryukyu Islands. It is unique among rhacophorid frogs in laying eggs in a small quantity of water accumulated in the tree hollows or bamboo stumps in forested regions of mountainous area. Breeding season is from April to July. The author recorded the calls of *C. eiffingeri* at Shitou on 12 June 1982 (18°C) and at Kuishanli on 18 June 1982 (25°C).

Most familiar calls of this species were composed of a short note (Fig. 12A), and at high level of calling activity there were long calls consisting of a series of notes (Fig. 12C). The single-note call recorded at Shitou and Kuishanli did not differ in frequency characteristics, but the note length was significantly longer in Kuishanli than in Shitou (Table 9). By time waveform analyses, most of the

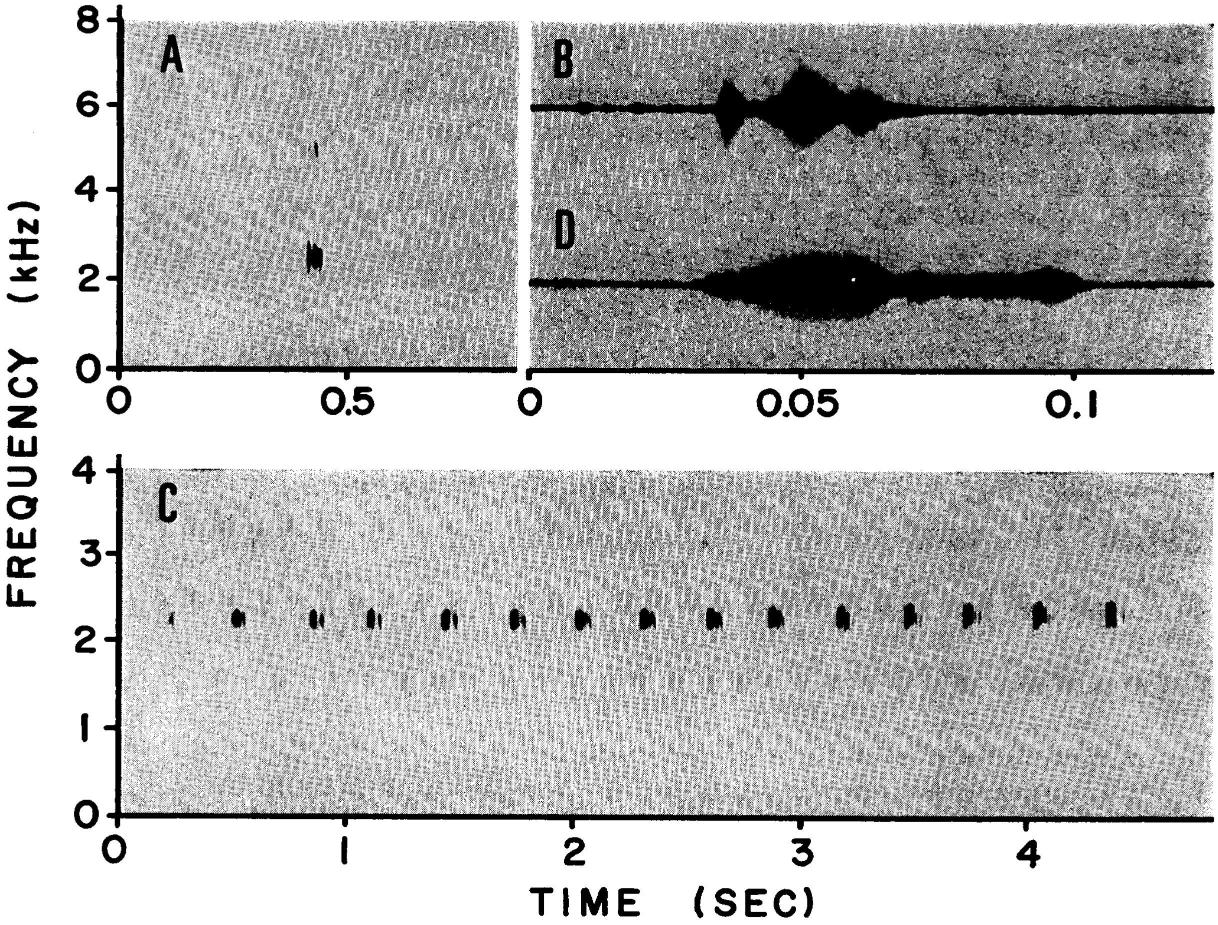

Fig. 12. Single-note call (A), multi-note call (C), and waveform of single-note call (B) and multi-note call (D) of *C. eiffingeri* recorded at Shitou (18°C, 300 Hz filter).

TABLE 9
Acoustic parameters of single-note calls of *C. eiffingeri*
($\bar{x}\pm$SE, range in parenthesis)

Locality Temp	N	Call duration (10^{-2} sec)	Frequency (kHz)	
			Fundamental	2nd harmonic
Shitou 18°C	13	3.6±0.5 (3– 4)	2.6±0.05 (2.4–2.8)	5.2±0.10 (4.9–5.7)
Kuishanli 25°C	13	7.2±0.6 (4–12)	2.6±0.03 (2.4–2.8)	5.3±0.04 (5.1–5.5)

TABLE 10

Acoustic parameters of multi-note calls of *C. eiffingeri* ($\bar{x}\pm$SE, range in parenthesis)

Locality Temp	N	Call duration (10^{-2} sec)	No. note	Note duration (10^{-2} sec)	Note repetition rate	Frequency (kHz)	
						Fundamental	2nd harmonics
Shitou	10	368.1±25.5	14.0±0.7	4.6±0.5	3.4±0.1	2.3±0.03	4.6*
18°C		(208–437)	(9–16)	(3–6)	(3.3–3.6)	(2.2–2.5)	
Kuishanli	12	127.0± 7.1	7.0±0.3	2.3±0.1	4.9±0.2	2.5±0.03	5.0±0.06
25°C		(85–174)	(6– 9)	(2–3)	(4.1–6.0)	(2.3–2.6)	(4.6–5.3)

* N=3

notes were resolved into several pulses (Fig. 12B), the number of pulses being much fewer in Shitou than in Kuishanli.

The multi-note call was much shorter and the note repetition rate was higher in Kuishanli than in Shitou (Table 10). This may be largely due to differences in temperature as the same trend was reported for many frogs (ZWEIFEL, 1968; WAHL, 1969; LÖRCHER and SCHNEIDER, 1973). In the calls recorded at Kuishanli, the note in the multi-note calls had significantly shorter duration than the note in the single-note calls. Since the waveform in the multi-note calls could not be resolved into pulses, the nature of notes differed from that of single-note calls. In contrast, the note of some multi-note calls recorded at Shitou could be resolved into pulses. In Kuishanli, fundamental frequency of the multi-note calls was lower than that of the single-note calls. There were clear 2nd and 3rd harmonic bands. Frequency modulation was obvious in the calls of Kuishanli but not in the calls of Shitou.

DISCUSSION

1. Acoustic comparison of rhacophorid frogs

All of the six rhacophorid frogs of Taiwan have calls consisting of a short pulse or pulses. This feature has also been reported in Japanese rhacophorids (KURAMOTO, 1975). The acoustic differences of the species are in the number of pulses, pulse repetition rate and energy distribution over the frequency range.

R. taipeianus and *R. moltrechti* of Taiwan, *R. owstoni* and *R. viridis* of the Ryukyu Islands, and *R. schlegelii* and *R. arboreus* of Japan proper are very similar to each other in external morphology and breeding ecology. Obviously, they form a species group most distinct among Far Eastern rhacophorid frogs. Acoustic features of the Japanese species were described previously (KURAMOTO, 1975) and a preliminary acoustic analysis of *R. taipeianus* and *R. moltrechti* was made by KURAMOTO and UTSUNOMIYA (1981). The present study made a more detailed acoustic comparison of the Japanese and Taiwanese members of this group possible.

The call structures of *R. moltrechti* and *R. owstoni* (KURAMOTO, 1975), an endemic species of Yaeyama group of the Ryukyu Islands, are nearly identical. Because the calls of the two species are of the most complicated structure among the anurans both in frequency and temporal features, it is highly improbable that the acoustic similarity has resulted from convergence. Apparently *R. owstoni* has been derived rather recently from the ancestral stock of *R. moltrechti*. On the other hand, *R. taipeianus* which has been previously confused with *R. owstoni* or *R. viridis* (OKADA, 1931; CHEN, 1969) constitutes a separate phyletic line so far as the call structures are concerned.

In the genus *Rhacophorus*, call structures of three other species of Southeast Asia are available for comparison, *R. appendiculatus* and *R. bimaculatus* of Thailand (HEYER, 1971) and *R. pardalis* of Philippines (KURAMOTO, unpubl. data). All of the three species have single-pulse calls as well as multi-pulse calls, and the pulses do not show clear harmonic bands. On the other hand, the Taiwanese and Japanese species never give single-pulse call. Furthermore, the calls of these species have clear harmonic bands except for *R. arboreus* of Japan proper (KURAMOTO, 1975). The Taiwanese and Japanese species seem to have highly specialized calls among the species of the genus *Rhacophorus*.

HEYER (1971) reported on the call structure of *P. leucomystax* of Thailand. It consists of 2–5 pulses and dominant frequency range is nearly the same as that of *P. leucomystax* of Taiwan. Pulse repetition rate is much higher in Thailand than in Taiwan probably, in part, due to difference in temperature. Unfortunately, temperature record was not presented. Whether the Thailand population lacks single-pulse call remains to be confirmed. The pulse of *P. leucomystax linki*, a subspecies of Palawan Island, is very long (KURAMOTO, unpubl. data), suggesting geographic variations in call features of this widely spreading species. No call structures are available for the other species of this genus.

The calls of *B. robusta* differed mainly in frequency features from the calls of *B. buergeri*, the Japanese representative occupying the same ecological niche. In contrast to the pulse of *B. robusta* involving a wide frequency range, the pulse of *B. buergeri* has a few narrow harmonic bands with a dominant band at about 1.8 kHz (KURAMOTO, 1975). The call of *B. buergeri* is significantly longer than the call of *B. robusta*. Probably the modification in frequency characteristics has led to the well-tuned call of *B. buergeri* from the poorly-tuned call of *B. robusta*.

The calls of *B. japonica* showed a considerable acoustic, and underlying genetic, divergence of the three populations examined. The long trill of *B. japonica* recorded in Amami Island of the Ryukyu Islands (KURAMOTO, 1975) is similar to the long trill of Kuishanli but not to that of Hualien. The dominant frequency and pulse repetition rate are nearly identical in Amami and Kuishanli populations when the differences in temperature at the time of recordings are taken into account. In the long trills of Amami population, there is a remnant of the first and main phase of Kuishanli population. Apparently minor modification of the long trill of Kuishanli has led to the long trill of Amami population. Further studies on call repertoire of Amami as well as Okinawa and Yaeyama group of the Ryukyu Islands will reveal more clearly the relationships between these populations and the process of acoustic divergence.

Single-note calls of *C. eiffingeri* of Taiwan resemble those of Yaeyama group (KURAMOTO, 1975). Two Thailand species of the genus *Chirixalus*, C. *nongkhorensis* and *C. vittatus*, have calls consisting of a single short note as in *C. eiffingeri*. According to HEYER (1971), *C. vittatus* evoked multi-note calls (up to 4 notes per call) later in the season.

2. Acoustic divergence in the Rhacophoridae

From a bio-acoustic view point, single-pulse call of *P. leucomystax* is the most simple call type. The pulse is a noisy sound containing a wide frequency range. Probably the other more complex call types were derived from this primitive call structure through modifications in temporal and frequency features.

The first step from the primitive to complex calls may be the formation of either (1) a multi-pulse call or (2) a harmonic pulse. The multi-pulse calls of *P. leucomystax* and *B. robusta* represent the direction (1), and the single-note call of *C. eiffingeri* represents the direction (2). Because the long pulse that is comparable to the call of *Rana ishikawae* (KURAMOTO, 1980b) has not been reported in rhacophorid frogs, the direction toward a long pulse has been of minor importance in the acoustic divergence in the family Rhacophoridae.

The advanced calls are composed of many pulses with more or less clear harmonic bands. This call type can be derived either from changes in energy distribution over the frequency range of multi-pulse calls or from the duplication of single-pulse calls with harmonic bands. Further divergence is accompanied with the note formation and differentiation of notes or note groups into different phases. Fig. 13 schematically represents the process of acoustic divergence postulated above.

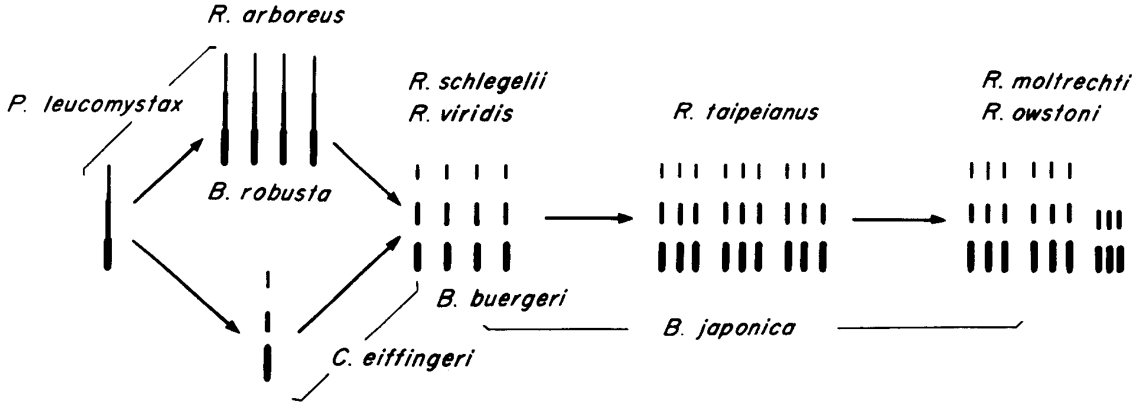

Fig. 13. A possible course of acoustic divergence in the rhacophorid frogs of Taiwan and Japan.

The genera *Rhacophorus* and *Buergeria* involve species that are in various stages of acoustic divergence. Apparently the acoustic divergence took place in parallel within the two different genera. For the genera *Polypedates* and *Chirixalus*, more species should be studied in order to confirm whether or not the same acoustic divergence have occurred. Even if the call structure of these genera is demonstrated to be of simple type, it does not necessarily imply the primitiveness of the genera, because there are ecological constraint affecting the acoustic properties of the calls.

As discussed by KONISHI (1970) and NELSON (1973), the animal call should have acoustic features that maximize the sound transmission in a given habitat and the effectiveness of sound localization. MARTEN and MARLER (1977) and MARTEN, QUINE and MARLER (1977) measured the sound attenuation in various habitats. Attenuation increases with frequency but near the ground level attenuation of lower frequency increases. They found that the pattern of sound attenuation was similar in various habitats and that there was minimum excess attenuation between 0.5 and 2 kHz when the sound source was within 1 m above ground level. Except for *B. japonica* and *C. eiffingeri*, the fundamental (dominant) frequencies of rhacophorid frogs studied here are within this range.

Probably, small species meets physical constraint for producing sounds of lower frequency, and this explains a relatively high dominant frequency of the calls of *B. japonica* and *C. eiffingeri*. Acoustic features of *C. eiffingeri* agree with those of microhylid frogs with similar habitat in having short, high-pitched, and relatively pure single-note call (NELSON, 1973). This type of call may have some advantages over other call types in relation to the habitat.

The calls involving a wide frequency range are restricted to large rhacophorid frogs, *R. arboreus*, *P. leucomystax* and *B. robusta*. This kind of sound may carry much information compared with the sound with a narrow frequency range. In addition, the sound with a wide frequency range may enhance the efficiency of transmission through various kinds of acoustic obstacles that attenuate or confuse specific frequency ranges. Allocation of the sound energy over a wide frequency range may be possible in large species, while in small species the energy should be concentrated to a narrow frequency range for effective sound transmission.

From the acoustic data available to date, the primitive call structures are confined to the arboreal species inhabiting forested regions. On the other hand, the calls of species breeding in more or less open habitats are of more advanced, complex structures. If some factors associated with open habitats have enhanced the complexity of sound signal, the process of acoustic divergence reflects the evolutionary changes in habitats rather than the taxonomic relationships.

For sound localization in small animals, the binaural time differences of the sound rather than the intensity differences or phase differences are efficient, and calls consisting of many short pulses are most favorable for this purpose (NELSON, 1973). Rhacophorid frogs have this type of calls, suggesting that the sound localization of this group of frogs depends on the binaural time differences of the sound.

Most of the calls reported herein are certainly so-called mating call, while the different call types of *B. japonica* may have different ecological roles that will be clarified later. Mating call and territorial call, for example, have different call structures as shown by many authors (SCHNEIDER, 1967; CAPRANICA, 1968; WAHL, 1969; BRZOSKA, WALKOWIAK and SCHNEIDER, 1977; WELLS, 1978). Also, two phases of *R. moltrechti* may play two different roles. NARINS and CAPRANICA (1978, 1980) found in *Eleutherodactylus coqui* that the two notes (phases according to the present definition) which differed in acoustic features elicited different responses to males and females. The first note ("Co") elicited another male to evoke "Co" note, but the male did not respond to "Qui" note. The females, on the other hand, responded to "Qui" note. Playback experiments may reveal the possible role of the two phases of *R. moltrechti* and different call types of *B. japonica.*

SUMMARY

1. The calls of six rhacophorid frogs from Taiwan, *Rhacophorus taipeianus*, *R. moltrechti*, *Polypedates leucomystax*, *Buergeria robusta*, *B. japonica* and *Chirixalus eiffingeri*, were recorded and their structure was sonagraphically analyzed.

2. *R. taipeianus* had long calls consisting of many well-tuned pulses that repeated rapidly. The pulses constituted 1–4 notes. Multi-note calls were associated with high vocal activity.

3. The calls of *R. moltrechti* were composed of two phases that differed in pulse repetition rate, fundamental frequency and waveform of the pulses. The calls involved many harmonic bands. The call structure closely resembled that of *R. owstoni* of the Ryukyu Islands, suggesting a direct phylogenetic relationships between the two species.

4. The calls of *P. leucomystax* consisted of 1–5 or more short pulses. Neither clear fundamental nor harmonic frequencies were recognized. Multi-pulse calls were associated with high vocal activity.

5. The calls of *B. robusta* consisted of 7–12 short pulses with very weak harmonic structure. When two or more males were in close proximity, they emitted rapid calls in which the pulses were repeated rapidly and dominant frequency bands were high compared with the normal calls.

6. *B. japonica* had three call types, short trill, long trill and whistle, and each call type differed in structure among three populations examined. All kinds of calls consisted of several to many well-tuned pulses.

7. *C. eiffingeri* had single-note and multi-note calls. Frequency range was very narrow. Waveform and dominant frequency differed between single- and multi-note calls in one population but not in the other populations.

8. Acoustic data of rhacophorid frogs available to date were compared. All the calls consisted of one or more short pulses with or without harmonic frequencies. The call structures of the conspecific populations in the Ryukyu Islands were similar to, or slightly differed from, those of the Taiwanese populations.

9. A possible course of acoustic divergence in rhacophorid frogs of Taiwan and Japan was postulated. The genera *Rhacophorus* and *Buergeria* involve the species at different stages of acoustic divergence. Acoustic divergence seemed to be associated with habitats and body size of the species rather than the taxonomic relationships.

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ADDENDUM

Later studies on breeding and life history of Taiwan populations of *C. eiffingeri* revealed that the Kuishanli and several other populations differed from those of

Shitou and the Ryukyu Islands, and that they should be recognized as a distinct species. Furthermore, LIEM's generic allocation of *C. eiffingeri* is obviously erroneous. These results will be given elsewhere.