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Acoustic Characteristics of Treefrogs from Sichuan, China, with Comments on Systematic Relationship of *Polypedates* and *Rhacophorus* (Anura, Rhacophoridae)

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ABSTRACT—Advertisement call characteristics of *Polypedates chenfui*, *P. dugritei*, and *P. omeimontis*, all from Sichuan, China, are described. Calls of the three species differ considerably from each other both in temporal and frequency patterns. Acoustically, these three species cannot be differentiated from some *Rhacophorus* species from Japan and Taiwan, and the systematic relationship of *Polypedates* and *Rhacophorus* needs reassessment.

INTRODUCTION

Rhacophorus Kuhl et van Hasselt, 1822 and *Polypedates* Tschudi, 1838 represent two major genera among the treefrog subfamily Rhacophorinae [4]. There are, however, conflicting opinions about the taxonomic relationship of these two genera. *Polypedates* has long been synonymized with *Rhacophorus* [13,18], but Liem [12], in revising the family Rhacophoridae, split the two genera on the basis of adult morphology. Later, Dubois [3] placed *Polypedates* as a synonym of *Rhacophorus* after reinterpreting Liem's data on adults [12] and utilizing Inger's data on tadpoles [6]. On the other hand, Jiang et al. [7] considered that *Polypedates* and *Rhacophorus* are separate lineages in China. Similarly, Channing [1] reanalyzed Liem's data [12] and showed that the two genera were not sister groups. Thus there is at present disagreement about the taxonomic relationship of *Polypedates* and *Rhacophorus*.

On the other hand, non-morphological characteristics including acoustic ones have been studied on some members of these two genera, and their bearing on systematics has been discussed [5, 9, 10, 11, 15]. The data hitherto accumulated, however, are still insufficient to utilize for outlining phylogenetic relationship of *Polypedates* and *Rhacophorus*. Regarding acoustic data of east Asian species, the knowledge of members from Japan and Taiwan is considerable, but nothing is known about Chinese members. Although China is famous for its rich amphibian fauna [21], very few studies have been made on the call characteristics of frog species [16, 17], and members of *Polypedates* and *Rhacophorus* are not exceptions. In order to better understand systematic relationship of these two genera, acoustic data on Chinese members are badly needed. In this communication, we will report acoustic characteristics of three rhacophorine species from China, i. e., *Polypedates omeimontis* Stejneger, 1924, *P. chenfui* (Liu, 1945), and *P. dugritei* David, 1871, and discuss phylogenetic relationship of the two genera.

MATERIALS AND METHODS

Recordings of calls were made in the field by the junior author using a cassette tape recorder (Sony WM-D3) with an external microphone (Sony ECM-909A). Ambient temperature was measured at the time of recording.

Calls of *P. chenfui* were recorded on Mt. Emei-shan at the altitude of 1400 m, Sichuan, China, on 13 May 1993. Air temperature at the time of recording was 13.0°C. Males were observed to call simultaneously with *P. omeimontis*. For the latter species, calls were recorded on Mt. Emei-shan at the altitude of 1400 m, on 13 and 15 May 1993. Air temperatures at the time of recording were 13.0°C and 11.0°C, respectively. Calls of *P. dugritei* were recorded on Mt. Wa-shan, Sichuan, China, at the altitude of 1600 m on 1 June 1993, and at the altitude of 2600 m on 2 June 1993. Air temperature at the time of each recording was 8.0°C and 4.0°C, respectively. For comparisons, data of the following species of Japanese and Taiwanese *Rhacophorus* are used: *R. arboreus* (Honshu, Japan); *R. schlegelii* (Honshu, Japan); *R. v. viridis* (Okinawajima and Kume-jima, eastern Ryukyus); *R. owstoni* (Ishigakijima and Iriomotejima, western Ryukyus); *R. prasinatus* (northern Taiwan).

The recorded calls were analyzed using computer programs, SoundEdit Vers. 2 or SoundEdit Pro (MacroMind-Paracomp, Inc.) by a Macintosh computer. Advertisement calls as defined by Wells [19] were compared among the three species. In the following description, note means a pulse group, note duration the time from the beginning of the first pulse to the end of the last pulse in a note, and pulse repetition rate number of pulses per second. In order to examine relationships among call parameters, analysis-of-covariance (ANCOVA) was performed. Kruskal-Wallis tests with nonparametric multiple comparisons (=Dunn test [20]) or Mann-Whitney U tests were performed to detect the presence or absence of differences in the frequency distributions. The significance level was set at 0.05.

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TABLE 1. Call characteristics of three Chinese rhacophorid species (Mean±1SD, followed by sample size)

Species	Note duration (sec)	Pulse rate (N of pulse/sec)	Initial frequency (Hz)	Climax frequency (Hz)
Polypedates dugritei	4.0°C			
10 pulsed note	0.700	14.29	1500	1600
	1	1	1	1
11 pulsed note	0.895	12.30	1275	1525
	2	2	2	2
12 pulsed note	0.970±0.046	12.39±0.60	1391.7±159.4	1675.0± 41.8
	6	6	6	6
13 pulsed note	0.965±0.025	13.48±0.34	1445.0±170.3	1657.5± 39.2
	10	10	10	10
14 pulsed note	1.015	13.80	1350	1625
	2	2	2	2
Polypedates dugritei	8.0°C			
2 pulsed note	0.075	26.67	1450	2500
	1	1	1	1
3 pulsed note	0.190	15.79	1150	1450
	1	1	1	1
6 pulsed note	0.310	19.54	1412.5	1875
	2	2	2	2
7 pulsed note	0.445	15.83	1075	1750
	2	2	2	2
8 pulsed note	0.517	15.50	1191.7	1766.7
	3	3	3	3
9 pulsed note	0.510±0.029	17.69±0.97	1192.8±196.7	1764.3± 69.0
	7	7	7	7
10 pulsed note	0.637±0.023	15.72±0.58	1133.3± 57.7	1900.0±132.3
	3	3	3	3
11 pulsed note	0.700	15.71	1050	1900
	1	1	1	1
Polypedates omeimontis	11.0°C			
3 pulsed note	0.318±0.011	9.45±0.32	865.8± 30.1	936.7± 21.6
	6	6	6	6
4 pulsed note	0.460±0.022	8.71±0.41	865.5± 21.2	977.1± 49.8
	42	42	42	42
Polypedates omeimontis	13.0°C			
2 pulsed note	0.166±0.015	12.12±1.16	817.5± 53.8	827.5± 38.6
	4	4	4	4
3 pulsed note	0.325±0.018	9.25±0.52	804.6± 35.5	884.6± 68.1
	13	13	13	13
4 pulsed note	0.439±0.007	9.11±0.14	845.4± 32.3	913.1± 48.9
	13	13	13	13
5 pulsed note	0.584	8.56	770	850
	1	1	1	1
Polypedates chenfui	13.0°C			
2 pulsed note	0.158	12.64	2000	2100
	1	1	1	1
4 pulsed note	0.385±0.027	10.44±0.70	2120.0±102.1	2348.8± 53.6
	8	8	8	8
5 pulsed note	0.514±0.018	9.74±0.33	2082.1±133.5	2334.4±132.7
	34	34	34	34
6 pulsed note	0.645±0.042	9.35±0.61	2033.3±111.8	2318.9±125.8
	9	9	9	9

RESULTS

Polypedates chenfui

The call recorded at 13.0°C was a well pulsed note (Fig. 1B) and included two to six pulses. The note duration increased with increasing number of pulses, and the mean duration varied from 0.158 sec in the note with two pulses to 0.645 sec in the note with six pulses (Table 1). The duration differed significantly among the notes with different number of pulse (Dunn's multiple comparison test, $P<0.05$). The relationship of the number of pulse (X) and the note duration (Y) was expressed as $Y=0.126X-0.116$ ($N=52$, $r=0.965$, $P<0.01$). The pulse repetition rate tended to decrease with the increment of the pulse number, means varying from 12.64 in the note with two pulses to 9.35 in the note with six pulses. The rate was significantly greater in the note with four pulses than in the notes with five or six pulses (Dunn's multiple comparison test, $P<0.05$), but the latter two did not differ from each other. The relationship between the number of pulse (X) and the pulse repetition rate (Y) was $Y=-0.682X+13.221$ ($N=52$, $r=-0.718$, $P<0.01$). Each pulse had harmonics, and a slight frequency modulation was seen within a note (Fig. 1A). The mean dominant frequency in the initial pulse was about 2000–2120 Hz, but it slightly increased to 2100–2349 Hz in the climax pulse. In the climax pulse, the second dominant frequency was about 6000–6500 Hz, and six harmonic bands in total were apparent between 0–7500 Hz. Average harmonic interval, therefore, was about 1250 Hz, and this value corresponded to the fundamental frequency. The first dominant frequency, therefore, was the second harmonic and the second corresponded to the fifth harmonic of the spectrogram. The dominant frequency of either the initial or the climax pulses did not differ significantly among the notes with different number of pulse (Kruskal-Wallis test, $P>0.05$). Thus, there were insignificant correlations between the number of pulse (X) and dominant frequencies (Y) of either the initial ($r=-0.111$, $P>0.05$) or the climax pulse ($r=0.097$, $P>0.05$).

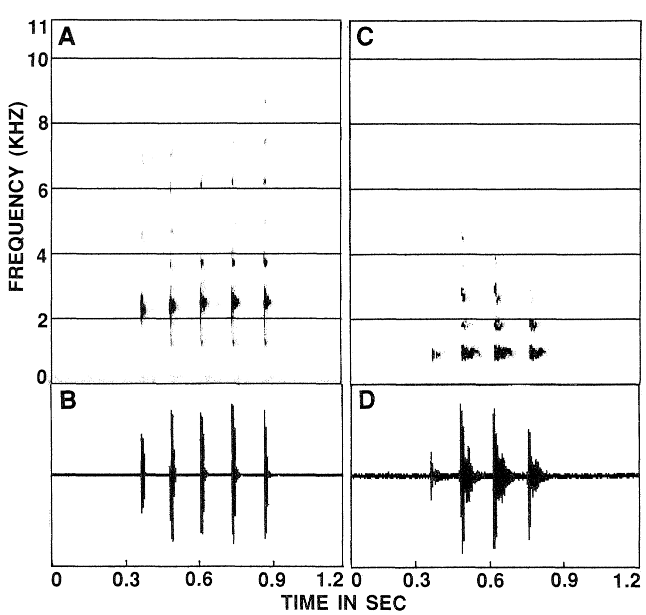

Fig. 1. Sonagrams (A, C) and sound wave forms (B, D) of advertisement calls of *Polypedates chenfui* (A, B, recorded at 13.0°C) and *P. omeimontis* (C, D, recorded at 11.0°C).

Polypedates omeimontis

Calls of *P. omeimontis* included several call types, but only the advertisement call [8, 19] is considered here. The advertisement call was a well pulsed note (Fig. 1C, D) and at 11.0°C, it included three or four pulses. The mean note duration of 0.318 sec in the note with three pulses was significantly shorter than 0.460 sec in the four pulsed note (Mann-Whitney *U* test, $P<0.05$). The mean pulse repetition rate in the three pulsed note (9.45) was significantly larger than that in the four-pulsed note (8.71; Mann-Whitney *U* test, $P<0.05$). Each pulse had harmonics, but they are usually not clear in the initial pulse. A weak frequency modulation was seen within a note. Parameters of frequencies did not differ between notes with three and four pulses (Mann-Whitney *U* test, $P>0.05$). The dominant frequency in the initial pulse was about 866 Hz, but it increased to 936–977 Hz in the climax pulse. In the climax pulse, the second dominant frequency was about 2300 or 2900 Hz. Seven harmonic bands in total could be traced between 0–7350 Hz. Average harmonic interval was about 1050 Hz and corresponded to the fundamental frequency. The first dominant frequency was judged to be the fundamental and the second corresponded to the second or third harmonic of the spectrogram. The dominant frequency in either the initial or the climax pulse did not differ between the notes with three and four pulses (Mann-Whitney *U* test, $P>0.05$).

The calls recorded at 13.0°C had basically similar traits, but the number of pulses included in a note tended to be smaller than in 11.0°C (median=three pulses in 13.0°C, compared with four in 11.0°C). The mean note durations varied from 0.166 sec in the note with two pulses to 0.584 sec in the note with five pulses (Table 1), but they were statistically not different (Kruskal-Wallis test, $P>0.05$). Similarly, the note durations did not differ significantly between the notes with the same number of pulses, and recorded at 13°C and 11.0°C (Mann-Whitney *U* test, $P>0.05$). The pulse repetition rates varied from 12.12 in the note with two pulses to 8.56 in the note with five pulses, but their difference was insignificant (Kruskal-Wallis test, $P>0.05$). In the four-pulsed notes, repetition rate in 13.0°C (9.11) was larger than that in 11.0°C (8.71; Mann-Whitney *U* test, $P<0.05$). The dominant frequency slightly increased from 777–845 Hz in the initial pulse to 828–913 Hz in the climax pulse. Dominant frequencies in the initial and climax pulses were significantly lower in some calls recorded at 13.0°C than in 11.0°C (initial pulse in the three-pulsed note, and climax pulse in the four-pulsed note: Mann-Whitney *U* test, $P<0.05$).

Comparisons with calls of syntopic *P. chenfui* simultaneously recorded at 13.0°C, using the four-pulsed note resulted in the followings. The note duration of *P.*

omeimontis was significantly longer than that of *P. chenfui* (Mann-Whitney *U* test, $P<0.05$), and in the pulse repetition rate *P. omeimontis* was slightly smaller than in *P. chenfui* (Mann-Whitney *U* test, $P<0.05$). Much greater interspecific differences were found in frequency characteristics. The dominant frequency in the climax pulse was significantly lower in calls of *P. omeimontis* than in *P. chenfui* (Mann-Whitney *U* test, $P<0.01$), so was the dominant frequency in the initial pulse (Mann-Whitney *U* test, $P<0.01$).

The relationship of the number of pulse (X) and the note duration (Y) was expressed as $Y=0.166X-0.201$ ($N=48$, $r=0.762$, $P<0.01$) and $Y=0.131X-0.079$ ($N=31$, $r=0.986$, $P<0.01$) in the calls recorded at 11°C and 13°C, respectively. The slope of the former equation was significantly steeper than the latter (ANCOVA, $P<0.05$). The latter slope was not significantly different from syntopic *R. chenfui*. The number of pulse (X) and the pulse repetition rate (Y) had the relationships of $Y=-5.951X+32.773$ ($N=48$, $r=-0.660$, $P<0.01$) and $Y=-1.043X+13.038$ ($N=31$, $r=-0.694$, $P<0.01$) in the calls recorded at 11°C and 13°C, respectively. The slope of the former regression line was significantly steeper than that of the latter (ANCOVA, $P<0.05$), which in turn was insignificantly different from the slope in syntopic *R. chenfui* (ANCOVA, $P>0.05$). In the calls recorded at 11.0°C, there were significant correlations between the number of pulse (X) and dominant frequencies (Y) of both the initial ($Y=-86.167X+1226.72$, $N=48$, $r=-0.495$, $P<0.01$) and the climax pulse ($Y=-53.048X+1197.25$, $N=48$, $r=-0.353$, $P<0.01$), but correlations were insignificant in the calls recorded at 13.0°C ($P>0.05$).

Polypedates dugritei

The call was again a well pulsed note (Fig. 2B, D) and at 4.0°C, it included ten to 14 pulses. The note duration tended to increase with increasing number of pulses, and the mean duration varied from 0.700 sec in the note with ten pulses to 1.015 sec in the note with 14 pulses. However, the duration did not differ significantly (Kruskal-Wallis test, $P>0.05$) among the notes with different number of pulses, probably because of small sample size. The mean pulse repetition rate varied from 12.30 to 14.29 but showed no correlation with the number of pulses ($r=0.378$, $P>0.05$). Each pulse had clear harmonics, and a frequency modulation was seen within a note. The dominant frequency in the initial pulse was about 1275–1500 Hz, but it increased to 1525–1675 Hz in the climax pulse, and slightly decreased to about 1500 Hz in the final pulse. In the climax pulse, the second dominant frequency was about 4500–4800 Hz. A total of seven harmonic bands could be traced between 0–11000 Hz, and average harmonic interval was about 1570 Hz. Thus, the first dominant frequency was the fundamental and the second corresponded to the third harmonic.

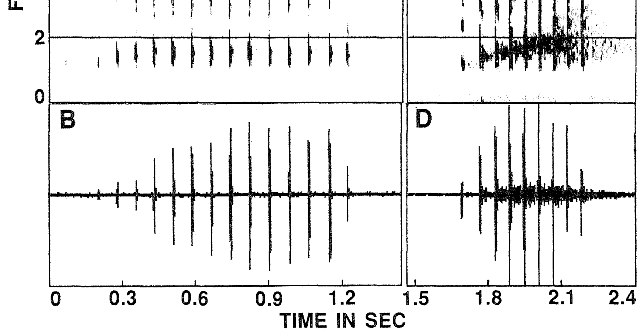

FIG. 2. Sonagrams (A, C) and sound wave forms (B, D) of advertisement calls of *Polypedates dugritei* (A, B, recorded at 4.0°C; C, D recorded at 8.0°C).

The calls recorded at 8.0°C (Fig. 2C, D) had basically similar traits, but a note tended to have smaller number of pulses (median=nine in 8.0°C and 13 in 4.0°C). Note durations seemed to be shorter than in 4.0°C, but the limited number of corresponding samples prohibited statistical comparisons. The mean note durations varied from 0.075 sec in the note with two pulses to 0.700 sec in the note with 11 pulses (Table 1), but they did not differ significantly in duration (Dunn's multiple comparison test, $P>0.05$), again probably due to small sample size. The pulse repetition rates varied from 15.50 to 26.67, but the mean was insignificantly different from that in 4.0°C (Dunn's multiple comparison test, $P>0.05$). The dominant frequency slightly increased from 1050–1450 Hz in the initial pulse to 1450–2500 Hz in the climax pulse. In the climax pulse, three harmonic bands were apparent at about 1850, 5600, and 9300 Hz. The harmonic interval was thus judged to be about 1850 Hz, and this corresponded to the fundamental and the first dominant frequency. The second and the third dominant frequencies corresponded to the third and fifth harmonic, respectively. The dominant frequency in either the initial or the climax pulse did not differ among the notes with different number of pulses regardless of the temperature difference (Dunn's multiple comparison test, $P>0.05$).

The relationship of the number of pulse (X) and the note duration (Y) was expressed as $Y=0.052X+0.303$ ($N=21$, $r=0.726$, $P<0.01$) and $Y=0.065X-0.042$ ($N=20$, $r=0.963$, $P<0.01$) in the calls recorded at 4.0°C and 8.0°C, respectively. Similarly, the relationship between the number of pulse (X) and the pulse repetition rate (Y) was expressed as $Y=-0.669X+22.637$ ($N=20$, $r=-0.557$, $P<0.01$) in the calls recorded at 8.0°C, but, as noted above, the relationship was statistically insignificant in the calls recorded at 4.0°C. In the calls recorded at either 4.0°C or 8.0°C, there were insignificant correlations between the number of pulse (X) and dominant frequencies (Y) of either the initial ($r=0.076$, $P>0.05$ and $r=-0.336$, $P>0.05$) or the climax pulse ($r=0.326$, $P>0.05$ and $r=-0.220$, $P>0.05$).

Interspecific comparisons

Although some parameters, such as the dominant frequency, did not vary with variant temperatures, others, such as the pulse repetition rate, varied in relation to temperatures. Interspecific comparisons of acoustic parameters, therefore, should be made by adjusting parameters at a standard temperature. Because calls of *P. chenfui* and *P. omeimontis* were recorded at 13°C, values of parameters at this temperature were calculated from the regression lines for *P. dugritei*. Figure 3 shows the relationships of the pulse rate and dominant frequency of the climax pulse among the above three Chinese species and some Japanese and Taiwanese species (Table 2). As clearly seen, the three Chinese species differ from each other completely. *Polypedates dugritei* had a high repetition rate and moderately high frequency. *Polypedates omeimontis*, on the other hand, had low repetition rates and low frequencies, which are in contrast to *P. chenfui* that was characterized by low repetition rates and high frequencies. *Polypedates chenfui* was placed near *R. schlegelii* and *R. viridis*, while *P. omeimontis* lay near *R. owstoni* and *R. arboreus*. *Rhacophorus prasinatus* was closest to *P. dugritei* on this graph.

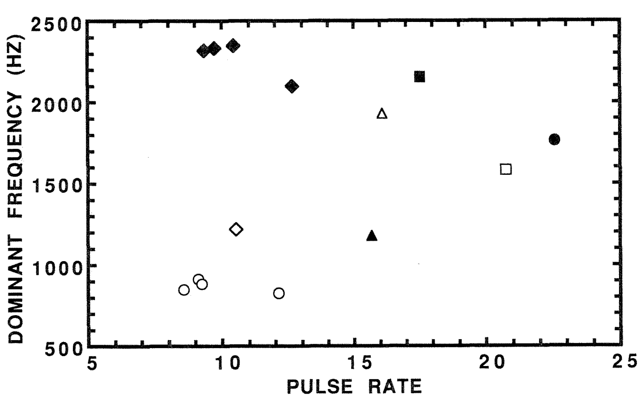

FIG. 3. Relationships of pulse repetition rate and dominant frequency of the climax pulse in the calls of *Polypedates chenfui* (closed diamond), *P. dugritei* (closed circle), *P. omeimontis* (open circle), *Rhacophorus schlegelii* (open triangle), *R. arboreus* (closed triangle), *R. viridis* (closed rectangle), *R. owstoni* (open diamond), and *R. prasinatus* (open rectangle). Values are adjusted to the ambient temperature of 13.0°C in all the species, except for *P. chenfui* and *P. omeimontis*, both of which represent the raw data.

TABLE 2. Parameters for regression lines Y=aX+B, where X =air temperature (in °C) and Y=pulse repetition rate, in *Polypedates dugritei* and some Japanese and Taiwanese species of *Rhacophorus* (data from Matsui, unpublished)

	a	B	r
P. dugritei	1.049	8.930	0.735
R. schlegelii	1.584	−4.554	0.944
R. viridis	1.570	−2.859	0.927
R. arboreus	1.460	−3.302	0.850
R. owstoni	0.452	4.645	0.804
R. prasinatus	1.583	0.156	0.994

DISCUSSION

From a cladistic analysis of adult morphology, Jiang et al. [7] classified 14 Chinese rhacophorid species into five genera, which classification is essentially the same as that proposed by Liem [12]. In their classification, all the three species treated in the present paper were classified as *Polypedates*, together with *P. dennysi*, *P. hungfuensis, P. nigropunctatus, P. leucomystax* (type species of the genus), and *P. mutus*. On the other hand, *R. rhodopus* and *R. reinwardtii* (type species of the genus) were placed in *Rhacophorus*. According to Jiang et al. [7], these two genera commonly possess Y-shaped terminal phalange, unopposable hand, and lack anterior process of hyale, but are distinguished from each other by heart-shaped intercalary cartilage, no skin fold, slightly or half webbed hand, and low vegetation habitat of *Polypedates*, in contrast to a wing-shaped intercalary cartilage, a broad skin fold, full hand webbing, and inhabiting on tall trees of *Rhacophorus*.

These differences, however, are not necessarily reliable, because all the Japanese and Taiwanese species currently assigned to *Rhacophorus* lack broad skin fold and full hand webbing [14]. Also, the habitat of an anuran species is very difficult to specify, and the above Chinese species are not sharply differentiated in this character. As to the shape of the intercalary cartilage, available information is too meager to assess whether or not it could be appropriately used for splitting the two genera.

Calls of the three species here reported completely differed from the call of *Polypedates leucomystax* [15] or from those of several *Rhacophorus* species from Southeast Asia [2]. Rather, the calls of the three species fairly resembled calls of some Japanese and Taiwanese species of *Rhacophorus* (see Fig. 3). Of the three Chinese species treated here, *P. omeimontis* and *P. chenfui* are syntopic on Mt. Emei-shan. The two species differ greatly in morphology and ecology; *P. omeimontis* is larger and lays an egg nest on the tree or grass [13], while *P. chenfui* is small and breeds on land. As shown above, these species differ greatly in acoustic characteristics, *P. omeimontis* with much lower frequency and slightly longer note duration. Interestingly, similar morphological, ecological, and acoustic relationships are found in the Japanese rhacophorids, *R. arboreus* and *R. schlegelii* from the Japan mainland [14]. The oviposition site of the larger species, *R. arboreus* is on the tree or on the grass, whereas the syntopic, smaller *R. schlegelii* lays an egg mass under the ground and never on the tree [14]. As shown in Fig. 3, calls of *R. arboreus* and *P. omeimontis* have similar temporal and frequency characteristics, so do calls of *R. schlegelii* and *P. chenfui*. Although another species, *R. owstoni* also lay close to *P. omeimontis* in Fig. 3, their calls are actually quite dissimilar. *Rhacophorus owstoni* occurs in the western Ryukyus, and has characteristically long calls that are composed of slow and fast units [9]. The two unit calls have variant pulse rates, and only the initial, slow unit resembles the call of *P. omeimontis*.

The relationships of the above allopatric species pairs, i. e., *P. chenfui* vs. *R. schlegelii* and *P. omeimontis* vs. *R. arboreus*, may be regarded as reflecting results of ecological convergence, but actual close phylogenetic relationships of these pairs are also plausible. This is inferred from the fact that there are some species pairs of *Rhacophorus* that are allopatric in distribution, similar in call characteristics, and deemed closely related phylogenetically. *Rhacophorus moltrechti* from Taiwan and *R. owstoni* from the western Ryukyus, or *R. schlegelii* from Japan mainland and *R. viridis* from the eastern Ryukyus are examples of such pairs [11].

Anyhow, the available evidence indicates that at least three Chinese species of *Polypedates* reported here cannot be differentiated acoustically from some *Rhacophorus* species from Japan and Taiwan. Acoustic studies of species from wider regions will surely contribute to better understanding the relationship of *Polypedates* and *Rhacophorus*.

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