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Vocalizations of mossy frogs (Anura: Rhacophoridae: *Theloderma*)

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The species-rich rhacophorid genus *Theloderma* Tschudi, commonly referred to as mossy or warty frogs, comprises large, predominantly arboreal species that are often highly cryptic in appearance (Poyarkov *et al.* 2015). To date, thirty species have been formally recognized, widely distributed across Southeast Asia, with numerous molecularly identified lineages still awaiting formal description (Luo *et al.* 2023; Frost 2024). Although the phylogenetic relationships and biogeography of the genus are generally well resolved, taxonomic revisions have lagged behind, primarily due to a lack of integrative data (Nguyen *et al.* 2015; Poyarkov *et al.* 2015; Chan *et al.* 2018; Luo *et al.* 2023).

An integrative approach that incorporates molecular, morphological, larval development and bioacoustics data provides the most robust framework for amphibian taxonomy (Padial *et al.* 2010). Among these, advertisement calls have proven especially valuable as species-specific traits for identifying cryptic diversity in anuran amphibians (e.g. Köhler *et al.* 2017). The bioacoustic data within *Theloderma* have only been documented for seven species: *Theloderma albopunctatum* Liu and Hu, *T. auratum* Poyarkov, Kropachev, Gogoleva and Orlov, *T. corticale* Boulenger, *T. lateriticum* Bain, Nguyen and Doan, *T. licin* McLeod and Ahmad, *T. stellatum* Taylor and *T. vietnamense* Poyarkov, Orlov, Moiseeva, Pawangkhanant, Ruangsuwan, Vassilieva, Galoyan, Nguyen and Gogoleva (Poyarkov *et al.* 2015, 2018; Chen *et al.* 2019; Ginal *et al.* 2021). To expand the bioacoustic dataset for the genus, the aim of this study is to provide comparative descriptions of the advertisement calls of two additional species, *T. asperum* Boulenger and *T. leporosum* Tschudi, along with additional data for *T. corticale*. Furthermore, this study aims to summarize the current understanding of bioacoustic characteristics across the genus.

A total of six adult specimens (one *Theloderma leporosum*, one *Theloderma corticale* and four *Theloderma asperum*) were obtained through the pet trade (La Ferme Tropicale, Paris) and kept in heavily planted terrariums at the National Museum of Natural History's life animal collection (Supplementary Fig.). Specimen identification was based on adult morphology (e.g. Chan-Ard *et al.* 1999, Poyarkov *et al.* 2015, Ginal *et al.* 2021). Recordings were conducted at night with live specimens kept in a terrarium under the same environmental conditions for all species. Calls were recorded at 23–25°C from a distance of 15cm. The calls of *Theloderma leporosum* (three recordings) and *T. corticale* (one recording) were recorded using a DPA 6060 series omnidirectional microphone connected to a Tentacle Track E digital audio recorder with the following settings: sampling rate = 48 kHz and 32-bit dynamic range, frequency response in 20–20,000 Hz range. Calls of *T. asperum* (one recording) were recorded using a DPA 4006C series omnidirectional microphone connected to a Nagra Seven digital audio recorder with the following settings: sampling rate = 48 kHz and 24-bit dynamic range, frequency response in 20–20,000 Hz range. Recordings were resampled to 24-bit for analyses using GoldWave (https://goldwave.com/). All original recordings are available at the sonothéque of MNHN (https://sonotheque.mnhn.fr/) under accession numbers MNHN-SO-2024-3543 and MNHN-SO-2024-3545 (*T. leporosum*), MNHN-SO-2024-3546 (*T. asperum*) and MNHN-SO-2024-3547 (*T. corticale*) and in the FONOZOO repository under 14932–14934 (*T. leporosum*), 14935 (*T. asperum*) and 14936 (*T. corticale*). All recordings were analyzed using SASLab Pro version 5.3.2 (Avisoft) with the following specifications: Spectrum (FFT of calls; Hamming window size =32,769 points; filter bandwidth =1.46 Hz, T =1/F =683 ms), Hilbert transformation for envelope and instantaneous frequency. We visualized oscillograms and

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spectrograms using Seewave version 2.2.3 in R (Sueur *et al.* 2008), with individual parameters of FFT provided in figure captions. Call parameters and terminology follows Boistel (2003) and Boistel *et al.* (2011) and includes the following temporal parameters: number of tonal calls (i.e. notes); note duration, providing the duration of notes in ms; inter-note duration, providing the time between notes within a series in s; repetition rate, providing the 'temporal density' of notes in notes per min; tempo, providing the overall ratio between note duration and inter-note duration in %; as well as the following spectral parameters: dominant frequency, describing the frequency that carries the maximal energy in the spectrum in Hz; spectral centroid, representing the weighted (by magnitude) mean of the spectrum in Hz; energy below 1,500 Hz, providing the fraction of the total energy that is allocated in the lower frequency range in %; quality factor, estimating the frequency selectivity by providing the ratio between dominant frequency and bandwidth at -3 dB (no unit); number of harmonics, providing the count of multiple frequency components above the fundamental frequency. Descriptive statistics for call parameters were presented as mean ± standard deviation with range in brackets. For single measurements, the exact value is provided instead.

Theloderma asperum (Fig. 1). The description is based on 24 advertisement calls. Calls consisted of tonal notes with a duration of 68.5 ± 6.3 ms (58.6–78.4 ms). Calls were emitted at a rate of 10.8 calls per minute and a tempo of 1.3 %, with inter-call intervals of 5.7 ± 2.7 s (3.8–17.7 s). Spectral analysis using a Fast Fourier Transform (FFT) showed that each call contained three harmonics with a dominant fundamental frequency at 2,128 ± 23 Hz (2,080–2,168 Hz) without frequency modulation (FM). The quality factor (QF) of the carrier frequency was 61.5 ± 18.9 (30.3–3.7), indicating that it functions as a frequency-selective resonator. 93.0 ± 0.01 % (89.95–95.4 %) of the acoustic energy was concentrated below 1,500 Hz. The spectral center of gravity, representing the energy-weighted mean frequency, was located at 2,357 ± 43 Hz (2,280–2,432 Hz; Table 1).

Theloderma corticale (Fig. 1). The call was previously described in detail by Ginal *et al.* (2021). However, since the author did not report all bioacoustic metrics, we supplemented Table 1 with additional values based on our own recordings. Our recording included 73 tonal notes. As some of the parameters differed slightly from the original description, we also provide additional information on call variation (Table 1). Tonal notes in our recording were emitted at a rate of 21.4 calls per minute (vs. 28 ± 0 in Ginal *et al.* 2021). The dominant fundamental frequency was followed by 4.0 ± 0.3 (3–5) harmonics (vs. 7 in Ginal *et al.* 2021; Table 1). All other metrics from our recording overlap broadly in their range with the description of Ginal *et al.* (2021), extending variation in some parameters (Table 1).

Theloderma leporosum (Fig. 1). The description is based on 64 advertisement calls. Each call consisted of tonal notes with a duration of 243.7 ± 17.3 ms (212.4–292.1 ms) emitted in long sequences. The calls were emitted at a rate of 11.4 ± 2.6 calls per minute (9.8–14.4), with a tempo of 4.7 ± 1.2 % (3.9–6.0 %), and inter-call intervals of 5.5 ± 6.3 s (3.1–5.1 s). Spectral analysis using a Fast Fourier Transform (FFT) showed that each call contained 6.3 ± 2.2 (2–12) harmonics, with a dominant fundamental frequency at 1,045 ± 27 Hz (990–1,087 Hz), without FM. The QF of the carrier frequency was 118.4, indicating that it functions as a frequency-selective resonator. 89.4 ± 2.8 % (85–96 %) of the acoustic energy was concentrated below 1,500 Hz. The spectral center of gravity, which represents the energy-weighted mean frequency, was located at 1,518 ± 178 Hz (1,084–1,813 Hz; Table 1).

Table 1 summarizes bioacoustic metrics for all *Theloderma* species with described calls and provides information on vocal sac morphology based on Poyarkov *et al.* (2015, 2018); Bain *et al.* (2009); McLeod & Norhayati (2007); Mian *et al.* (2017); Anh & Trường (2018) and phylogenetic clade based on Luo *et al.* (2023).

The average note duration of *Theloderma leporosum* is slightly shorter than that of *T. corticale*, but 3.6 times longer than that of *T. asperum* (Table 1). The amplitude envelopes of the three species can be distinguished as follows: those of *T. leporosum* are Gaussian shaped, *T. asperum* exhibits an amplitude peak at the beginning of calls and *T. corticale* shows an intermediate pattern, with the peak occurring in the first half of the calls (Fig. 1C). While note duration is considerably shorter in *T. asperum* when compared to the other two species, inter-note duration is shortest in *T. corticale* and equally longer in both *T. asperum* and *T. leporosum*, resulting in approximately twice the repetition rate in *T. corticale* (Table 1). Tempo clearly distinguishes all three species (Table 1). *Theloderma corticale* produce the lowest-pitched calls among the three species and indeed, the lowest within the genus, while *T. asperum* has the highest pitched calls. In all three species, the dominant fundamental frequency accounts for over 89% of the total energy present in the spectrum.

Theloderma leporosum does not exhibit frequency modulation, whereas *T. corticale* shows a slight increase of 137 Hz and *T. asperum* displays pronounced frequency modulation (Fig. 1D). The QF measured at -3 dB from the dominant frequency indicates that *T. leporosum* has a high degree of frequency selectivity, reflected in its high QF. In *T. asperum*, QF is intermediate, while in *T. corticale*, it is lower, likely due to variation in the instantaneous frequencies of the dominant frequency. Quality factor (QF) measurements are not available for most species with previously described calls.

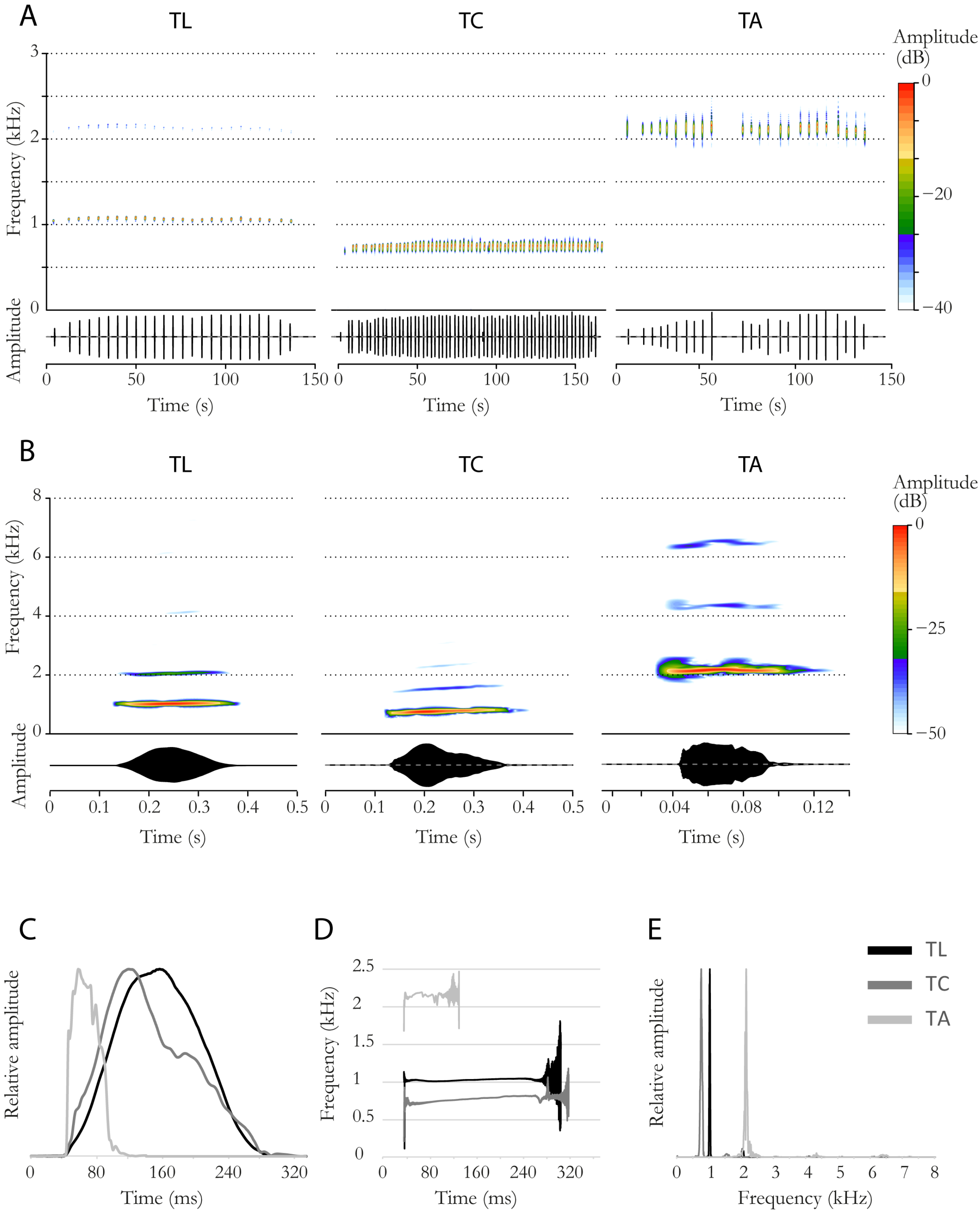

FIGURE 1. Oscillogram and spectrogram of the (A) advertisement call series and (B) tonal notes of *Theloderma leporosum* (TL), *T. corticale* (TC) and *T. asperum* (TA). (C) envelope, (D) instantaneous frequency and (E) spectrum of the three species. For (A) and (B), FFT at 65,536 points, 0.73 Hz, 1.36 ms, zero padding at 8 and overlap at 95%, for (E), FFT at 16,385 points, 2.9 Hz, 341.3 ms.

TABLE 1. Overview of bioacoustic metrics for the genus *Theloderma*, an update and refinement of Ginal *et al.* (2021), who only included six species. Values for *T. corticale* and *T. licin* are weighted mean and pooled variance from Ginal *et al.* (2021), where notes were separated in two types, which, however, show no differentiation except their posterior interval. Phylogenetic clades follow Luo *et al.* (2023). Information on vocal slits and SVL summarized from Poyarkov *et al.* (2015, 2018); Bain *et al.* (2009); McLeod & Norhayati (2007); Mian *et al.* (2017); Anh & Trường (2018) and this study for *T. asperum*, *T. corticale* and *T. leporosum*. SVL = snout-vent length, F1 to F4 indicates the first four harmonics. Where available, data is shown as mean ± standard deviation and range in brackets.

	T. albopunctatum	*T. asperum*	*T. auratum*	*T. corticale*	*T. corticale*	*T. lateriticum*	*T. leporosum*	*T. licin*	*T. stellatum*	*T. vietnamense*
Clade	B1	B1	C2	C1	C1	C3	C4	B1	A	A
SVL male (mm)	30.5–32	25	24.9 (21.8–26.1)	not specified	66.8	23.5 holotype	69.9	27.8 (27.7–28.0)	30.69 (36.9–22.7)	31.2 (28.0–35.1)
Vocal slits	present	present	absent	absent	absent	absent	absent	present	present	present
N calls (tonal notes) analyzed	26	24	15	40	73	unknown	64	40	32	16
Note duration (ms)	300 ± 30 (220–360)	68.5 ± 6.3 (58.6–78.4)	61 ± 0.5 (30–75)	250 ± 34.9 (190–380)	260.8 ± 27.7 (174.5–332.0)	~220	243.7 ± 17.3 (212.4–292.1)	255 ± 40.7 (200–390)	85 ± 2 (65–108)	161 ± 3 (125–175)
Inter-note duration (s)	10.21 ± 5.17 (6.38–26.82)	5.7 ± 2.7 (3.8–17.7)	0.529 ± 0.007 (0.411–0.842)	1.95 ± 0.24 (0.18–3.36)	2.6 ± 0.6 (0.7–4.0) 71	0.2–0.7	5.5 ± 6.3 (3.1–5.1)	3.64 ± 0.53 (1.06–6.58)	0.88 ± 0.08 (0.38–2.39)	2.0 ± 0.02 (1.91–2.2)
Repetition rate (notes/min)	7.4 ± 2.1 (4–10)	10.8	100.8 ± 1.8 (91.8–118.8)	28 ± 0	21.4	NA	11.4±2.6 (9.8–14.4)	16 ± 0.42 (14–18)	57.0	28.2
Tempo (%)	NA	1.3	NA	NA	10.24	NA	4.7 ± 1.2 (3.9–6.0)	NA	NA	NA
Dominant frequency (Hz)	1,676 ± 0,031 (1,635–1,764)	2,128 ± 23 (2,080–2,168)	2,856 ± 4 (2,710–3,090)	819± 17.2 (794–881)	767 ± 14 (772–803)	2,500–3,500	1,045 ± 27 (990–1,087)	1,626 ± 16.4 (1,611–1,672)	1,530 ± 30 (1,370–1,720)	1,300 ± 10 (1,270–1,330)
Spectral centroid (Hz)	NA	2,357 ± 43 (2,280–2,432)	NA	NA	857 ±15 (775–877)	NA	1,518 ± 178 (1,084–1,813)	NA	NA	NA

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TABLE 1. (Continued)

	T. albopunctatum	*T. asperum*	*T. auratum*	*T. corticale*	*T. corticale*	*T. lateriticum*	*T. leporosum*	*T. licin*	*T. stellatum*	*T. vietnamense*
Energy below 1,500 Hz (%)	NA	93.0 ± 0.01 (89.95–95.4)	NA	NA	95.0 ± 0.01 (94.2–97.6)	NA	89.4 ± 2.8 (85–96)	NA	NA	NA
Quality factor	NA	61.5 ± 18.9 (30.3–93.7)	NA	NA	20.9 ± 12.2 (11.8–77.6)	NA	118.4 ± 39.6 (42.9–211.5)	NA	NA	NA
N harmonics	4–5	3.0 ± 0.0 (3–3)	NA	7	4.0±0.3 (3–5)	3	6.3 ± 2.2 (2–12)	3–6	2.1 ± 0.1 (2–3)	2.6 ± 0.1 (2–3)
F1 (Hz)	3,388 ± 114 (3224–3615)	4,256 ± 35 (4,143–4,365)	NA	1,639 ± 53 (1,366–1,737)	1,567 ± 25 (1,443–1,620)	5,800–6,800	2,091 ± 55 (1,976–2,172)	3,246 ± 59 (3,134–3,327)	2910 ± 10 (2,840–2,970)	2,550 ± 10 (2,540–2,560)
F2 (Hz)	5,203 ± 198 (4934–5655)	6,382 ± 92 (6,229–6,533)	NA	2,419 ± 45 (2,329–2,574)	2,325 ± 61 (1,893–2,433)	8,000–9,000	3,143 ± 86 (2,965–3,262)	4,864 ± 116 (4,521–5,111)	NA	NA
F3 (Hz)	6,770 ± 130 (6,434–7,112)	NA	NA	3,262 ± 80 (3,102–3,531)	3,105 ± 86 (2,965–3,262)	NA	4,184 ± 119 (3,948–4,349)	6,562 ± 136 (6,348–6,799)	NA	NA
F4 (Hz)	8,047 ± 99 (7,949–8,201)	NA	NA	4,144 ± 162(3,836–4,679)	NA	NA	5,281 ± 163 (4,985–5,435)	8,359 ± 61 (8,201–8,514)	NA	NA
Reference	Ginal *et al.* (2021)	this study	Poyarkov *et al.* (2018)	Ginal *et al.* (2021)	this study	Chen *et al.* (2019)	this study	Ginal *et al.* (2021)	Poyarkov *et al.* (2015)	Poyarkov *et al.* (2015)

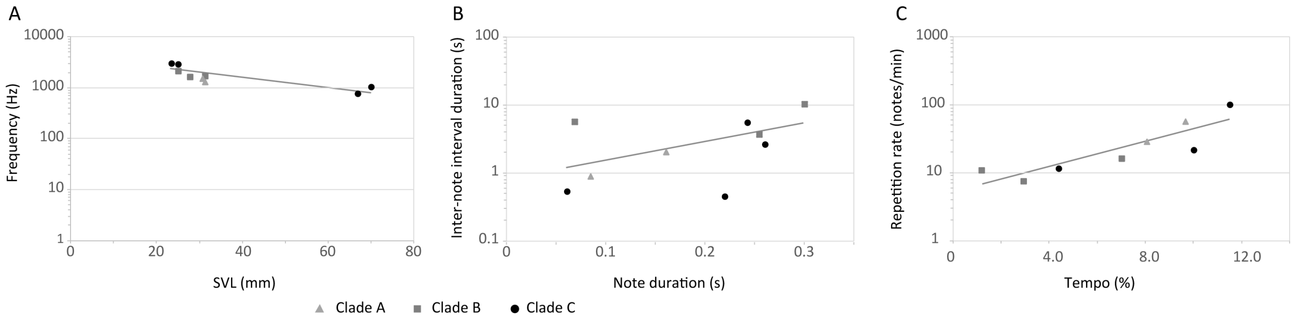

FIGURE 2. Interspecific variation in acoustic parameters of *Theloderma* calls: Variation in (A) dominant fundamental frequency as a function of size; (B) duration of inter-note intervals as a function of note duration; (C) repetition rate as a function of tempo; *T. lateriticum* was not included due to lack of data. Clades *sensu* Luo *et al.* (2023) are indicated by the shape and color of the markings.

We suggest five parameters as highly discriminatory across the genus, three of which are temporal (tempo, note duration, inter-note duration) and two frequential (dominant fundamental frequency and number of harmonics) parameters (Table 1, Fig. 2). For comparative purposes, we estimated tempo as the ratio between note duration and inter-note duration (Fig. 2B). Because harmonic values are integer multiples of the dominant fundamental frequency, we only included the latter and the number of harmonics in our analysis. Notably, vocal slits are absent in clade C (*sensu* Luo *et al.* 2023) in contrast to their presence in the other two clades (at least for species with described calls; Table 1), highlighting a potentially significant anatomical difference. This difference may reflect distinct patterns of call activity across the *Theloderma* phylogeny, although further comparative anatomical studies are needed to provide a more detailed anatomical description of the vocal apparatus within the genus. Generally, the presence or absence of a vocal sac may influence both temporal and frequency characteristics of the calls (Boistel 2001, 2003, 2011; Pauly *et al.* 2006; Starnberger *et al.* 2014). In contrast, we did not observe a clear phylogenetic signal in the acoustic metrics analyzed (Fig. 2) and clades broadly overlap in bioacoustic metrics or combinations of those (Table 1), although this may be confounded by the substantial gap in bioacoustics sampling within the genus. Instead, other factors such as body size may influence bioacoustic parameters (e.g. dominant fundamental frequency, Gerhardt 1994; Tonini *et al.* 2020; Fig. 2A). As descriptions are based on single specimens from which calls were recorded or single recordings, intraspecific variation remains to be studied (Poyarkov *et al.* 2015, 2018; Chen *et al.* 2019; Ginal *et al.* 2021; this study). Currently, fewer than one–third of *Theloderma* species have described calls, limiting our understanding of interspecific acoustic variation and constraining integrative taxonomic approaches. We conclude that when combined, note and inter-note duration, tempo, dominant fundamental frequency and QF are highly species-specific characters in the genus. Given that the ecological and phylogenetic contexts remain unknown, future work may integrate bioacoustic information with anatomic and behavioral data to shed light on the functional and evolutionary background of the observed patterns.

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SUPPLEMENTARY MATERIALS. The following supporting information can be downloaded at the DOI landing page of this paper.

SUPPLEMENTARY FIGURE. Adult male specimens from which calls were recorded. (A, C) *Theloderma leporosum,* (B) *T. corticale* and (D) *T. asperum*. (A–C) Photos By Boistel Renaud, (D) Photos by Christophe Flick.

SUPPLEMENTARY TABLE. Mean values of bioacoustic metrics used for Fig. 2. Asterisk indicates estimated values (see text). SVL = snout-vent length, DF = dominant fundamental frequency, ND = note duration, IND = inter-note duration, RR = repetition rate. Data is based on Table 1 and references therein.

species	Clade	SVL (mm)	DF (Hz)	ND (s)	IND (s)	Tempo* %	RR (notes/min)
T. leporosum	C4	69,9	1045	0,24	5,5	4,4	11,4
T. corticale	C1	66,8	767	0,26	2,6	10,0	21,4
T. albopunctatum	B1	31,3	1676	0,30	10,2	2,9	7,4
T. vietnamense	A	31,2	1300	0,16	2	8,1	28,2
T. stellatum	A	30,7	1530	0,09	0,9	9,7	57
T. licin	B1	27,8	1626	0,26	3,6	7,0	16
T. asperum	B1	25,0	2128	0,07	5,7	1,2	10,8
T. auratum	C2	24,9	2856	0,06	0,5	11,5	100,8
T. lateriticum	C3	23,5	3000	0,22	0,5	48,9	unknown