

Advertisement call variation in the *Leptodactylus mystaceus* species complex (Amphibia: Leptodactylidae) with a description of a new sibling species

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Abstract. Whereas morphological analysis of populations recognized as *Leptodactylus mystaceus* indicates there is one species with modest geographic variation, analysis of advertisement calls indicates there are at least two or perhaps three species involved. The differences found in advertisement calls are sufficient to act as species isolating barriers to recognize at least two species, which action is taken. A consequent result is the description of a new sibling species. The significance of sibling species in the genus *Leptodactylus* is discussed briefly.

Introduction

Heyer (1978: 41) stated that the distribution of *Leptodactylus mystaceus* (as *L. amazonicus*) was characterized as occurring "Throughout the greater Amazon Basin, Guianas, northern Atlantic Forest, and cerrados bordering the Amazon Basin". At that time, recordings of advertisement calls were available only from a single site. Since then, recordings of *L. mystaceus* have been made at several other localities. Analysis of these recordings, together with those of two other members of the *L. mystaceus* complex, form the basis of the characterization of the acoustic variation within the group.

Materials and methods

Museum abbreviations follow Leviton et al. (1985) with the exception that MHNSM is the Museo de Historia Natural, Universidad San Marcos, Peru.

The recordings analyzed and associated data of morphologically identified *L. mystaceus* are (arranged roughly from East to West and North to South):

Brazil: Pará; near Altamira. ASN-AJC (Archivo Sonoro Neotropical, Adão J. Cardoso recording) Tape 64 (cut 1, 3), December 1986, 21:35 h, 25°C air temperature, voucher specimen ZUEC 7196, recorded by Adão J. Cardoso. ASN-AJC Tape 67 (cut 7), 7 December 1986, 25.5°C air temperature, voucher specimen ZUEC 7249, recorded by Adão J. Cardoso.

Brazil: Pará; Parque Nacional da Amazônia (Rio Tapajós). USNM (tape archive at National Museum of Natural History, Smithsonian Institution) Tape 53 (cut 6), 21 January 1981, 18:00-23:00 h, 24.6°C air temperature, voucher specimen USNM 288748, recorded by Ronald I. Crombie.

Brazil: Amazonas; Biological Dynamics of Forest Fragments sites, N of Manaus. USNM Tape 149 (cuts 1 and 2), 12 January 1984, 20:23 h, unvouchered, recorded by Barbara L. Zimmerman. USNM Tape 161 (cut 1), 9 April 1987, 19:30 h, unvouchered, recorded by Barbara L. Zimmerman.

Venezuela: Amazonas; Neblina base camp. USNM Tape 70 (cut 2), 24 February 1985, 19:00 h, 25.2°C air temperature, voucher specimen USNM 332867, recorded by Reginald B. Cocroft. USNM Tape 70 (cut 3), 24 February 1985, 20:15 h, 24.4°C air temperature, voucher specimen USNM 332868, recorded by Reginald B. Cocroft.

Ecuador: Napo; Limoncocha. USNM Tape 16 (cut 3), 20 June 1971, 22.9°C air temperature, unvouchered, recorded by W. Ronald Heyer. USNM Tape 16 (cut 4), 20 June 1971, 23.2°C air temperature, unvouchered, recorded by W. Ronald Heyer. USNM Tape 18 (cut 2), 15 July 1971, about 20:00 h, 22.9°C air temperature, unvouchered, recorded by W. Ronald Heyer. USNM Tape 18 (cut 3), 15 July 1971, 20:30-21:00 h, 22.9°C air temperature, voucher specimen LACM 92111, recorded by W. Ronald Heyer.

Brazil: Mato Grosso; Chapada dos Guimarães. ASN-AJC Tape 32 (cut 1), 12 November 1982, 23:00 h, 22°C air temperature, voucher specimen ZUEC 5093, recorded by Adão J. Cardoso.

Brazil: Amazonas; Rio Juruá, Barro Vermelho. USNM Tape 254 (cut 1), 23 October 1991, 18:30 h, 27°C, voucher specimen INPA 3272; recorded by Claude Gascon.

Brazil: Acre; Rio Juruá, Porongaba. USNM Tape 256 (cut 5), 19 February 1993, 18:30 h, 26°C, unvouchered, recorded by Claude Gascon.

Brazil: Acre; Rio Acre, Xapuri. ASN-AJC Tape 54 (cut 4), 24 December 1983, 20:10 h, voucher specimen ZUEC 5745, recorded by Adão J. Cardoso. ASN-AJC Tape 113 (cut 8), 16 November 1991, 17:00 h, 24°C air temperature, unvouchered, recorded by Adão J. Cardoso.

Peru: Madre de Dios; Tambopata. USNM Tape 204 (cut 3), 1 January 1989, 17:45 h, unvouchered, recorded by Reginald B. Cocroft. USNM tape 204 (cut 4), 1 January 1989, 18:10 h, 25.5°C air temperature, voucher specimen USNM 332861, recorded by Reginald B. Cocroft. USNM Tape 204 (cut 5), 1 January 1989, 18:30 h, 25.4°C air temperature, voucher specimen USNM 332862, recorded by Reginald B. Cocroft. USNM Tape 205

(cut 10), 4 January 1989, 19:10 h, 24.2°C air temperature, 24.8°C substrate, voucher specimen USNM 332863, recorded by Reginald B. Cocroft. USNM Tape 205 (cuts 11 and 12), 4 January 1989, 19:35 h, 23.8°C air temperature, 25.0°C substrate, voucher specimen USNM 332864, recorded by Reginald B. Cocroft.

For convenience, the above recordings are referred to by abbreviated specific localities throughout the rest of the text.

Leptodactylus elenae Paraguay: Itapua; El Tirol. USNM Tape 180 (cut 7), 16 November 1976, voucher specimen USNM 253384, recorded by Mercedes S. Foster.

Leptodactylus notoaktites Brazil: Paraná; 12 km W of São João da Graciosa on PR 410 to Curitiba. USNM Tape 10 (cut 11), 26 December 1978, 20:45 h, 16.9°C, voucher specimen USNM 217791, recorded by W. Ronald Heyer. Brazil: Paraná; Morretes. ASN-AJC Tape 23 (cut 3), 3 February 1982, 18:00 h, 24°C air temperature, voucher specimen ZUEC 4717, recorded by Adão J. Cardoso.

Advertisement calls were analyzed using a Kay Digital Sona-Graph model 7800, Uniscan II equipment, or "Canary" software (Charif et al., 1993) on a Macintosh IICI computer.

Measurements were analyzed using SAS software (1988) for an IBM personal computer.

Advertisement calls

Altamira ($n = 20$ calls analyzed). Calls of single notes; call rate 1.6-2.2 per s; call duration 0.14-0.20 s; dominant frequency modulated from 720 to 2120 Hz, with or without a brief terminal drop in frequency; call intensity low initially, rising to a peak about 2/3 duration of call; call distinctly pulsed, of about 9-12 pulses, pulses very distinct at beginning of call, call usually pulsatile terminally; harmonic structure present (fig. 1).

Tapajós ($n = 5$, entire recording has a microhylid frog calling simultaneously with the *Leptodactylus*, precluding some analyses). Calls of single notes; call rate 1.4 per s; call duration 0.14-0.16 s; dominant frequency modulated from 680 to 1320 Hz, no drop in terminal frequency; call of lower intensity initially and terminally; call very distinctly pulsed throughout, of 9 pulses; harmonic structure present (fig. 2).

Manaus ($n = 30$). Calls of single notes, call rate 1.8-2.2 per s; call duration 0.16-0.23 s; dominant frequency modulated from 600 to 1440 Hz, with or without a brief terminal drop in frequency; call intensity low initially, rising to maximum intensity from 1/2 to 2/3 duration of call; call distinctly pulsed, of about 10-13 pulses, pulses either distinct throughout call or distinct through most of call and pulsatile at end of call; harmonic structure present (fig. 3).

Neblina ($n = 20$). Calls of single notes; call rate 1.6 per s; call duration 0.16-0.23 s; dominant frequency modulated from 600 to 1440 Hz, with or without a brief terminal drop in frequency; call intensity low initially, rising to maximum intensity from 1/2 to 2/3 duration of call; call distinctly pulsed, of about 12-16 pulses, pulses

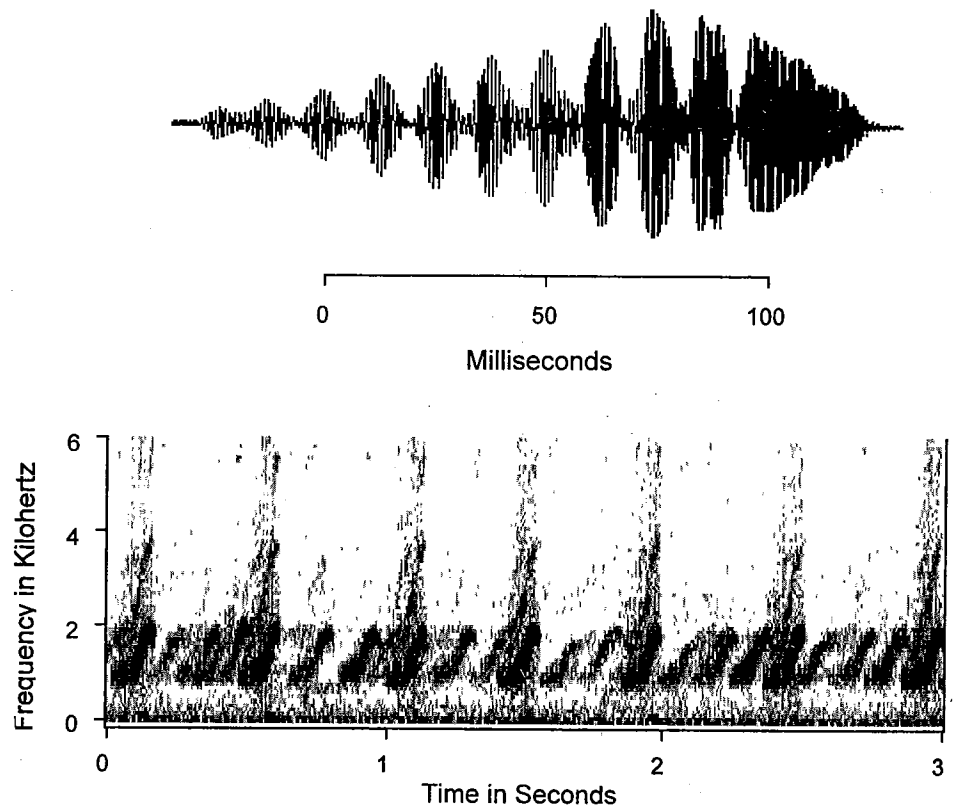


Figure 1. Audiospectrogram (below) and wave form (above) of advertisement call of *Leptodactylus mystaceus* cluster member from Altamira, Pará, Brazil, ASN-AJC Tape 67, cut 7.

very distinct at beginning of call, terminal 1/4-3/5 of call pulsatile; harmonic structure present (fig. 4).

Limoncocha ($n = 40$). Calls of single notes; call rate 1.0-2.0 per s; call duration 0.15-0.25 s; dominant frequency modulated from 560 to 1760 Hz, with or without a brief terminal drop in frequency; call intensity low initially, reaching maximum about 1/2 to 2/3 duration of call; call distinctly pulsed, of about 11-17 pulses, either distinctly pulsed, throughout or (usually) terminal 1/5 to 1/7 of call pulsatile; harmonic structure present (fig. 5).

Chapada dos Guimarães ($n = 29$). Calls of single notes; call rate 1.0-1.6 per s; call duration 0.18-0.27 s; dominant frequency modulated from 620 to 1480 Hz, with or without a brief terminal drop in frequency; call intensity low initially, rising to maximum about 1/2 to 2/3 call duration; call distinctly pulsed, of 10-13 pulses, pulses either more or less distinct throughout call or terminal 1/3 to 1/4 of call pulsatile; harmonic structure present (fig. 6).

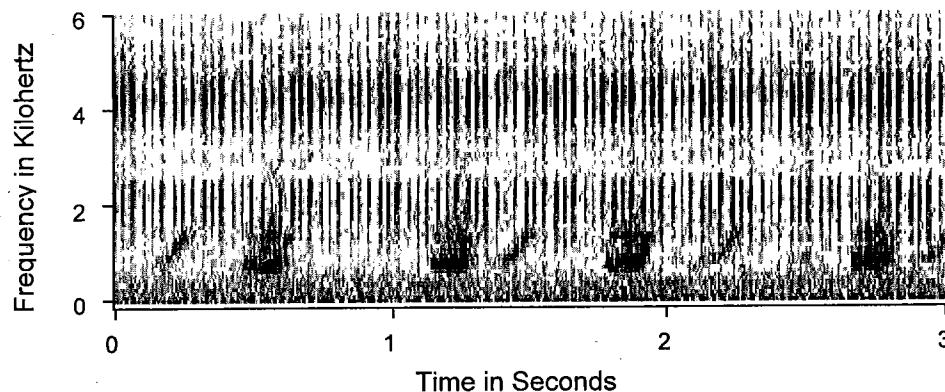


Figure 2. Audiospectrogram of advertisement call of *Leptodactylus mystaceus* cluster member from Parque Nacional da Amazônia (Rio Tapajós), Pará, Brazil, USNM Tape 53, cut 6.

Barro Vermelho ($n = 10$). Calls of single notes; call rate 1.4 per s; call duration 0.26-0.32 s; dominant frequency modulated from 520 to 1470 Hz, call without terminal drop in frequency; call intensity low initially, rising to maximum from 3/4 to just before end of call; call not distinctly pulsed, of either single pulse or two partial pulses; harmonic structure present (fig. 7).

Porongaba ($n = 9$). Calls of single notes; call rate 1.6 per s; call duration 0.19-0.22 s; dominant frequency modulated from 550 to 1470 Hz, call without terminal drop in frequency; call intensity low initially, rising to maximum about mid-call; call not distinctly pulsed, of either single pulse or two partial pulses; harmonic structure present (fig. 8).

Xapuri ($n = 126$). Calls of single notes; call rate 1.7-3.1 per s; call duration 0.09-0.13 s; dominant frequency modulated from 510 to 1510 Hz, calls with brief terminal drop in frequency; call intensity low initially, rising to maximum from about mid-call to 3/4 call duration; call not distinctly pulsed, of either single pulse or two partial pulses; harmonic structure present (fig. 9).

Tambopata ($n = 60$). Calls of single notes; call rate 1.4-2.3 per s; call duration 0.09-0.13 s; dominant frequency modulated from 560 to 1480 Hz, with or without a brief terminal drop in frequency; call intensity low initially, rising to maximum about 2/3 call duration; call not distinctly pulsed, of either single pulse or two partial pulses; harmonic structure present (fig. 10).

Leptodactylus elenae ($n = 10$). Calls of single notes; call rate 1.2 per s; call duration 0.21-0.24 s; dominant frequency modulated from 800 to 1520 Hz, call without terminal drop in frequency; call intensity low initially, rising to maximum about 3/4 to 4/5 duration of call; call of single pulse; harmonic structure present (fig. 11).

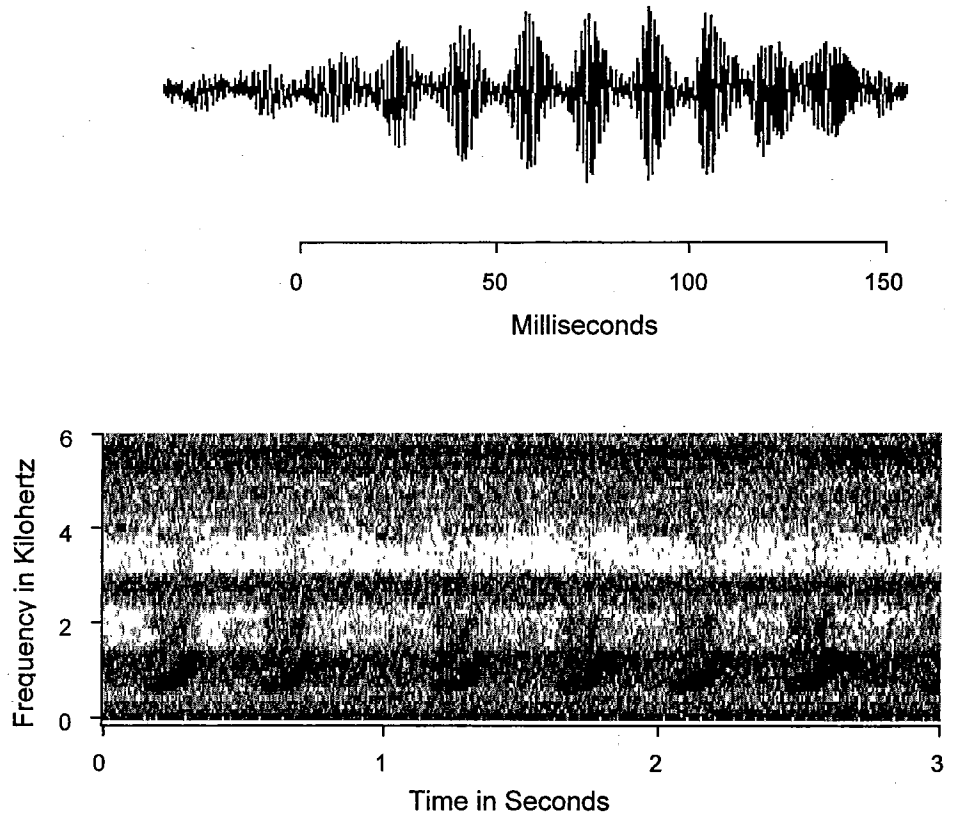


Figure 3. Audiospectrogram (below) and wave form (above) of advertisement call of *Leptodactylus mystaceus* cluster member from Biological Dynamics of Forest Fragments sites, N of Manaus, Amazonas, Brazil, USNM Tape 149, cut 1.

Leptodactylus notoaktites ($n = 15$). Calls of single notes; call rate 1.5-2.0 per s; call duration 0.06-0.09 s; dominant frequency modulated from 470 to 1990 Hz, call without terminal drop in frequency; call intensity low initially, rising to maximum intensity about 2/5 call duration; call of single pulse; harmonic structure present (fig. 12).

Advertisement call comparisons

All calls have (1) the same general range of call rates, (2) harmonic structure, (3) the same kind of frequency and intensity modulation, and (4) the same broadcast frequency range with some differences among ranges. There are consistent differences in pulsation.

Among the pulsed calls, intrapopulation variation exists in whether there is a brief terminal drop in frequency. The exception, the calls from Tapajós which all lack a terminal

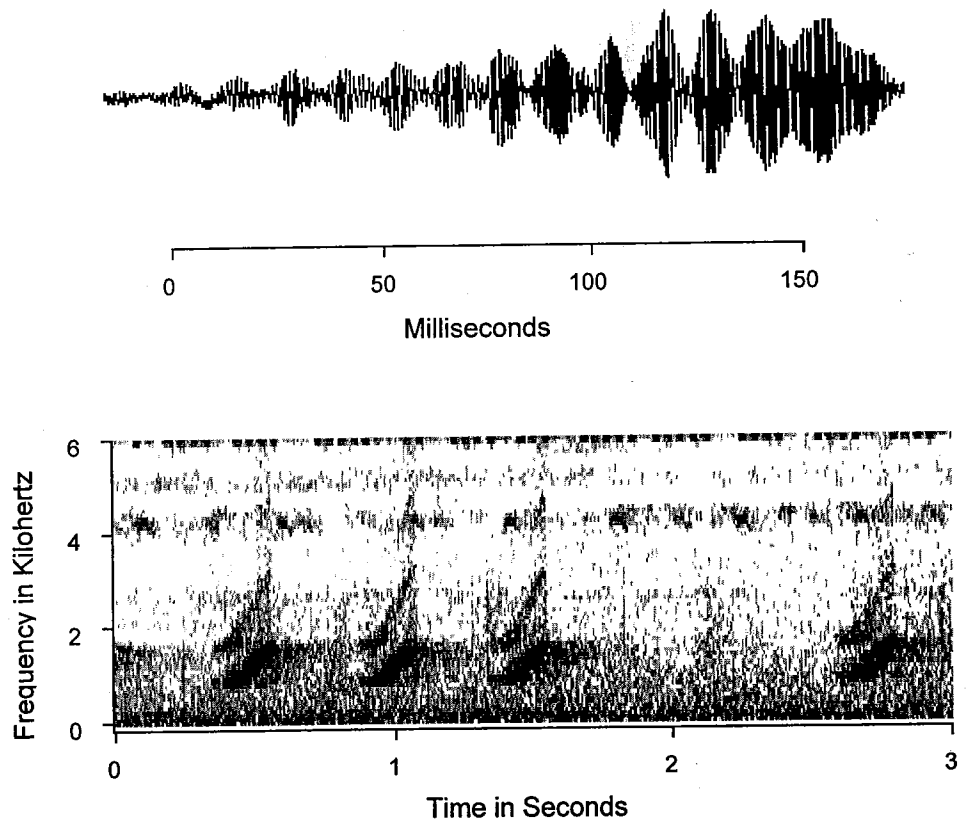


Figure 4. Audiospectrogram (below) and wave form (above) of advertisement call of *Leptodactylus mystaceus* cluster member from Neblina base camp, Amazonas, Venezuela, USNM Tape 70, cut 3.

drop in frequency, may be related to the small number of calls available for analysis from the Tapajós locality ($n = 5$). The most distinctive frequency range exhibited by pulsed calls is that from Altamira, in which the broadcast frequency range is 720-2120 Hz, whereas the combined frequency range of all other pulsed calls is 560-1760 Hz. The number of pulses per call is similar among all pulsed calls.

In contrast, there is more variation among non-pulsed calls. The calls of *L. notoaktites* are the shortest and overlap the duration minimally with those from Xapuri and Tambopata, which also are relatively short. None of these calls overlap in duration with the longer calls from Barro Vermelho, Porongaba, or the call duration of *L. elenae*, the latter three of which are quite similar. Only at Tambopata was evidence found of intrapopulation variation in the presence of a brief terminal drop. All Xapuri calls have a brief terminal frequency drop; all Barro Vermelho, Porongaba, *L. elenae*, and *L. notoaktites* calls lack this feature.

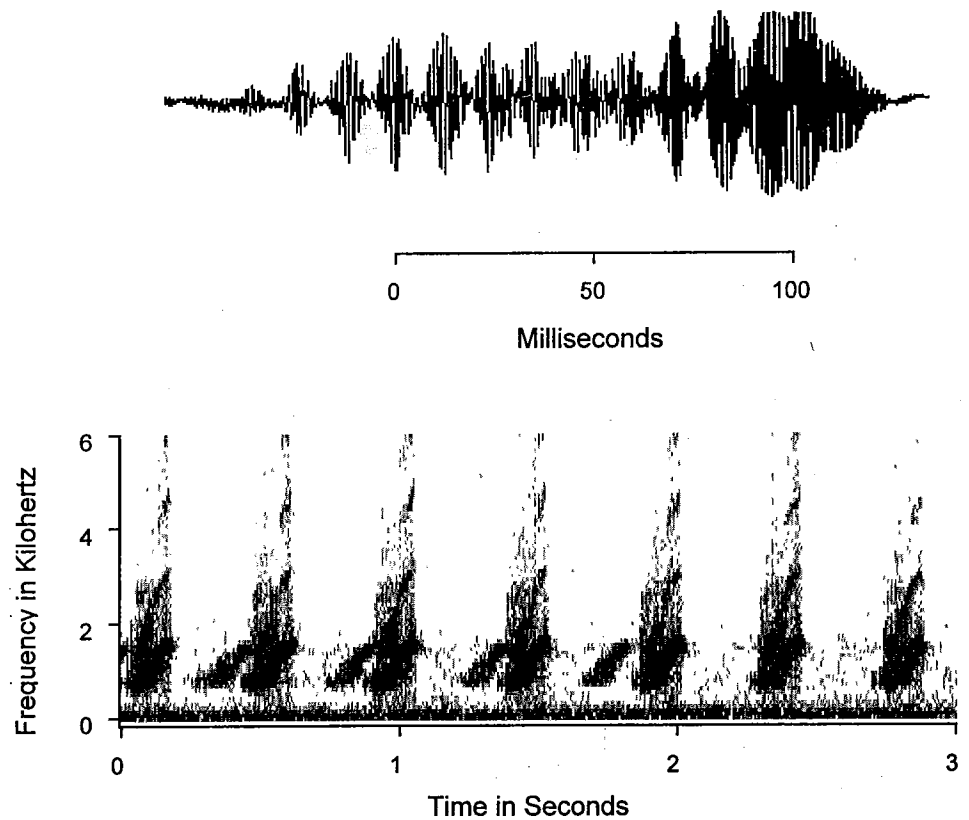


Figure 5. Audiospectrogram (below) and wave form (above) of advertisement call of *Leptodactylus mystaceus* cluster member from Limoncocha, Napo, Ecuador, USNM Tape 16, cut 4.

The advertisement calls can be placed into the following groups: (1) Pulsed calls (Altamira, Tapajós, Manaus, Neblina, Limoncocha, Chapada dos Guimarães); (2) Very short, non-pulsed calls, lacking terminal frequency drop (*L. notoaktites*); (3) Short, non-pulsed calls, at least some calls with terminal frequency drop (Xapuri, Tambopata); (4) Relatively long, non-pulsed calls, lacking terminal frequency drop (Barro Vermelho, Porongaba, *L. elenae*).

Morphological comparisons and species delimitations

Leptodactylus elenae, *mystaceus* (as *amazonicus*, see Heyer, 1983, for nomenclatural change justification), and *notoaktites* differ morphologically (Heyer, 1978). All specimens reported herein, except for *L. elenae* and *notoaktites*, are morphologically like *mystaceus*.

