HERPETOZOA 12 (1/2): 23 - 38
Wien, 30. Juli 1999

On the geographic variation of the advertisement call of *Dendrobates histrionicus* BERTHOLD, 1845 and related forms from north-western South America
(Anura: Dendrobatidae)

Zur geographischen Variation des Anzeigerufes von *Dendrobates histrionicus* BERTHOLD, 1845 und verwandter Formen aus dem nordwestlichen Südamerika
(Anura: Dendrobatidae)

STEFAN LÖTTERS & FRANK GLAW & JÖRN KÖHLER & FERNANDO CASTRO

KURZFASSUNG

Anzeigerufe von sechs Populationen von *Dendrobates histrionicus* BERTHOLD, 1845 und *D. occultator* MYERS & DALY, 1976 wurden untersucht. Unter Einbeziehung von Literaturdaten zum Anzeigeruf anderer Populationen von *D. histrionicus* und *D. lehmanni* MYERS & DALY, 1976 zeichnen sich zwei Gruppen ab: Die nördlichen Populationen mit relativ langen Lauten (≥ 125 ms) und einer niedrigen Lautwiederholungsrate (2-3,5/Sekunde) sowie die südlichen Populationen mit deutlich kürzeren Lauten (≤ 100 ms) und einer höheren Lautwiederholungsrate (mindestens 5/Sekunde). Die nördlichen Populationen haben zudem ähnliche Dominanzfrequenzen und werden daher als artgleich aufgefaßt. Wir ordnen sie *D. histrionicus* sensu stricto zu. Es wird vorläufig vorgeschlagen, daß die südlichen Populationen mindestens drei Arten angehören: Dem hier revalidierten *Dendrobates sylvaticus* FUNKHOUSER, 1956 sowie *D. lehmanni* und *D. occultator*, deren Status weiterer Untersuchungen bedarf.

ABSTRACT

Advertisement calls of six populations of *Dendrobates histrionicus* BERTHOLD, 1845 and *D. occultator* MYERS & DALY, 1976 were studied. When we combine our results with published data on advertisement calls of other populations of *D. histrionicus* and *D. lehmanni* MYERS & DALY, 1976, two groups become evident: northern populations with relatively long notes (≥ 125 ms) and a low note repetition rate (2-3.5/second) and southern populations with distinctively shorter notes (≤ 100 ms) and a higher note repetition rate (at least 5/second). The northern populations, in addition, are similar in dominant frequency; hence, they are regarded to be conspecific. We assign them to *D. histrionicus* sensu stricto. The southern populations are tentatively suggested to belong to at least three species: *Dendrobates sylvaticus* FUNKHOUSER, 1956, which is revalidated here, and *D. lehmanni* as well as *D. occultator*, the statuses of which deserve further investigation.

KEY WORDS

Amphibia, Anura, Dendrobatidae, *Dendrobates histrionicus* sensu stricto, *D. lehmanni*, *D. occultator*, *D. sylvaticus* bona species, advertisement call, taxonomy, Colombia, Ecuador.

INTRODUCTION

Along the Pacific coast of Colombia and northern Ecuador, poison frogs related to *Dendrobates histrionicus* BERTHOLD, 1845 are widely distributed (fig. 1). Interpopulation variation of coloration and pattern is enormous, occasionally even between neighboring populations (MYERS & DALY 1976). In the past, this led to the description of several species or subspecies (see SILVERSTONE 1975). However, comprehensive studies by SILVERSTONE (1975) and MYERS & DALY (1976) revealed that throughout the entire geographical range of these dendrobatids external morphology and skin toxins vary but slightly. As a result, these authors regarded most populations (including those for which scientific names were suggested previously) to belong to a single polychromatic species, *D. histrionicus*. In contrast, two Colombian populations were described as new species, *D. lehmanni* MYERS & DALY, 1976 and *D. occultator* MYERS & DALY, 1976. While both differ from *D. histrionicus* mainly in components of skin toxins (MYERS & DALY 1976; DALY & al. 1986), *D. lehmanni* was

suggested to differ also in color pattern (MYERS & DALY 1976). LÖTTERS (1992) reported color patterns intermediate between *D. histrionicus* and *D. lehmanni*. Moreover, ZIMMERMANN & ZIMMERMANN (1988) received fertile hybrids of both latter nominal species in captivity. These observations cast some doubt on the validity of *D. lehmanni*. In addition, recently it was proposed that at least some "dendrobatid alkaloids" result from dietary uptake and sequestering (DALY & al. 1994 a, 1994 b), thus drastically weakening the value of alkaloid profiles for dendrobatid taxonomy in general.

Recent field studies in Colombia revealed that *D. lehmanni* and a color morph of *D. histrionicus* (form 2 of LÖTTERS 1992) occur sympatrically (although, syntopic occurrence has not yet been discovered) in the Río Anchicayá valley, Departamento Valle del Cauca (LÖTTERS & WIDMER 1997). The authors found considerable differences in the advertisement calls of both forms, suggesting that the validity of *D. lehmanni* should probably be warranted. However, LÖTTERS & WIDMER (1997) also found differences in the advertisement calls of two non-sympatric populations referable to *D. histrionicus*. This led to the assumption that *D. histrionicus* probably comprises a complex of sibling species. But since the authors analyzed only a small sample, they were unable to verify this hypothesis.

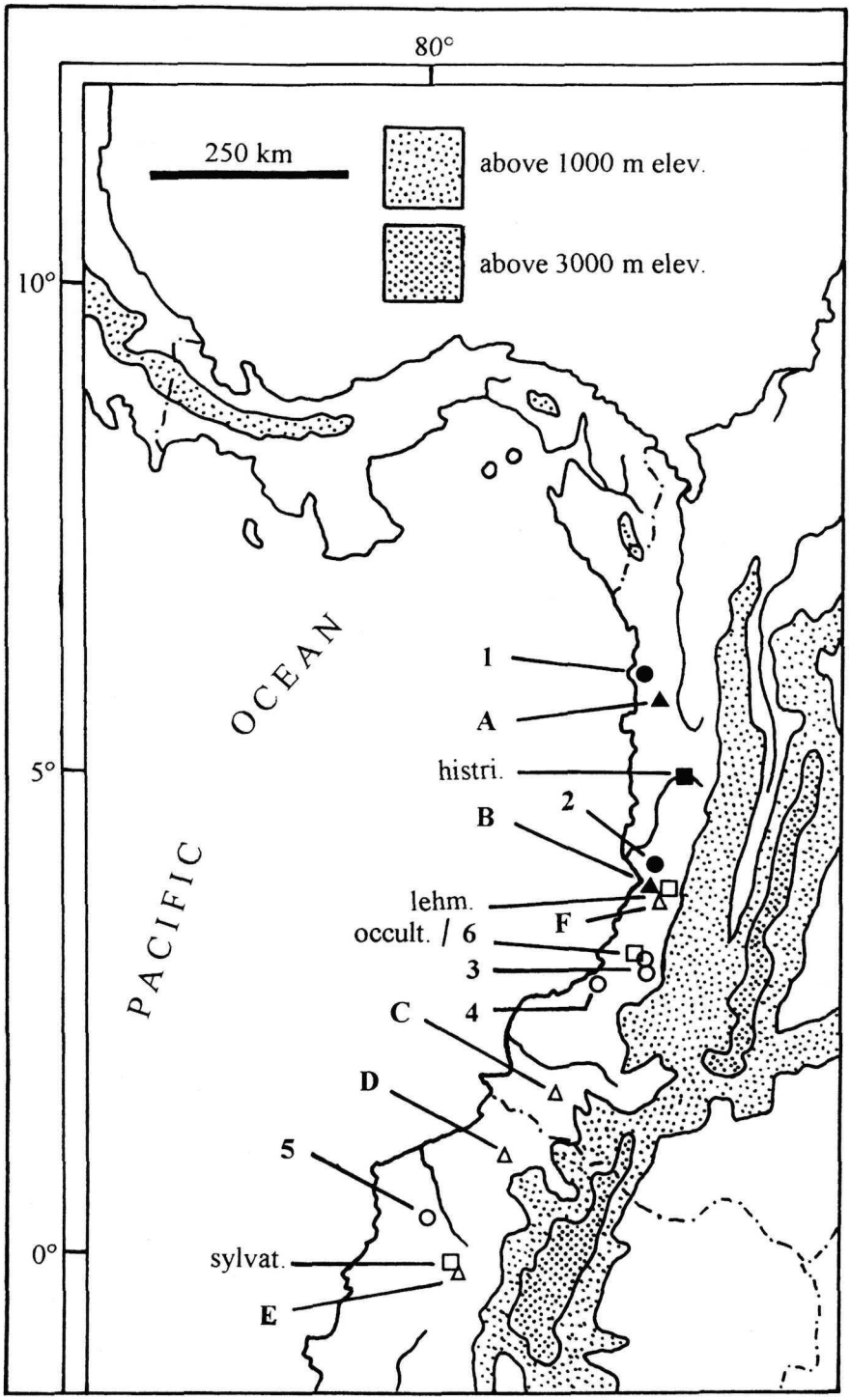
We studied advertisement calls of five further populations referable to *D. histrionicus* from almost all over its geographical range and one population of *D. occultator*. From all of them vocalizations were previously unknown. The objectives of this paper are (1) to describe the advertisement calls of the populations mentioned, (2) to compare them with data on vocalizations of *D. histrionicus* and *D. lehmanni* from the literature, and (3) to contribute to a better understanding of the geographic variation of advertisement calls of *D. histrionicus* and related forms with respect to possible consequences for taxonomy.

MATERIALS AND METHODS

Advertisement calls were recorded in the field or in captivity in rainforest terraria. Recording equipment included a Sony® WM-D6C tape recorder and a Sony® ECM- 121 microphone. Distance between calling frogs and microphone was about 50 cm during recordings. After each recording the air temperature was measured immediately. Recordings were analyzed using a Medav® MOSIP 3000 sound spectrograph with integrated software Spektro® 3.2 (version 1991). Frequency information was obtained through fast Fourier transformation (FFT width 512). According to MYERS & al. (1995), *D. pumilio* O. SCHMIDT, 1857, a Central American species related to *D. histrionicus*, often starts calling with irregular short notes which become constant throughout the rest of the call. For that reason, we always chose middle sections of calls for analysis in *D. histrionicus* and *D. occultator*. For each population, spectrograms and oscillograms of a two second section of a characteristic advertisement call are provided. The following parameters were studied: (1) note duration; (2) number of pulses per note; (3) note repetition rate (notes per second); (4) interval between two notes; (5) frequency range; and (6) dominant frequency. Terminology of call description follows HEYER & al. (1990). Repetition rates were calculated according to method "B" of SCOVILLE & GOTTLIEB (1978).

Fig. 1 (opposite page): Pacific coast of northwestern South America showing distributions of populations of *Dendrobates histrionicus* and related species involved in this paper. ■ □ - type localities; ● ○ - populations 1-6 studied here (where 6 = *D. occultator*); ▲ Δ - other populations mentioned in the text: A - Serranía de Baudó, B - Anchicayá, C - Guayacana, D - Lita, E - Santo Domingo, F - *D. lehmanni* from Anchicayá. The northern populations are indicated by full and the southern populations by open symbols (see text).

Abb. 1 (gegenüberliegende Seite): Pazifikküste des nordwestlichen Südamerikas und Verbreitung der hier einbezogenen Populationen von *Dendrobates histrionicus* und verwandter Arten. ■ □ - Typuslokalitäten; ● ○ - untersuchte Populationen 1-6 (wobei 6 = *D. occultator*); ▲ Δ - andere, im Text erwähnte Populationen: A - Serranía de Baudó, B - Anchicayá, C - Guayacana, D - Lita, E - Santo Domingo, F - *D. lehmanni* aus Anchicayá. Die Symbole für die nördlichen Populationen sind ausgefüllt, die für die südlichen offen (vgl. Text).


80°
250 km
above 1000 m elev.
above 3000 m elev.
10°
5°
0°
PACIFIC OCEAN
1
A
histri.
2
B
lehm.
occult. / 6
F
3
4
C
D
5
sylvat.
E

Since a permit for collecting material was not available, we were not able to deposit voucher specimens of all six populations studied in scientific collections. Nevertheless, from all populations in which voucher specimens could not be deposited, scientific material from previous collectors is available in different herpetological collections, as mentioned in the list of populations studied below:

Dendrobates histrionicus
BERTHOLD, 1845

1. Colombia: Departamento Chocó: Municipio Bahía Solano: vicinity N of Bahía Solano, about 50 m a.s.l. (see figs. 1, 2) – recorded in captivity. The individual recorded is part of a series deposited at Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK 69913-16).

2. Colombia: Departamento Valle del Cauca: Municipio Dagua: caserío el Rusio "El Naranjo", Quebrada La Rusia, about 560 m a.s.l. (see figs. 1, 3) – recorded in captivity. The individual recorded is part of a series deposited at Universidad del Valle, Cali (UVC 12431-52).

3. Colombia: Departamento Cauca: Municipio Micay: upper Río Saija (also called Río Patia), Quebrada Guanguí, about 0.5 km above its junction with the Río Saija, close to the indigenous settlement San Francisco, about 50 m a.s.l. (see figs. 1, 4) – recorded in the field. The specimen recorded was not collected. According to MYERS & DALY (1976) a large series of this population is deposited at the American Museum of Natural History, New York (AMNH).

4. Colombia: Departamento Cauca: Municipio Guapí: about 3 km SW of Guapí runway, about 10 m a.s.l. (see figs. 1, 5) – recorded in the field. The specimen recorded was not collected. A single individual from this locality is deposited at UVC (UVC 10391).

5. Ecuador: Provincia Esmeraldas: vicinity of the village of Rosa Zarrate (= Cuba) on the road Esmeraldas - Santo Domingo (see figs. 1, 6) – recorded in captivity. The specimen recorded is deposited at ZFMK (ZFMK 663345).

Dendrobates occultator
MYERS & DALY, 1976

6. Colombia: Departamento Cauca: Municipio Micay: upper Río Saija (also called Río Patia), Quebrada Guanguí, at about its junction with the Río Saija, near the indigenous settlement San Francisco, about 150 m a.s.l. (see figs. 1, 7) – recorded in the field. The specimen recorded was not collected. The type series of this poison frog at AMNH includes specimens from the same locality and the nearby type locality La Brea (MYERS & DALY 1976).

For comparison we used data referring to vocalizations of *D. histrionicus* and *D. lehmanni* from the literature, in part from SILVERSTONE (1973), MYERS & DALY (1976), ZIMMERMANN & ZIMMERMANN (1982), MEYER (1996), and LÖTTERS & WIDMER (1997).

RESULTS AND DISCUSSION

The results of the analysis of the advertisement calls of populations 1 to 6 are shown in figures 8 to 13 and table 1. Populations 1 and 2 from the northern portion of the distribution area of *D. histrionicus* sensu SILVERSTONE (1975) and sensu MYERS & DALY (1976) are similar in note repetition rate and intervals between notes. The slightly shorter note duration of population 2 may be explained by the higher temperature during recording, whereas the differences in frequency range cannot be explained by the temperature. However, high overlap, especially in the dominant frequencies, is obvious. For none of the parameters studied the significance with respect to species-specific discrimination is known. The largest difference was found in the number of pulses per note, but we suggest that this is probably less important because of the following reasons: although advertisement calls in *D. histrionicus* and related species have a pulsed structure in principal, the pulses are rather indistinct and do not show distinct temporal patterns. As a result, single pulses are not recogniz-

Fig. 2: *Dendrobates histrionicus* from near Bahía Solano, Colombia (population 1).
Abb. 2: *Dendrobates histrionicus* aus der Nähe von Bahía Solano, Kolumbien (Population 1).

Fig. 3: *Dendrobates histrionicus* from Quebrada La Rusia, Colombia (population 2).
Abb. 3: *Dendrobates histrionicus* vom Quebrada La Rusia, Kolumbien (Population 2).

Fig. 4: *Dendrobates histrionicus* from Quebrada Guanguí, Colombia (population 3). We assign this population to *D. sylvaticus* sensu lato.

Abb. 4: *Dendrobates histrionicus* vom Quebrada Guanguí, Kolumbien (Population 3). Wir stellen diese Population zu *D. sylvaticus* sensu lato.

Fig. 5: *Dendrobates histrionicus* from near Guapí, Colombia (population 4). We assign this population to *D. sylvaticus* sensu lato.

Abb. 5: *Dendrobates histrionicus* aus der Nähe von Guapí, Kolumbien (Population 4). Wir stellen diese Population zu *D. sylvaticus* sensu lato.

Fig. 6: *Dendrobates histrionicus* from the vicinity of Cuba, Ecuador (population 5).
We assign this population to *D. sylvaticus* sensu lato.
Abb. 6: *Dendrobates histrionicus* aus der Umgebung von Cuba, Ecuador (Population 5).
Wir stellen diese Population zu *D. sylvaticus* sensu lato.

Fig. 7: *Dendrobates occultator* from Quebrada Guanguí, Colombia (population 6).
Abb. 7: *Dendrobates occultator* vom Quebrada Guanguí, Kolumbien (Population 6).

able for the human ear and sometimes cannot be counted on oscillograms (figs. 8-13). Considering these aspects, populations 1 and 2 do apparently not represent different species. Additional data on advertisement calls of two other populations from the northern geographical range of *D. histrionicus* were provided by previous authors. One is from Serranía de Baudó in the Departamento Chocó, Colombia (fig. 1); SILVERSTONE (1973: 297) reported its repetition rate to be three notes per second. The other is from Anchicayá in the Departamento Valle del Cauca, Colombia (fig. 1), and was studied by LÖTTERS & WIDMER (1997); data are summarized in table 2. Since parameters of advertisement calls of both populations coincide well with populations 1 and 2, we regard all four northern populations being conspecific.

In contrast, populations 3 to 6 from the more southern portion of the distribution area of *D. histrionicus* sensu SILVERSTONE (1975) and sensu MYERS & DALY (1976) are considerably different from the northern populations, especially by having a shorter note duration and higher note repetition rates. The number of pulses per note in populations 3 through 6 is similar to population 2. Although the means of the intervals between two consecutive notes are significantly shorter in populations 3 to 6, the interval range of population 4 (and of population 5 in part) shows overlap with that of the northern populations. However, we observed that interval length depends highly on individual motivation. Consequently, this character can be extremely variable. The frequency ranges as well as the dominant frequencies in populations 3 to 6 differ from each other and from the northern populations. As a result, populations 3 to 6 can be grouped together based on the note duration and note repetition rate. We suggest that these southern populations are not conspecific with the northern populations: the differences noted are comparable to those among other species related to *D. histrionicus*, e. g., when comparing *D. arboreus* MYERS, DALY & MARTÍNEZ, 1984 to *D. pumilio* (MYERS & al. 1984). Nevertheless, we are uncertain whether the southern populations belong to just one or several species, because of considerable differences in the frequency ranges and dominant frequencies (even at identical or similar recording temperatures). Published data on advertisement calls of *D. histrionicus* populations of the southern geographical range are provided in table 2. A population from Guayacana in the Departamento Nariño, Colombia (fig. 1), studied by MYERS & DALY (1976), and another from Lita in the Provincia Esmeraldas, Ecuador (fig. 1), studied by LÖTTERS & WIDMER (1997) coincide well with the southern populations studied here, especially by having a relatively short note duration and high note repetition rate. *Dendrobates lehmanni* from Anchicayá in the Departamento Valle del Cauca, Colombia (fig. 1), is also referable to our southern populations based on data provided by LÖTTERS & WIDMER (1997) (table 2). However, coincidence in frequency ranges or dominant frequencies can only be found in part (e. g., in the dominant frequencies of the Guayacana and Lita populations, or *D. lehmanni* and population 4). Further investigation of populations from the southern geographical range of *D. histrionicus* is necessary.

A population from Santo Domingo in the Provincia Pichincha, Ecuador (fig. 1), analyzed by MEYER (1996) is neither referable to our southern nor to our northern group. In note duration and note repetition rate it appears to be intermediate between the northern and southern populations studied by us (see table 2). Neither much coincidence with southern nor with northern populations is evident in the data on advertisement calls of *D. histrionicus* and *D. lehmanni* (both from unknown localities) provided by ZIMMERMANN & ZIMMERMANN (1982). Note duration is also intermediate whereas the note repetition rate resembles more the northern populations (table 2). However, as indicated by the authors, they analyzed a mixed sample of *D. lehmanni* (which is similar to our southern populations) and a color morph of *D. histrionicus* which most probably belongs to the northern group postulated in the present paper. According to the illustrations and color variant descriptions by ZIMMERMANN & ZIMMERMANN (1982), their material of *D. histrionicus* is comparable to population 2 (fig. 3) as well as material from the Río Azul in the northern Departa-

Table 1: Advertisement call parameters of populations 1 to 6. SD - Standard deviation.

Tabelle 1: Parameter der Anzeigerufe der Populationen 1 bis 6. SD - Standardabweichung.

Population analyzed (see Materials and Methods) / Unteruchte Population (siehe Materials and Methods)	Number of individuals studied / Anzahl untersuchter Individuen	Number of notes analyzed / Anzahl untersuchter Laute	Temperature [°C] / Temperatur [°C]	Note duration [ms] $\bar{x}\pm$ SD (range) / Lautdauer [ms] $\bar{x}\pm$ SD (Spannweite)	Number of pulses per note $\bar{x}\pm$ SD (range) / Anzahl Pulse je Laut $\bar{x}\pm$ SD (Spannweite)	Note repetition rate (notes/second) / Lautwieder-holungsrate (Rufe/Sekunde)	Interval between two notes [ms] $\bar{x}\pm$ SD (range) / Intervall zwischen zwei Lauten [ms] $\bar{x}\pm$ SD (Spannw.)	Frequency range [Hz] / Frequenz-bereich [Hz]	Dominant frequency [Hz] / Dominanz-frequenz [Hz]
Population 1 (figs. 2, 8)	1	31	21.5	184.9 ± 6.3 (174-199)	44.7 ± 1.6 (42-48)	2-3	175.3 ± 5.1 (166-188)	1000-4650	1850-2200 2600-2800
Population 2 (figs. 3, 9)	1	20	26.0	148.6 ± 9.2 (125-162)	18.6 ± 9.2 (16-22)	3	170.9 ± 24.9 (131-239)	900-1300 1700-3000 8000-8600	2450-2800
Population 3 (figs. 4, 10)	1	20	30.0	61.6 ± 3.1 (57-68)	21.6 ± 1.0 (20-23)	6-7	89.9 ± 7.7 (76-113)	700-5300 7000-8350	1700-2950
Population 4 (figs. 5, 11)	1	20	30.0	89.9 ± 4.8 (82-100)	27.0 ± 1.2 (25-29)	5-6	104.2 ± 24.44 (90-174)	1350-3050 3200-5300	3450-3700
Population 5 (figs. 6, 12)	1	20	23.0	95.2 ± 4.0 (86-100)	19.0 ± 1.4 (16-21)	5-6	109.3 ± 6.5 (100-121)	800-3000	1750-1950 2300-2450
Population 6 (figs. 7, 13)	1	20	25.0	74.4 ± 4.3 (68-84)	19.5 ± 1.4 (18-22)	6-7	91.7 ± 5.3 (82-104)	1100-3000 3400-5100 7100-9450	3750-3900

Table 2: Chronological compilation of literature data of advertisement calls of different populations of *Dendrobates histrionicus* and *D. lehmanni*. In those data of *D. lehmanni* provided by MYERS & DALY (1976) it is uncertain if they refer to advertisement calls (see text). SD - Standard deviation; * - Mixed sample. Data which are estimated from figures in the literature source mentioned are indicated by: [1]. Data which are not available from the source mentioned but which were reinvestigated by us using the original recordings are indicated by: [2].

Tabelle 2: Chronologische Zusammenstellung von Literaturdaten zum Anzeigeruf verschiedener Populationen von *Dendrobates histrionicus* und *D. lehmanni*. Bei den Daten zu *D. lehmanni* von MYERS & DALY (1976) ist es unsicher, ob sie sich auf Anzeigerufe beziehen (vgl. Text). SD - Standardabweichung; * - Gemischte Stichprobe. Angaben, die aufgrund von Abbildungen in der angegebenen Quelle gemacht werden, sind gekennzeichnet durch: [1]. Daten, die aus der angegebenen Quelle nicht hervorgehen, aber anhand der Originalaufnahmen nachträglich von uns erhoben wurden, sind gekennzeichnet durch: [2].

Species name Locality (Literature source)	Number of individuals studied	Number of notes analyzed	Temperature [°C]	Note duration [ms] $\bar{x}\pm$ SD (range)	Number of pulses per note $\bar{x}\pm$ SD (range)	Note repetition rate (notes/second)	Interval between two notes [ms] $\bar{x}\pm$ SD (range)	Frequency range [Hz]	Dominant frequency [Hz]
Artname Fundort (Literaturquelle)	Anzahl untersuchter Individuen	Anzahl untersuchter Laute	Temperatur [°C]	Lautdauer [ms] $\bar{x}\pm$ SD (Spannweite)	Anzahl Pulse je Laut $\bar{x}\pm$ SD (Spannweite)	Lautwieder-holungsrate (Rufe/Sekunde)	Intervall zwischen zwei Lauten [ms] $\bar{x}\pm$ SD (Spannw.)	Frequenz-bereich [Hz]	Dominanz-frequenz [Hz]
D. histrionicus Guayacana, Colombia (MYERS & DALY 1976)	1	?	27	~ 80-90 [1]	?	6	~ 70-90 [1]	1500-3500	~ 1700-3400 [1]
D. lehmanni ? (MYERS & DALY 1976)	1	?	28	~ 140 [1]	?	2-3	~ 180-200 [1]	1500-3500	~ 1700-3200 [1]
D. histrionicus + *D. lehmanni* * ? (ZIMMERMANN & ZIMMERMANN 1982)	?	?	?	100-160	?	2-4	~ 330 [1]	500-3500	?
D. histrionicus Sta. Domingo, Ecuador (MEYER 1996)	1	29	?	108.0 ± 6.0 (92-119)	?	4.22	129.0 ± 10.0 (111-169)	2254-4356	3187-3445
D. histrionicus Anchicayá, Colombia (LÖTTERS & WIDMER 1997)	3	21	all at /alle bei 22.5	192.7 ± 6.2 (162-222)	47.3 ± 3.4 (37-59)	3-3.5 [2]	161.9 ± 23.9 (119-254)	800-3100	1700-2800
D. histrionicus Lita, Ecuador (LÖTTERS & WIDMER 1997)	1	16	21	86.1 ± 1.7 (76-100)	32-38	5 [2]	153.0 ± 10.9 (113-233)	900-3000	1800-3000
D. lehmanni Anchicayá, Colombia (LÖTTERS & WIDMER 1997)	3	21	all at /alle bei 26	79.0 ± 6.1 (66-92)	23.5 ± 2.0 (20-27)	5 [2]	143.0 ± 4.2 (127-158)	2200-4900	3000-3800

mento Valle del Cauca, Municipio Darién, Colombia (UVC 6937-39). Because the study of ZIMMERMANN & ZIMMERMANN (1982) does not provide separate data for each of their color morphs, it is excluded from further discussion.

MYERS & DALY (1976) reported call characteristics for *D. lehmanni* similar to our northern populations (table 2). Nevertheless, as indicated above, following the data of LÖTTERS & WIDMER (1997) we refer this species to the southern populations. The latter is supported by the following argumentation. LÖTTERS & WIDMER (1997) with certainty analyzed advertisement calls recorded from three different males in the field (close to the type locality). In contrast, MYERS & DALY (1976) recorded a single specimen from an unknown locality in a plastic bag. Several times the senior author observed males of *D. histrionicus* or *D. lehmanni* crowded in transport bags which produced release calls. According to ZIMMERMANN & ZIMMERMANN (1982) this call type consists of a single note with a duration of 220 to 280 ms (in *D. lehmanni* and *D. histrionicus* from unknown localities, but the latter most probably from a northern population as indicated above) and is produced when males are touched or clasped by other individuals. Release calls in the same population of *D. lehmanni* as studied by LÖTTERS & WIDMER (1997) recorded in a plastic bag had a duration of 131 to 139 ms ($\bar{x}$=133.1 ms, n = 3; the two inter-call intervals with 487 and 510 ms duration) (fig. 14). Thus, at least in duration they are similar to notes of the advertisement call recognized in northern populations. Moreover, if a male is rather stressed (as is possible when confined in a plastic bag with other individuals) and the air temperature is relatively high (as during the recording by MYERS & DALY 1976; see table 2) release calls may be given more frequently, and inter-call intervals may become shorter, thus almost resembling a series of notes.

CONCLUSIONS

Our results show that, at least two species are involved with *D. histrionicus* sensu SILVERSTONE (1975) and sensu MYERS & DALY (1976). They are represented by a northern and southern group of populations. The former is relatively constant in most parameters analyzed; hence we regard the populations involved as conspecific. The southern populations are similar in note duration and note repetition rate; however, they vary extremely in frequency range and dominant frequency. For that reason we cannot contribute to the question if the southern populations belong to just one species or if they comprise a complex of species. Due to our results we further conclude:

(1) the northern populations should be referred to *D. histrionicus* sensu stricto. Recently MYERS & BÖHME (1996) showed that the type locality of *D. histrionicus* most probably is located in the upper Río San Juan drainage, Departamento Chocó, Colombia. Thus, it lies within an area surrounded by the northern populations studied by us (fig. 1). Consequently, we hold the view that this name is applicable to the northern populations analyzed in the present paper. Nevertheless, advertisement calls of *D. histrionicus* from the type locality have not yet become available and final resolution is needed.

(2) only those names persist in the synonymy of *D. histrionicus* sensu stricto which were based on material originating from within the range of the northern populations (fig. 1). These are *Dendrobates tinctorius* var. *cocteani* STEINDACHNER, 1864 [error typographicus pro *cocteaui*], *D. tinctorius* var. *coctaei* BOULENGER, 1913, *D. tinctorius* var. *chocoensis* BOULENGER, 1913, and *D. tinctorius wittei* LAURENT, 1942 (compare STEINDACHNER 1864; SILVERSTONE 1975). However, since advertisement call data from type localities of these forms are not available, synonymy can only be supposed.

(3) the southern populations - which are not conspecific with *D. histrionicus* sensu stricto - should be referred to *D. sylvaticus* FUNKHOUSER, 1956. Originally named *D. histrionicus sylvaticus*, this name and *D. histrionicus confluens* FUNKHOUSER, 1956 are the oldest names avail-

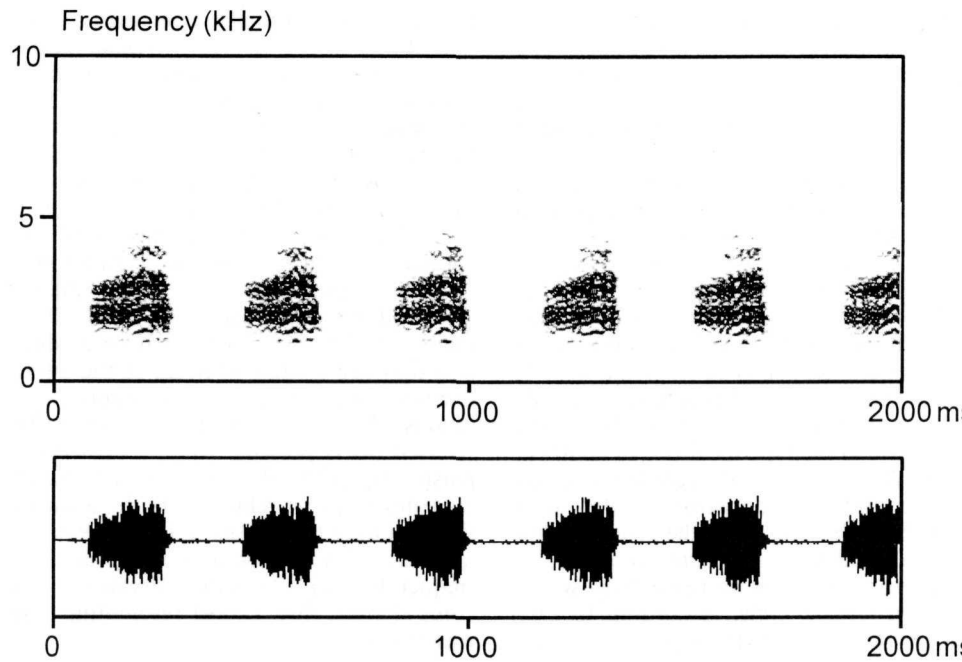


Fig. 8: Spectrogram and oscillogram of the advertisement call of population1 (Bahía Solano; fig. 2).
Abb. 8: Spektrogramm und Oszillogramm des Anzeigerufs von Population 1 (Bahía Solano; Abb. 2).

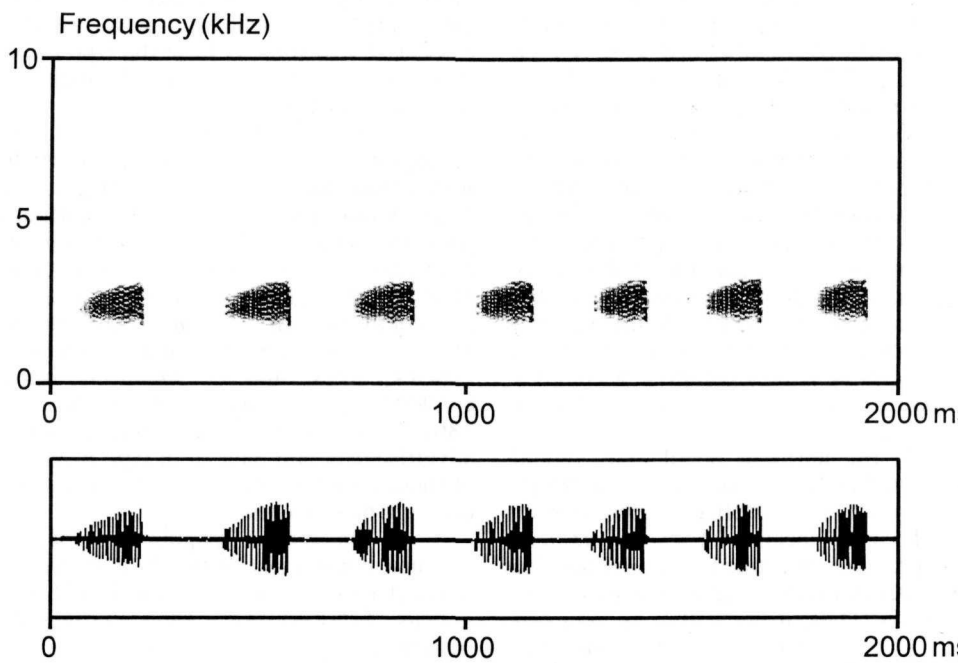


Fig. 9: Spectrogram and oscillogram of the advertisement call of population 2 (Quebrada La Rusia; fig. 3).
Abb. 9: Spektrogramm und Oszillogramm des Anzeigerufs von Population 2 (Quebrada La Rusia; Abb. 3).

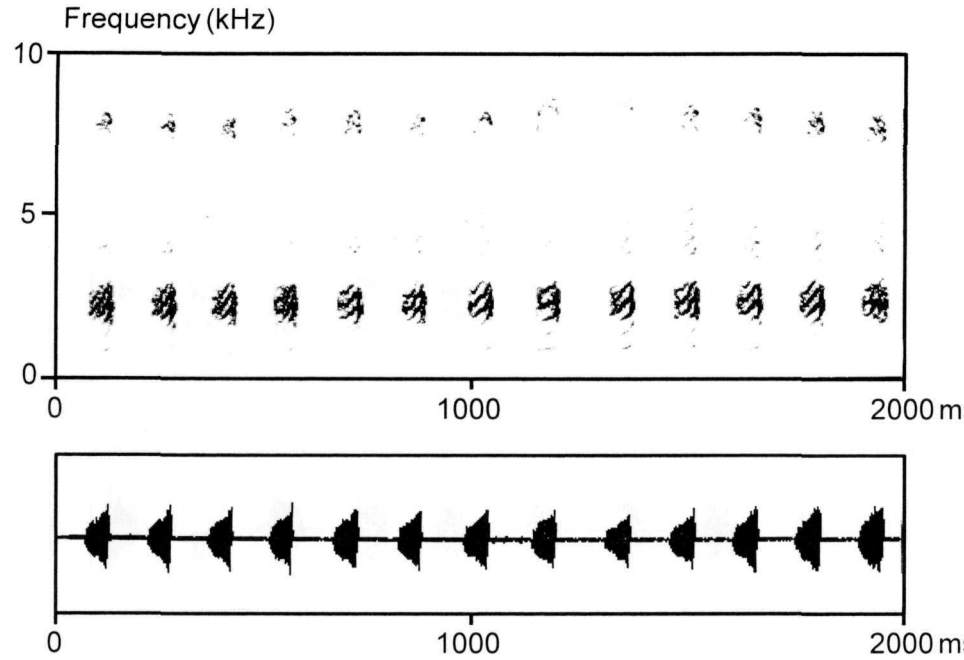


Fig. 10: Spectrogram and oscillogram of the advertisement call of population 3 (Quebrada Guanguí; fig. 4).
Abb. 10: Spektrogramm und Oszillogramm des Anzeigerufs von Population 3 (Quebrada Guanguí; Abb. 4).

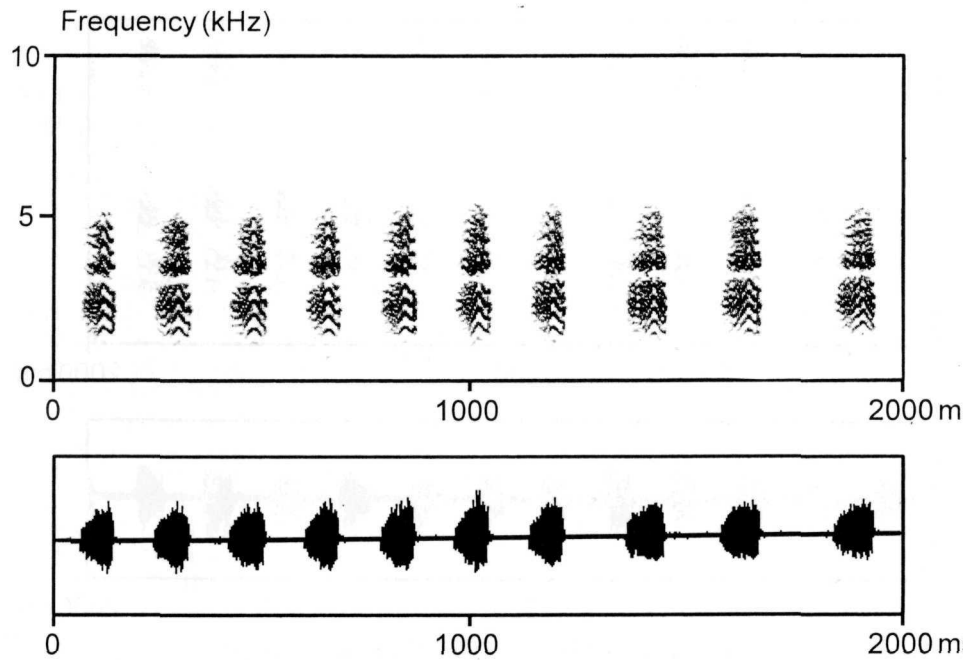


Fig. 11: Spectrogram and oscillogram of the advertisement call of population 4 (Guapí; fig. 5).
Abb. 11: Spektrogramm und Oszillogramm des Anzeigerufs von Population 4 (Guapí; Abb. 5).

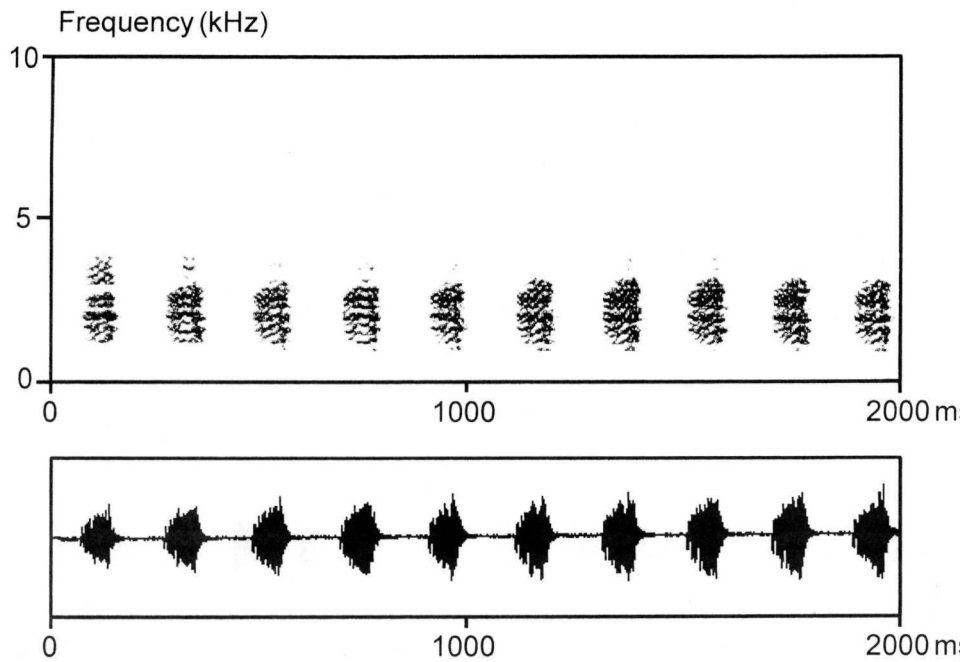


Fig. 12: Spectrogram and oscillogram of the advertisement call of population 5 (Cuba; fig. 6).
Abb. 12: Spektrogramm und Oszillogramm des Anzeigerufs von Population 5 (Cuba; Abb. 6).

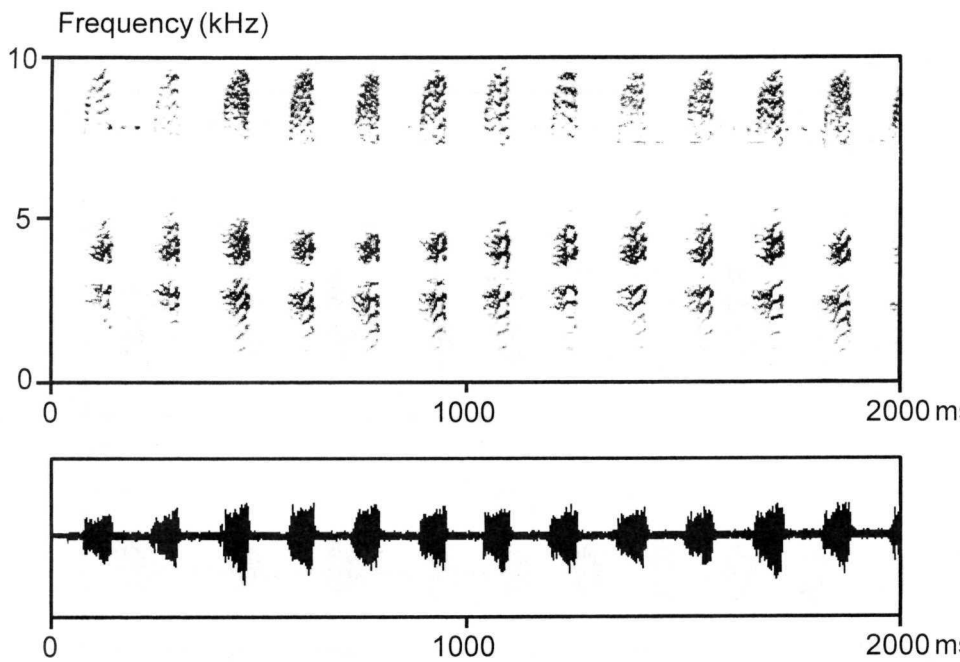


Fig. 13: Spectrogram and oscillogram of the advertisement call of population 6 (*Dendrobates occultator*, Quebrada Guanguí; fig. 7).
Abb. 13: Spektrogramm und Oszillogramm des Anzeigerufs von Population 6 (*Dendrobates occultator*, Quebrada Guanguí; Abb. 7).

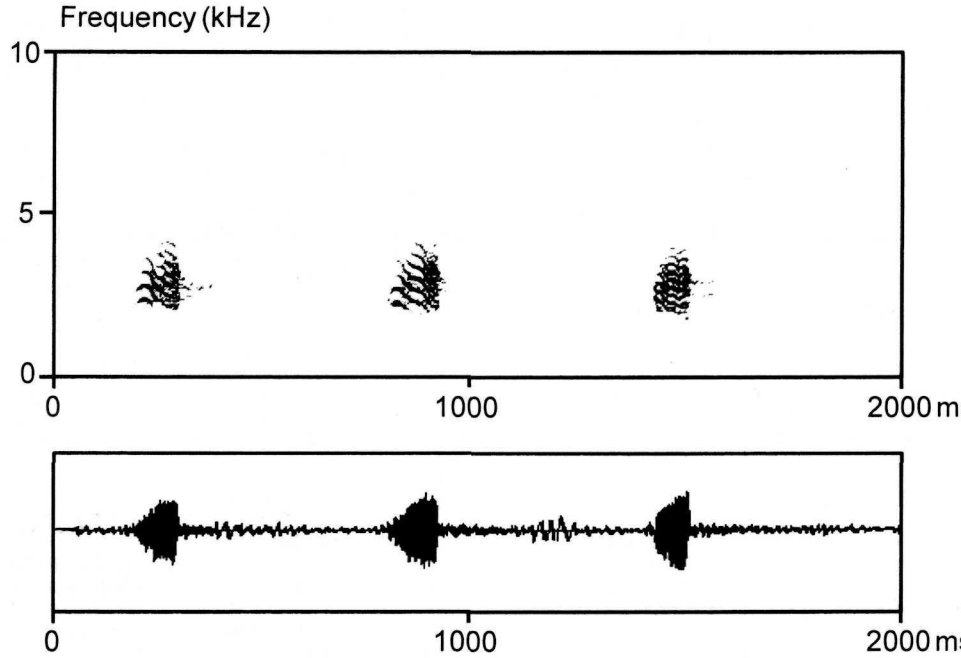


Fig. 14: Spectrogram and oscillogram of release calls of *Dendrobates lehmanni* (from Alto Anchicayá, Departamento Valle del Cauca, Colombia) recorded from one of two males in a plastic bag (air temperature 24°C).
Abb. 14: Spektrogramm und Oszillogramm von Befreiungsrufen von *Dendrobates lehmanni* (aus Alto Anchicayá, Departamento Valle del Cauca, Kolumbien), aufgenommen von einem von zwei Männchen in einem Plastikbeutel (Lufttemperatur 24°C).

able for populations which occur within the geographical range of the southern populations. Currently, both names are junior synonyms of *D. histrionicus* (e. g., SILVERSTONE 1975). Taking first reviser's action, we revalidate *sylvaticus* and elevate it to the species level. *Dendrobates histrionicus confluens* from the same general area is provisionally treated as its junior synonym. Although the type locality of *D. sylvaticus* is close to population 5 (fig. 1) and both have a similar color pattern [compare fig. 5 with description of *D. sylvaticus* provided by FUNKHOUSER (1956) and SILVERSTONE (1975)], we have to remark that advertisement calls of topotypic specimens of *D. sylvaticus* are not known. Since the southern populations possibly comprise a complex of species, the allocation of the name *D. sylvaticus* to all of them remains tentative. As a result, we suggest the combination *D. sylvaticus* sensu lato.

(4) *Dendrobates lehmanni* and *D. occultator* (the only other names set up for dendrobatids from within the range of the southern populations studied; fig. 1) are considered not synonymous with *D. sylvaticus* sensu lato, because the taxonomic relationship of the southern populations remains to be resolved. Noteworthy, *D. occultator* is likely to become a junior synonym of *D. sylvaticus* since - according to MYERS & DALY (1976) - both look very similar. In addition, the bio-acoustic differences of the sympatric populations 3 and 6 (i. e., *D. occultator*) are much smaller than usually found between sympatric species. As a result, the southern populations currently contain *D. occultator*, *D. lehmanni*, and *D. sylvaticus* sensu lato.

Further research which focuses especially on advertisement calls of populations from type localities is necessary to (1) confirm or reject the northern populations to represent *D. histrionicus* sensu stricto, and to (2) analyze the variation within the southern populations.

Diagnoses of species

Dendrobates histrionicus sensu stricto can be distinguished from *D. lehmanni*, *D. occultator*, and *D. sylvaticus* sensu lato in its advertisement call by having a longer note duration (≥ 125 ms versus ≤ 100 ms) and a lower note repetition rate (2-3.5/second versus at least 5/second). Concerning the dorsal color pattern, *D. histrionicus* sensu stricto often is symmetrically, brightly spotted (with one to many spots larger than the eye diameter and/or few to many dots smaller than the eye diameter), sometimes with brightly colored or spotted flanks, and occasionally with bracelets and/or spots on the limbs (SILVERSTONE 1975; MYERS & DALY 1976) (e. g., figs. 2, 3). The southern populations (*D. lehmanni*, *D. occultator*, and *D. sylvaticus* sensu lato) include the dorsally more washed patterns, close-set-spotted, mottled or marbled, as well as cross-banded (i. e., *D. lehmanni*) populations (SILVERSTONE 1975; MYERS & DALY 1976) (e. g., figs. 4 - 7).

ACKNOWLEDGMENTS

For field or laboratory assistance, hospitality and/or discussions we are indebted to C. ARROYO (Guapí), W. BÖHME (ZFMK, Bonn), E. CHAMAPURNY MEHIO (chief of the Emberá indigenous people of the Departamento Cauca, Colombia), A. EUFINGER (Bonn), P. H. GERBER (Kandersteg), T. "P." GRANT (UVC; Cali), R. RICHTER (Rüsselsheim), M. VENCES (Bonn), and A. WIDMER (Zürich).

REFERENCES

DALY, J. W. & SPANDE, T. F. & WHITTAKER, N. & HIGHET, R. J. &. FEIGL, D. & NISHIMORI, N. & TOKUYAMA, T. & MYERS, C. W. (1986): Alkaloids from dendrobatid frogs: structures of two ω-hydroxy congeners of 3-butyl-5-propylindolizidine and occurrence of 2,5-disubstituted pyrrolidines and a 2,6-disubstituted piperidine.- J. nat. Products; 49 (2): 265-280.

DALY, J. W. & GARRAFFO, H. M. & SPANDE, T. F. & JARAMILLO, C. & RAND, A. S. (1994 a): Dietary source for skin alkaloids of poison frogs (Dendrobatidae)?- J. chem. Ecol.; 20 (4): 943-955.

DALY, J. W & SECUNDA, S. I. & GARRAFFO, H. M. & SPANDE, T. F. & WISNIESKI, A. & COVER Jr., J. F. (1994 b): An uptake system for dietary alkaloids in poison frogs (Dendrobatidae).- Toxicon; 32 (6): 657-663.

FUNKHOUSER, J. W. (1956): New frogs from Ecuador and southwestern Colombia.- Zoologica, New York; 41: 73-80.

HEYER, W. R. & RAND, A. S. & DA CRUZ, C. A. G. & PEIXOTO, O. L. & NELSON, C. E. (1990): Frogs of Boracéia.- Arqu. Zool., São Paulo; 31: 237-410.

LÖTTERS, S. (1992): Zur Validität von *Dendrobates lehmanni* MYERS & DALY, 1976 aufgrund zweier neuer Farbformen von *Dendrobates histrionicus* BERTHOLD, 1845.- Salamandra, Bonn; 28 (2):138-144.

LÖTTERS, S. & WIDMER, A. (1997): Bioacoustic comparisons of the advertisement calls of the poison frogs *Dendrobates histrionicus* and *Dendrobates lehmanni*, pp. 237-245. In: BÖHME, W. & BISCHOFF, W. & ZIEGLER, T. (eds.): Herpetologia Bonnensis; Bonn (SEH).

MEYER, E. (1996): Ökologie und Biogeographie des zentralamerikanischen Pfeilgiftfrosches *Dendrobates granuliferus* TAYLOR; Dissertation Universität Ulm.

MYERS, C. W. &. BÖHME, W. (1996): On the type specimens of two Colombian poison frogs described by A. A. BERTHOLD (1845), and their bearing on the locality "Provinz Popayan".- American Mus. Novitates, New York; 3185:1-20.

MYERS, C. W. & DALY, J. W. (1976): Preliminary evaluation of skin toxins and vocalizations in taxonomic and evolutionary studies of poison-dart frogs (Dendrobatidae).- Bull. American Mus. Nat. Hist., New York; 157: 173-262.

MYERS, C. W. & DALY, J. W. & MARTÍNEZ, V. (1984): An arboreal poison frog (*Dendrobates*) from western Panama.- American Mus. Novitates, New York; 2783 :1-20.

MYERS, C. W. & DALY, J. W. & GARRAFFO, H. M. & WISNIESKI, A. & COVER Jr., J. F. (1995): Discovery of the Costa Rican poison frog *Dendrobates granuliferus* in sympatry with *Dendrobates pumilio*, and comments on taxonomic use of skin alkaloids.- American Mus. Novitates, New York; 3144:1-21.

SCOVILLE, R. &. GOTTLIEB, G. (1978): The calculation of repetition rate in avian vocalizations.- Animal Behavior; 26: 962-963.

SILVERSTONE, P. A. (1973): Observations on the behaviour and ecology of a Colombian poison-arrow frog, the kõkoé-pá (*Dendrobates histrionicus* BERTHOLD).- Herpetologica; 29: 295-301.

SILVERSTONE, P. A (1975): A revision of the poison-arrow frogs of the genus *Dendrobates* WAGLER.- Nat. Hist. Mus. Los Angeles County, Sci. Bull.; 21: 1-55.

STEINDACHNER, F. (1864): Batrachologische Mitteilungen.- Verh. zool.-bot. Ges. Wien; 14: 239-288.

ZIMMERMANN, E. & ZIMMERMANN, H. (1982): Soziale Interaktionen, Brutpflege und Zucht des Pfeilgiftfrosches *Dendrobates histrionicus* (Amphibia: Salientia: Dendrobatidae).- Salamandra, Frankfurt/Main; 18 (3/4):150-167.

ZIMMERMANN, H. & ZIMMERMANN, E. (1988): Etho-Taxonomie und zoogeographische Artengruppenbildung bei Pfeilgiftfröschen.- Salamandra, Bonn; 24 (2/3): 125-160.

DATE OF SUBMISSION: September 25th, 1998 Corresponding editor: Heinz Grillitsch

AUTHORS: STEFAN LÖTTERS, JÖRN KÖHLER, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany [email: uzs5r6@uni-bonn.de]; FRANK GLAW, Zoologische Staatssammlung, Münchhausenstraße 21, D-81247 München, Germany; FERNANDO CASTRO, Universidad del Valle, Facultad de Ciencias, Departamento de Biología, Apartado 25360, Cali, Colombia.