EVOLUTION OF ACOUSTIC BEHAVIOUR IN AFRICAN *BUFO* (ANURA: BUFONIDAE)

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ABSTRACT

Mating calls are known for 29 species of African *Bufo* belonging to 11 species groups. Twenty-five African species, representing eight species groups (including four groups or complexes having 2N=22) have calls which Martin (1972) termed Type I. This call type is also found in *Schismaderma carens*, *Nectophrynoides tornieri* and *N. occidentalis*. It is known in only four species of *Bufo* outside Africa and in *Odontophrynus americanus* which is thought to be closely related to leptodactylids that gave rise to the genus *Bufo*. Four African species of *Bufo* have Type II calls.

Geographic distribution of three call types indicates large radiations of one or two call types in South America, North America and Africa. The European and Asian *Bufo* faunas appear to be derived primarily from American radiations.

The radiation of bufonids in Africa appears to be equal to that of South America. An explanation of this may be that *Bufo* or its progenitor evolved prior to the continental separation of South America and Africa.

INTRODUCTION

The importance of anuran mating calls as premating isolating mechanisms and the usefulness of these calls for species identification are now well established. Call structure is also useful for determining relationships between species (Blair 1958, 1962; Bogert 1960; Mecham 1961; Martin 1972; Tandy & Keith 1972; Schiøtz 1973; Straughan 1973).

Martin (1967, 1971, 1972) showed that call structure in *Bufo* accompanied by detailed physiological study of sound-producing structures could be used to discern phylogenetic patterns in that genus. These patterns were supported by data from other sources such as hybridization experiments (Blair 1972a) and biochemical composition of parotoid gland secretions (Low 1972). Martin (1972) described three basic types of mating call in different species of *Bufo*, based on pulsatile structures and their anatomical correlates. He compared 75 species among African (16), Eurasian (7), North American (36) and South American (16) members of the genus. Using these data, he supported theories proposed by Blair (1972a, b) and others suggesting the origin of *Bufo* in South America and its subsequent dispersal to other continents.

Tandy & Keith (1972) presented information on the mating calls of *Schismaderma carens* and 17 African *Bufo* species belonging to eight species groups. Most of these species were the same ones used by Martin (1972) for evaluation of the African radiation. Mating calls are now known for 29 species of African *Bufo* belonging to at least 11 species groups and for the African bufonids *Schismaderma carens*, *Nectophrynoides occidentalis* and *N. tornieri*. Data are also available on mating behaviour and/or laryngeal morphology of four species of *Bufo*, including two additional species groups and one other complex that probably lack mating calls. Such in-

Zoologica Africana 11(2): 349–368 (1976)

formation has also accumulated on the four known species of *Werneria,* two species of *Wolterstorffina* and *Nectophryne afra* (see Appendix).

This study is a re-examination of the African radiation of bufonids and its relationship to the evolution of the Family Bufonidae and the genus *Bufo*. Recent data on mating calls is the primary basis of this evaluation.

METHODS

Tape-recorded mating calls were analysed on a Kay Electric Sonagraph 6061A and a Tektronix 502A dual beam oscilloscope using standard methods. Durations and repetition rates based on time periods greater than two seconds were also measured with a stop-watch.

Data on the presence or absence of arytenoid valves in the larynx are based primarily on Martin (1971, 1972). The presence of such valves in additional species was inferred from the occurrence of passive amplitude modulation in their calls.

For African species, the presence of tympani was determined by examination of specimens, in most cases including the type material. Such data for Eurasian species are principally from Inger (1972). Martin (1972) presented such information for many American species; we have examined non-type material of most of these.

PHYSICAL STRUCTURE OF *BUFO* MATING CALLS

The physical components of the temporal and spectral structure of *Bufo* mating calls were described and illustrated by Tandy & Keith (1972). Such calls have temporal structures of five grades of complexity: (1) pulses, (2) pulse trains, (3) complex pulse trains, (4) first-order sequences of complex pulse trains and (5) second-order sequences of first-order sequences of complex pulse trains (Figures 1–3).

Structures of the same temporal grade of complexity, e.g. pulses, may not be homologous

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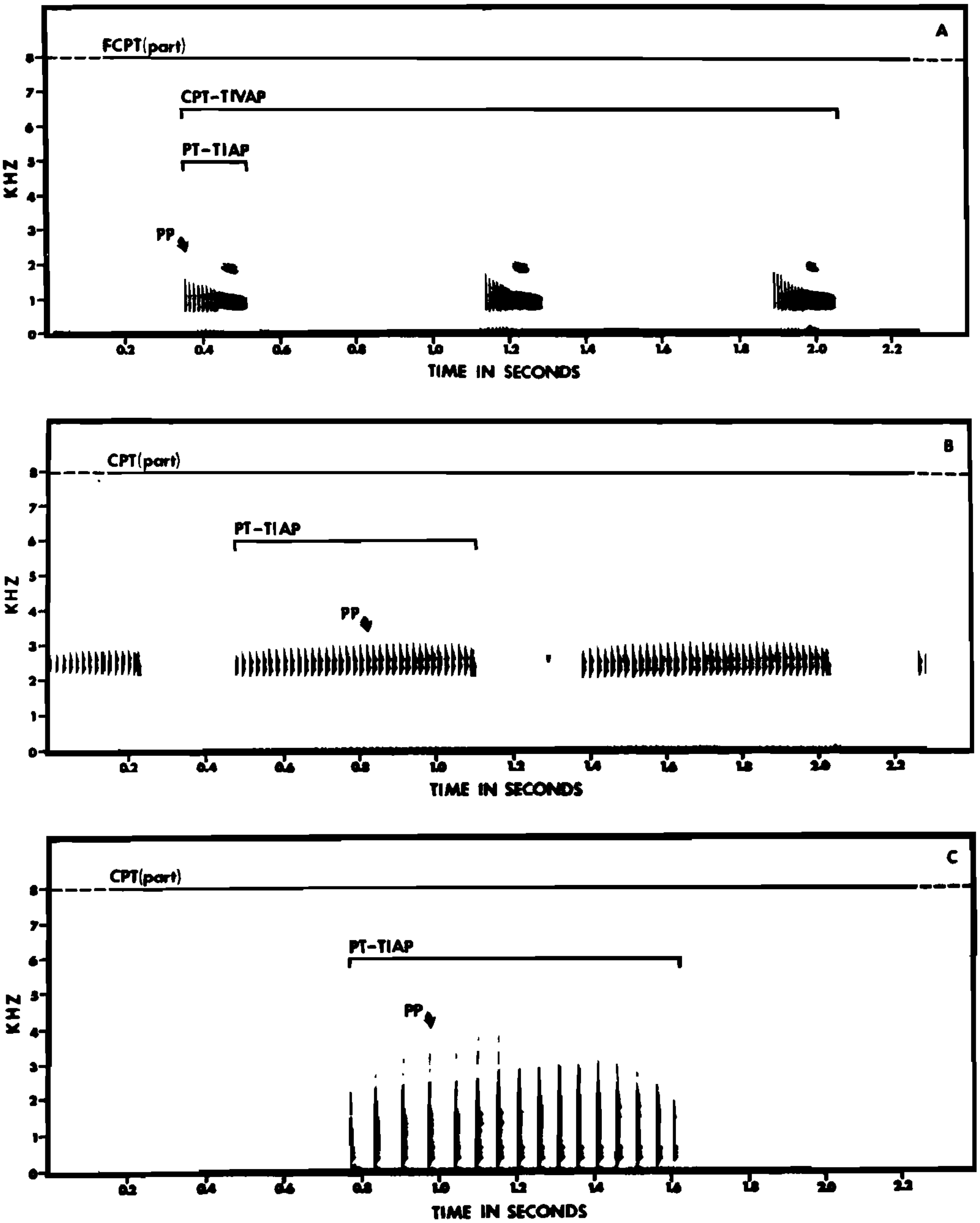
FIGURE 1

Sound spectrograms of parts of the mating calls of three species of *Bufo* which Martin (1972) would term Type I on the basis of their containing passive pulsation and Type I active pulsation but lacking Type II active pulsation. The physical complexity of each structure is labelled; actively produced components are followed by the type of active pulsatile mechanism responsible for their structure. Solid lines above structures represent durations. Dashed continuations of such lines at margins indicate that only part of the structure is shown. See Appendix for abbreviations. (A) *B. bufo*, near Bebenhausen, Germany, by H. Schneider, 29 March 1965, 22h30–23h00. Air temperature 2°C, water temperture 5°C. (B) *B. lughensis* TNHC 37529, snout-urostyle length 31,9 mm; Hoddur, Somalia, by M. and J. Tandy, 24 October 1970, 22h52. Air temperature 21,9°C, water and toad temperature 23,5°C, relative humidity 95%. (C) *B. gutturalis* TNHC 37847, snout-urostyle length 67,4 mm; 1,6 km NW Makindu, Kenya, by M. and J. Tandy, 7 November 1970, 21h00. Air temperature 20,8°C, toad temperature 19,3°C, relative humidity 83%. Effective filter band width 300 Hz. Band widths of most sonagrams illustrated in Tandy & Keith (1972) are at 300 Hz rather than 50 Hz as they were mislabelled. Those labelled 300 Hz in that article were at 50 Hz.


A
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PT-TIAP
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TIME IN SECONDS
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TIME IN SECONDS
C
CPT(part)
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TIME IN SECONDS

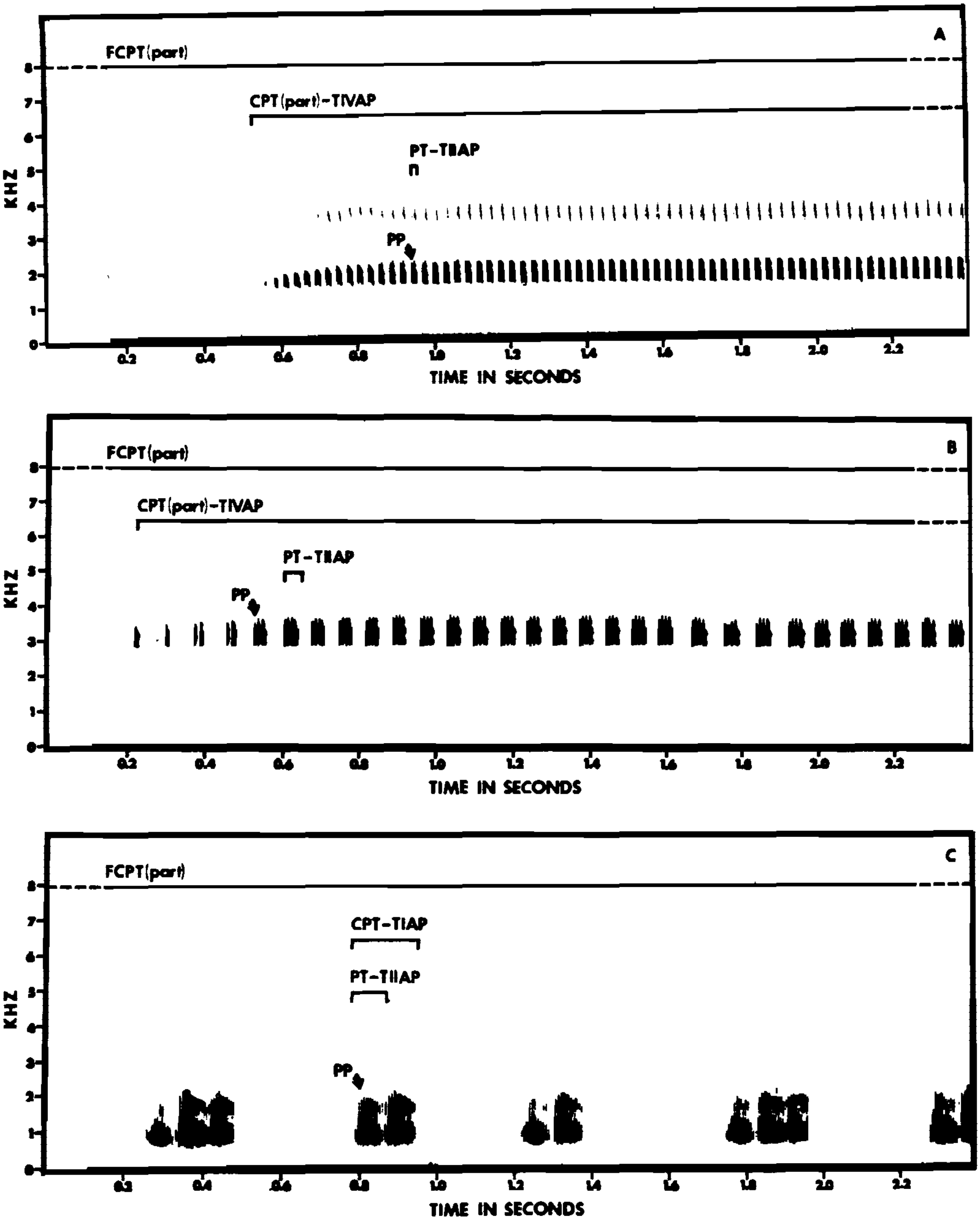
between different species. Martin (1967, 1971) demonstrated that there are two types of pulses with different physiological bases. One is produced passively by the arytenoid valves of the larynx acting as relaxation oscillators during flow of air from the lungs to the vocal sac. Each oscillation produces a high rise-time pulse which is referred to here as a passive pulse (Figures 1 & 2). Another type of pulsation may be produced actively by quasi-periodic contraction of the thoracic musculature, permitting reversal of direction of air flow between the lungs and the vocal sac. Such pulsation may give rise to low rise-time pulses repeated quasi-periodically to form simple pulse trains; it may also repeat simple pulse trains to form complex pulse trains as in the call of *Bufo viridis* (Schneider 1966; Martin 1972; Lörcher & Schneider 1973) (Figure 3). Such active mechanisms may also produce simple pulse trains of passive pulses (but not the pulses themselves) and complex pulse trains as in most species of the *Bufo regularis* complex (Figures 1 & 2). In the systematic sense we use 'complex' to refer to a group of species that are known to be related, such as the *Bufo regularis* complex which are all African and have a diploid chromosome number of 20, but which may not be a single species group as defined by reproductive compatibility by Blair (1972a). Active pulsation is also the basis for first-order sequencing of complex pulse trains in species such as *B. gracilipes* (Figure 2C), *B. perreti*, *B. mauritanicus* and *B. speciosus* and of second-order sequencing of first-order sequences in *B. canaliferus* and *B. marmoreus*. Thus, pulses are of either passive or active physiological origin. More complex temporal structures are of active origin.

Because temporal structures of the same physical grade of complexity may not be homologous between different species whereas structures of different grades of complexity may be homologous, calls of different species are here compared phylogenetically. Thus temporal components thought to be homologous are compared rather than those which may be of similar physical complexity. The physical complexities of entire calls are indicated in the Appendix. The complexity of each acoustic structure resulting from each pulsation of the different homologous pulsatile mechanisms is also indicated. See also Figures 1–3.

There is spectral variation of mating calls among *Bufo* species. In all species so far investigated, a carrier frequency is generated by air passing over the anterior membranes of the larynx (Martin 1967, 1971, 1972; Martin & Gans 1973). Because this study is based on apparently primitive versus derived but qualitatively different characteristics of mating calls, the carrier frequency will not be utilized because it varies only quantitatively among different species and apparently has the same physiological basis in all species. Variation in side-band harmonic structure will not be used because such variation results either from quantitative variation in

FIGURE 2

Sound spectrograms of parts of the mating calls of three *Bufo* species which Martin (1972) would designate Type II because they contain passive pulsation and Type II active pulsation. See Figure 1 and Appendix for explanation of labels. (A) *B. gemmifer*, 3,2 km N Las Cruces, Guerrero, Mexico, 6 July 1960, University of Texas library of anuran sounds, Station 374. Air temperature 26°C, water temperature 27°C. (B) *B. vertebralis* TNHC 38166, snout-urostyle length 24,9 mm; 4,0 km S Jamestown, Cape Province, South Africa, by M. and J. Tandy, 4 February 1971, 00h50. Air temperature 15,6°C, water temperature 17,3°C, relative humidity 86%. (C) *B. gracilipes* MT 5220, snout-urostyle length 26,9 mm; 9 km S Akonolinga, Cameroun, by M. and J. Tandy, 9 April 1971, 11h15. Air temperature 30,6°C, water temperature 21,0°C, relative humidity 70%. Effective filter band width 300 Hz.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TIME IN SECONDS
B
FCPT(part)
CPT(part)-TIVAP
PT-TIIAP
PP
KHZ
TIME IN SECONDS
C
FCPT(part)
CPT-TIAP
PT-TIIAP
PP
KHZ
TIME IN SECONDS

pulse repetition rates, in which case qualitatively different derived states of the characteristic are not represented, or from side-band emphasis related to pulse wave-form, which is already represented in this study by comparisons of passive and active pulses.

HOMOLOGIES OF TEMPORAL STRUCTURES OF *BUFO* MATING CALLS

Passive pulses can usually be recognized by their characteristic high rise-time wave-form in oscilloscopic display. This structure is often evident in sonagrams. The physiological basis of the pulses is understood. Pulses of this type are thus homologous between different species and their presence or absence can usually be determined with little difficulty. They are considered primitive in *Bufo* (Martin 1972).

Similarly, there is seldom any problem in identifying actively produced pulses. They are considered derived by Martin (1972) and representing the loss of passive arytenoid valve pulsation in most species that produce active pulses. *Melanophryniscus stelzneri* emits such pulses, but these are considered primitive because there is no evidence that this species or its ancestors contained arytenoid valves in the larynx. Martin (1972) termed the calls of *Bufo* species with active pulses Type III.

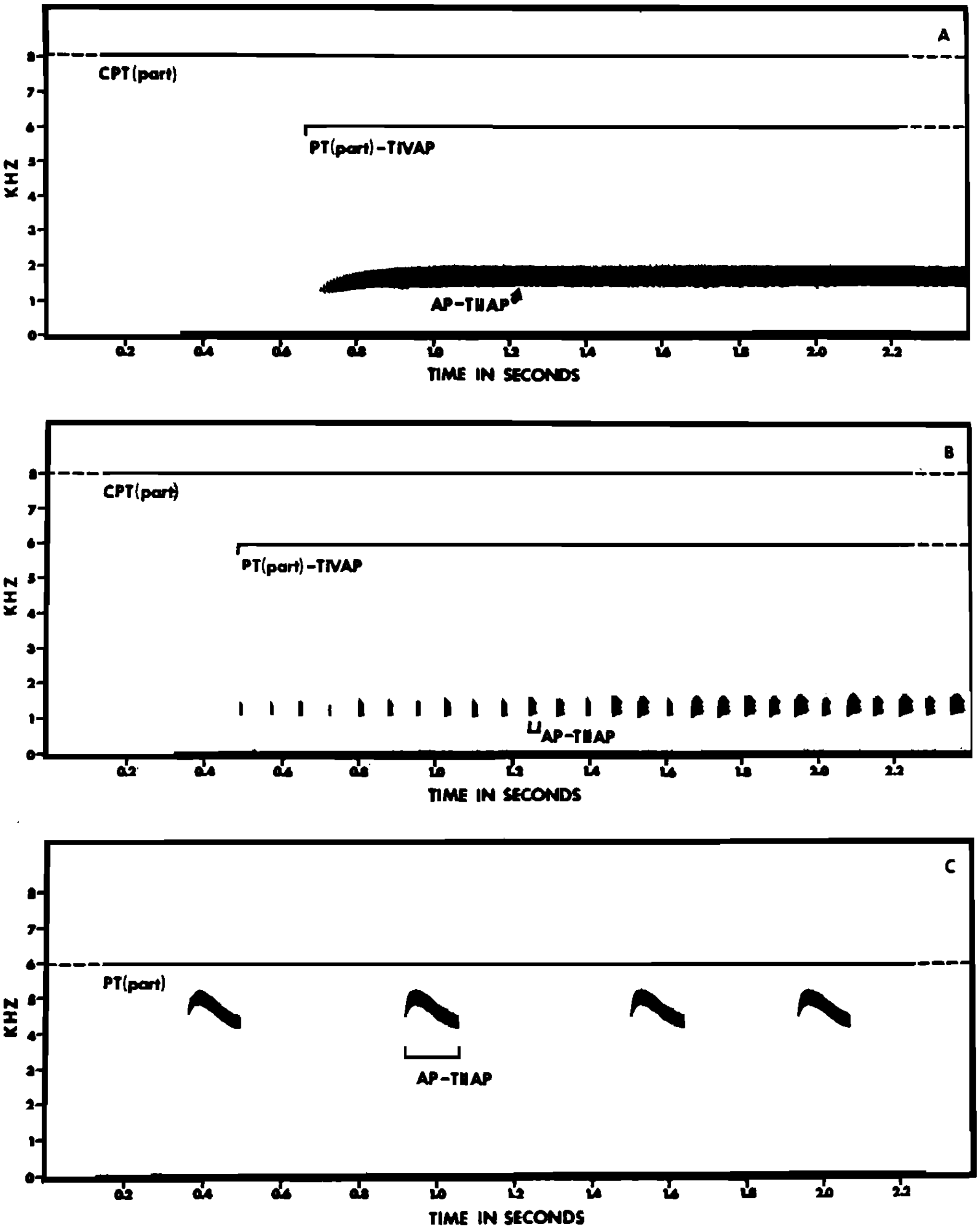
An exception is the mating call of *Schismaderma carens*. Apparently because of the very low carrier frequency of this species (250–500 Hz) and its pulse rate ($\bar{x}$ = 76 pulses/sec), the pulse wave-form is somewhat intermediate in appearance between those of typical passively and actively produced pulses. The larynx of *S. carens* has well-developed arytenoid valves (Martin, personal communication). It is assumed for purposes of this study that the pulses of the *S. carens* mating call are passive pulses.

As previously noted, the arytenoid valves of the larynx are responsible for passive pulses. In some species that lack passive pulses in their calls, arytenoid valves are present but do not oscillate during production of the mating call. In other species lacking passive pulses, arytenoid valves are reduced or absent (Martin 1972). Thus the presence or absence of arytenoid valves provides further evidence of acoustical evolution between species which may be similar or different in the pulse structure of their mating calls. These structures are considered, like passive pulses, to be primitive in this genus.

Determination of homologies of actively produced call structures other than active pulses is complicated by the existence of at least three different active pulsatile mechanisms. These mechanisms are characterized by three grades of pulsatile rates: (1) Relatively fast rates usually ranging from 15 to 100 per second. Extremes include *B. quercicus* with a rate as low as 1,5/second

FIGURE 3

Sound spectrograms of parts of the mating calls of three *Bufo* species which Martin (1972) termed Type III because they contain Type II active pulsation but lack passive pulsation. See Figure 1 and Appendix for explanation of labels. (A) *B. woodhousei*, 11,5 km S Luling, Texas, USA, 9 April 1954, University of Texas library of anuran sounds, Station 45. Air temperature 20°C, water temperature 20,5°C. (B) *B. viridis*, near Tübingen, Germany, by H. Schneider, 14 May 1965, 19h35. Air temperature 17°C, water temperature 19°C. (C) *B. quercicus*, 16 km NW Waycross, Georgia, USA, by F. C. Johnson, 7 July 1959, University of Texas library of anuran sounds, Station 424. Air temperature 25°C, water temperature 26°C. Effective filter band width 300 Hz.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PT(part)-TIVAP
AP-TIIAP
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TIME IN SECONDS
B
CPT(part)
PT(part)-TIVAP
AP-TIIAP
KHZ
TIME IN SECONDS
C
PT(part)
AP-TIIAP
KHZ
TIME IN SECONDS

and *B. woodhousei* as high as 200/second. Most American species have rates greater than 50/second. African species are not known with rates above 20/second. In this paper this category will be referred to as Type II active pulsation (TIIAP) after Martin (1972). He considered this pulsation rate primitive in *Bufo*. (2) Slower rates usually ranging from 0,3 to 2 per second. Extremes include some individuals of *B. kerinyagae* at 0,23/second and some *B. steindachneri* at 3,5/second. We refer to this category as Type I active pulsation (TIAP) after Martin (1972). It is also considered primitive. (3) Very slow rates usually ranging from 0,76 to 18 per minute. An extreme is *B. speciosus* at about 60/minute. This type of quasi-periodic repetition was not recognized by Martin (1972). It is termed Type IV active pulsation (TIVAP) in this paper to avoid confusion with Martin's Type III call designation.

Most Eurasian and American species that exhibit TIIAP also have TIVAP. It is equivalent to 'call repetition rate' for *B. viridis* in Lörcher & Schneider (1973) and for *B. americanus* and *B. woodhousei* in Zweifel (1968). Only three species have been recorded with both TIAP and TIVAP – *B. bufo* of Eurasia, *B. crucifer* of Brazil and *B. gariepensis* of South Africa. Published verbal descriptions of calls of *B. angusticeps* by Rose (1962) and of *B. amatolica* by Wager (1965) indicate that this combination of mechanisms may be typical of the *B. angusticeps* group. Because TIVAP occurs primarily in species that are otherwise considered primitive, this character is regarded likewise.

The three mechanisms of active pulsation are known to be different both because several species have two of the pulsation types present in their mating calls (Appendix, Figures 1–3) and because different anatomical bases for the acoustic structure have been demonstrated experimentally for some species (Martin 1967, 1972; Martin & Gans 1973). Tandy & Keith (1972) noted difficulties in determining homologies of active pulsatile structures between distantly related species, especially when only one active pulsatile rate was evident in the call of a given species and when the rate was in the overlap zone of the grades of TIIAP and TIAP. Information on additional species has somewhat alleviated these difficulties. In this study, four types of evidence have been used, when available, to assign active pulsatile components to one of the three mechanisms described above: (1) Experimental physiological demonstration of the anatomical basis of the acoustic structure. This is the work of Martin (1967, 1972) and Martin & Gans (1973). Many African species have not been studied in this way. (2) The rate grade of the pulsation. (3) The presence of two rate grades in a single species. (4) Comparison with closely related species and the presence of more than one rate grade within a species group or species complex.

Two other characters not parts of mating calls or their production mechanisms are used to compare similarities between species and species groups. One is presence or absence of a tympanum. This structure is part of the acoustic communication system and its presence is considered primitive. The diploid chromosome number is also utilized. This is either 20 or 22 in *Bufo* (Bogart 1968, 1972) and 22 is considered primitive.

DISTRIBUTION OF HOMOLOGOUS CALL STRUCTURES AMONG SPECIES GROUPS AND CONTINENTS

Twenty-five primarily African species of *Bufo*, representing eight species groups (one 20-chromosome complex and four probably 22-chromosome groups or complexes) plus *Schisma-*

derma carens, *Nectophrynoides tornieri* and *N. occidentalis* have calls which Martin (1972) would term Type I (Appendix). All exhibit passive pulsation. Except for the call of *B. gariepensis*, the only active pulsatile component present in these calls is TIAP. *B. bufo* occurs in north-west Africa, and its call is similar in basic structure to that of *B. gariepensis*. But *B. bufo* is primarily Eurasian in distribution, and biochemical evidence (Low 1972) indicates that *B. bufo* is not very closely related to *B. gariepensis*. Perhaps the acoustical similarity is a result of convergence. The Type I call is known in only four species of *Bufo* that occur outside Africa – *B. bufo* and *B. calamita* of Eurasia, and *B. crucifer* and *B. blombergi* of South America. The South American leptodactylid species *Odontophrynus americanus* also has this call type. This species is thought to be phylogenetically close to that group of leptodactylids which Blair (1972a, b) and others have suggested gave rise to the genus *Bufo*.

Four African *Bufo* species have calls which Martin (1972) would term Type II. The call of one of these, *B. vertebralis*, contains TIIAP and TIVAP. The calls of the other three species – *B. gracilipes*, *B. perreti*, and *B. mauritanicus* – contain TIIAP and TIAP.

B. viridis, another primarily Eurasian species, occurs in northern Africa. It has a Type IIIa call, which lacks passive pulsation, but the larynx of the species contains arytenoid valves which do not oscillate during production of the mating call (Martin 1972).

Two of the species complexes, including African species mentioned above, contain some species with one call type and other species with a second call type. The 20-chromosome *B. regularis* complex contains at least 20 species having Type I calls and also *B. perreti* which has Type II. The probably 22-chromosome *B. vertebralis* complex includes *B. lughensis* and *B. parkeri* with Type I calls and *B. vertebralis* with Type II.

Only three African species groups are strictly temperate in distribution – the *B. angusticeps* complex and the *B. pardalis* group in the south and the *B. mauritanicus* group in the north. The mating call of *B. pardalis* has not been recorded. Two other primarily tropical or subtropical groups have one species that is primarily temperate in distribution. These are *B. vertebralis* of the *B. vertebralis* complex and *B. rangeri* of the *B. regularis* group.

Call Types I, II and IIIa are represented in the acoustically poorly known *Bufo* of Eurasia. *B. bufo*, *B. calamita* and *B. viridis* were described above. *B. melanostictus* and *B. stomaticus*, representing different species groups, have Type II calls. These Type II calls contain TIIAP and TIVAP. From Inger's (1972) morphological study, one might predict that the Type II call is characteristic of the largest number of species of Asian *Bufo*.

Temperate North America contains seven species belonging to three species groups with Type II calls. All of these Type II calls contain TIIAP and TIVAP. One species, *B. alvarius*, has a Type IIIa call. Eight species belonging to three groups have Type IIIb calls. Each temperate North American species group is characterized by a single call type.

Tropical and subtropical North America have seven species with Type II calls belonging to four species groups. These calls contain TIIAP and TIVAP. The calls of *B. canaliferus* and *B. marmoreus* appear to contain two types of active pulsation in the TIIAP rate grade. Five species, belonging to two groups have Type IIIa calls. The *Bufo valliceps* group contains species with either Type II or Type IIIa calls. The other groups are characterized by single call types.

Eight South American *Bufo* species belonging to five species groups have Type II calls containing both TIIAP and TIVAP. This call type is also found in *Odontophrynus occidentalis*.

Two of the above *Bufo* species – *B. blombergi* and *B. crucifer* sometimes produce passive pulse trains by the TIAP mechanism. One species, *B. haematiticus*, has a Type III call which is apparently of different derivation than the Type III North American species listed above. *Melanophryniscus stelzneri* also has a call resembling Type III but of primitive origin according to Martin (1972).

The geographic distribution of the three call types in bufonids indicates large radiations of one or two call types in Africa, North America and South America. The same may be true of Eurasia (Table 1).

EVOLUTIONARY IMPLICATIONS OF THE ZOOGEOGRAPHIC PATTERNS

Blair (1972a, b) and others postulated an origin of *Bufo* in South America based partially on the common occurrence of the Type II call in the genus and its occurrence in other South American bufonids. They postulated successive migrations from the Americas to the Old World to account for the bufonid fauna of that region including the diverse African radiations as they were known at that time. They made strong cases for the relationship between *Bufo* and other South American genera and for proposed migrations of *B. marmoreus*-like ancestors leading to the *B. stomaticus* group, *B. valliceps*-like progenitors of the *B. melanostictus* group and *B. spinulosus-boreas*-like ancestors of the *B. viridis* line. Tandy & Keith (1972) noted the weaknesses of these arguments in explaining the African fauna. These include the presence of several bufonid radiations in Africa which appear to be too ancient to agree with Blair's proposed original Miocene migration and the absence of close relatives of African bufonids in tropical Eurasia.

The data presented in this paper indicate that there has been considerable endemism in major continental climatic zones during bufonid evolution. Continental faunas show closest similarities to adjacent faunas that have been ecologically accessible during geological time. There is little similarity between the bufonid fauna of Africa and that of Eurasia. A doubtful exception is the acoustic and morphological resemblance between the *Bufo angusticeps* complex and the *B. bufo* and *B. calamita* groups. The Sahara region seems to have acted as an effective barrier to tropical groups either as a desert in periods of relatively warm climates at northern latitudes or as a temperate zone during northern glacial periods. Inger's (1972) morphological data indicated similarities between *B. stomaticus*, *B. mauritanicus* and *B. pentoni*. These are warm temperate or tropical species. Blair (1972a, b) and others found similarities between *B. mauritanicus* and the *B. regularis* complex. It is conceivable that *B. stomaticus*, *B. mauritanicus* and *B. pentoni* form a line *via B. pardalis* to the *B. regularis* complex. But there are even greater biochemical similarities between *B. mauritanicus* and *B. blombergi* (Low 1972). No close relationships are evident between other species groups of African *Bufo* and extraterritorial forms. Neither are such relationships apparent for other African bufonid genera. The greatest similarities between African bufonids and those of other continents are with tropical American species. This is suggested by the call data presented here, in that tropical and subtropical Africa and tropical and subtropical South America are the only regions known to have *Bufo* species with both Type I and Type II calls and also other bufonids with these call types. Blair (1972a)

TABLE 1

Numbers of bufonid species exhibiting various call types and homologous characters in different geographic regions. N = total number of species evaluated for at least one character in each region. Data were not available for all characters for every species. Abbreviations as in Appendix.

Region	*N*	*Call Type*				*no*	*Homologous call characters*					*Tympanum*		*2N Number*	
		TI	*TII*	*TIII*	*TIIIb*	*mc*	*PP*	*AV*	*TIIAP*	*TIAP*	*TIVAP*	+	—	22	20 or 40
1. Tropical and subtropical Africa	58	26	2	0	0	10	29	31	2	29	0	38	21	9	15
2. Temperate Africa	10	2	2	0	0	1	3	4	2	2	2	8	1	4	1
3. Temperate Eurasia	3	2	0	1	0	0	2	3	1	2	2	3	0	3	0
4. Tropical and subtropical Eurasia	4	0	2	0	0	0	2	3	2	0	2	4	0*	2	0
5. Temperate North America	17	0	7	1	8	1?	7	9	16	0	15	17	0	17	0
6. Tropical and subtropical North America	14	0	7	5	0	2	7	13	12	0	12	12	2	8	0
7. Tropical and subtropical South America	13	3	9	0	0	0	10	14	11	2	8	12	1	15	0
8. Temperate South America	4	0	0	0	0	4	0	4	0	0	0	3	1	4	0
TOTALS	123	33	29	7	8	18	60	81	46	35	41	97	26	62	16

and Low (1972) also found greater similarities in genetic compatibility during hybridization experiments and composition of parotoid gland secretions respectively between African and American *Bufo* than between African *Bufo* and Eurasian species.

Present evidence indicates radiations of *Bufo* and other bufonids in Africa equal to those in South America. In Africa, the Type I call is most common in *Bufo* (both 20- and 22-chromosome species) and is known in *Schismaderma* and *Nectophrynoides*. In South America the Type II call is predominant. These and other data suggest long isolation between the faunas of the two areas, in spite of their similarities.

An explanation which could account for the large and diverse radiations of bufonids in Africa and South America and the presence of call Types I and II in the radiations of both continents is that bufonid progenitors evolved prior to the continental separation of Africa and South America. This is in accord with the ideas of Savage (1973) which suggest the presence of such bufonid ancestors in Gondwanaland during the Cretaceous.

ACKOWLEDGEMENTS

We express our gratitude to Dr W. F. Blair for providing funds *via* NSF Grant 5406X which supported much of the field work.

The following were most generous in making available their recordings of voices of African *Bufo*:

J.-L. Amiet, Université Fédérale du Cameroun;
A. Duff-MacKay, National Museum, Nairobi;
R. Keith, American Museum of Natural History;
M. Largen, Haili Selassi I University, Addis Ababa;
H. Schneider, Zoologisches Institut der Universität Bonn;
R. Siboulet, Universite d'Alger;
University of Texas Library of Anuran Sounds;
A. G. C. Grandison, British Museum (Natural History).

We are grateful to the following for providing preserved or living material:

J.-L. Amiet; American Museum of Natural History; Academy of Natural Sciences, Philadelphia; Umtali Museum; Museo Civico di Storia Naturale, Milano & Genova; Museo Nacional de Historia Natural, Madrid; Zoological Museum of Academy of Sciences U.S.S.R., Leningrad; Museum of Natural History, Univ. Kansas; A. Duff-MacKay; Univ. Michigan; A. G. C. Grandison; Muséum national d'Histoire naturelle, Paris; Transvaal Museum, Pretoria; H. Heusser; Rijksmuseum van Natuurlijke Historie, Leiden; H. Hoogstraal; Labo Allgem. Dierkunde, Antwerpen; Field Museum of Natural History, Chicago; Albany Museum, Grahamstown; Laboratoire Arago, Banyuls-sur-Mer; Ecole Normale Supérieure, Paris; California Academy of Sciences, San Francisco; McGregor Museum, Kimberley; Texas Memorial Museum, Univ. Texas; Carnegie Museum, Pittsburgh; Natur-Museum und Forschungs Institut Senckenberg, Frankfurt; Muséum d'Histoire Naturelle, Genève; Zoologisches Museum, Berlin; Smithsonian Institution; Naturhistorisches Museum, Basel; Museo Bocage, Lisboa; Instituto de Zoologia, Univ. Genova; R. Siboulet; Museum of Vertebrate Zoology, Berkeley & Ann Arbor; P. van den Elzen; Staatssammlung Museum für Naturkunde, Ludwigsburg; Museum of Comparative Zoology, Harvard; Institut Royal des Sciences Naturelles de Belgique; Los Angeles County Museum.

J. P. Bogart kindly provided unpublished data on the diploid chromosome numbers of various species.

W. F. Blair and J. P. Bogart read an earlier draft of the manuscript and offered helpful suggestions.

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APPENDIX

A list of mating call types, their physical complexity and homologous characters among species and species groups of bufonids. Martin call types refer to Types I, II, IIIa or IIIb as defined by Martin (1972). A dash in the first column indicates that the species probably has no mating call. Physical complexities of entire calls may be PT = pulse train, CPT = complex pulse train, FCPT = first-order sequence of complex pulse trains and SFCPT = second-order sequence of first-order sequences of complex pulse trains. Homologous call characters are: PP = passive pulsation, AV = arytenoid valves, TIIAP = Type II active pulsation, TIAP = Type I active pulsation, TIVAP = Type IV active pulsation. For these five characters and for tympanum, + indicates presence and — absence. (+) indicates that arytenoid valves are present but reduced. For TIIAP, TIAP and TIVAP, the physical complexity of each acoustical structure produced by a single pulsation of the mechanism is indicated in brackets after each +. Diploid number refers to the somatic chromosome number. Further explanation is in the text. Almost all African bufonid species currently recognized are listed. For Eurasia, North America and South America, only the species treated by Martin (1972) are listed. The lists for Eurasia and South America do not include many currently recognized species. The North American list is relatively complete. The placement of African species in groups or complexes follows Tandy & Tandy (in press). Placement of Eurasian species follows Inger (1972) except for *B. calamita* and *B. viridis* in which case Blair (1972*a*, *b*) is accepted. Species groups of North America and South America follow Blair (1972). Acoustic data are based on Schiøtz (1964), Schneider (1966), Keith (1968), Tandy & Keith (1972), Martin (1972), Lörcher & Schneider (1973) and unpublished data of J.-L. Amiet, A. Duff-MacKay, A. G. C. Grandison, R. Keith, M. Largen, R. Siboulet and M. Tandy. Information on diploid chromosome numbers is from Bogart (1968, 1972, and unpublished data). Asterisks indicate species which occur in Africa but are primarily Eurasian in distribution.

CONTINENT Species complex or non-*Bufo* genus Species group Species	*Martin call type*	*Physical complexity of entire call*	*Homologous call characters*					*Tympanum*	*Diploid number*
			PP	*AV*	*TIIAP*	*TIAP*	*TIVAP*		
AFRICA									
Bufo taitanus complex									
B. taitanus	—	—	—		—	—	—	—	
B. anotis	—	—	—	+	—	—	—	—	22
B. loennbergi	—	—	—?	+	—	—?	—	—	22
B. beiranus								—	
B. hoeschi								—	
B. chappuisi ?								—	
B. melanopleura								—	
B. osgoodi complex									
B. osgoodi	?	?	?	?	?	?	?	—	
B. angusticeps complex									
B. angusticeps group									
B. angusticeps								+	
B. gariepensis	I	FCPT	+	+	—	+ (PT)	+ (CPT)	+	22
B. amatolica								+	
B. tradouwi								+	
B. inyangae								+	22
B. rosei group									
B. rosei	—	—	—	+	—	—	—	—	22
B. vertebralis complex									
B. vertebralis	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	
B. dombensis								+	
B. fenoulheti								+	22
B. lughensis	I	CPT	+	+	—	+ (PT)	—	+	
B. parkeri	I	CPT	+	+	—	+ (PT)	—	+	
B. gracilipes group									
B. gracilipes	II	FCPT	+	+	+ (PT)	+ (CPT)	—	+	22
B. urunguensis								+	
B. regularis complex									
B. regularis group									
B. regularis	I	CPT	+	+	—	+ (PT)	—	+	20
B. garmani	I	CPT	+	+	—	+ (PT)	—	+	20
B. latifrons	I	CPT	+	+	—	+ (PT)	—	+	

CONTINENT Species complex or non-*Bufo* genus Species group Species	*Martin call type*	*Physical complexity of entire call*	*Homologous call characters*					*Tympanum*	*Diploid number*
			PP	*AV*	*TIIAP*	*TIAP*	*TIVAP*		
B. brauni	I	CPT	+	+	—	+ (PT)	—	+	20
B. gutturalis	I	CPT	+	+	—	+ (PT)	—	+	20
B. kisoloensis	I	CPT	+	+	—	+ (PT)	—	+	
B. poweri	I	CPT	+	+	—	+ (PT)	—	+	20
B. rangeri	I	CPT	+	+	—	+ (PT)	—	+	20
B. camerunensis	I	CPT	+	+	—	+ (PT)	—	+	20
B. kerinyagae	I	CPT	+	+	—	+ (PT)	—	+	20
B. sp. C	I	CPT	+	+	—	+ (PT)	—	+	20
B. sp. D	I	CPT	+	+	—	+ (PT)	—	+	40 (4x)
B. sp. F	I	CPT	+	+	—	+ (PT)	—	+	20
B. maculatus group									
B. maculatus	I	CPT	+	+	—	+ (PT)	—	+	20
B. blanfordi group									
B. blanfordi	I	CPT	+	+	—	+ (PT)	—	+	20
B. perreti group									
B. perreti	II	FCPT	+	+	+ (PT)	+ (CPT)	—	+	20
B. funereus group									
B. funereus								+	
B. steindachneri	I	CPT	+	+	—	+ (PT)	—	+	20
B. vittatus	I	CPT	+	+	—	+ (PT)	—	+	
B. fuliginatus								+	
B. villiersi	I	CPT	+	+	—	+ (PT)	—	+	
Group uncertain									
B. superciliaris								+	20
B. lemairi								+	
B. sp. A	I	CPT	+	+	—	+ (PT)	—	+	
B. sp. B								+	
B. sp. E	I	CPT	+	+	—	+ (PT)	—	+	
B. pardalis group									
B. pardalis								+	22
B. mauritanicus group									
B. mauritanicus	II	FCPT	+	+	+ (PT)	+ (CPT)	—	+	22
B. pentoni group									
B. pentoni	I	CPT	+	+	—	+ (PT)	—	+	
B. tuberosus group									
B. tuberosus	I	CPT	+	+	—	+ (PT)	—	+	
Schismaderma									
S. carens	I?	CPT	+?	+	—	+ (PT)	—	+	22

Werneria									
W. preussi	—	—	—		—	—	—	—	22
W. bambutensis	—	—	—		—	—	—	—	
W. mertensi	—	—	—		—	—	—	—	
W. tandyi	—	—	—		—	—	—	—	
Mertensophryne									
M. micranotis								—	
M. schmidti								—	
Didynamipus									
D. sjoestedti								—	
Wolterstorffina									
W. parvipalmata	—	—	—		—	—	—	—	
W. mirei	—	—	—		—	—	—	—	
Laurentophryne									
L. parkeri								—	
Nectophryne									
N. afra	—	—	—		—	—	—	—	22
N. batesi								—	
Nectophrynoides									
N. tornieri	I	CPT	+	+	—	+ (PP or PT)	—	+	22
N. viviparus								+	
N. occidentalis	I	CPT	+	+	—	+ (PT)	—	—	
N. cryptus								—	
N. minutus								+	
TEMPERATE EURASIA									
B. bufo group									
*B. bufo**	I	FCPT	+	+	—	+ (PT)	+ (CPT)	+	22
B. calamita group									
B. calamita	I?	CPT?	+	+	—	+ (PT?)	—	+	22
B. viridis group									
*B. viridis**	IIIa	CPT	—	+	+ (AP)	—	+ (CPT)	+	22
TROPICAL AND SUBTROPICAL EURASIA									
B. orientalis group									
*B. dodsoni**								+	

CONTINENT Species complex or non-*Bufo* genus Species group Species	Martin call type	*Physical complexity of entire call*	*Homologous call characters*					Tympanum	Diploid number
			PP	*AV*	*TIIAP*	*TIAP*	*TIVAP*		
B. stomaticus group									
B. stomaticus	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. melanostictus group									
B. melanostictus	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. asper group									
B. asper				+				+	?
TEMPERATE NORTH AMERICA									
B. boreas group									
B. boreas	—?			+				+	22
B. canorus	II	FCPT	+	—	+ (PT)	—	+ (CPT)	+	22
B. alvarius group									
B. alvarius	IIIa	CPT	—	+	+ (AP)	—	+ (PT)	+	22
B. punctatus group									
B. punctatus	IIIb	CPT	—	—	+ (AP)	—	+ (PT)	+	22
B. americanus group									
B. americanus	IIIb	CPT	—	—	+ (AP)	—	+ (PT)	+	22
B. houstonensis	IIIb	CPT	—	—	+ (AP)	—	+ (PT)	+	22
B. terrestris	IIIb	CPT	—	—	+ (AP)	—	+ (PT)	+	22
B. hemiophrys	IIIb	CPT	—	—	+ (AP)	—	+ (PT)	+	22
B. microscaphus	IIIb	CPT	—	—	+ (AP)	—	+ (PT)	+	22
B. woodhousei	IIIb	CPT	—	—	+ (AP)	—	+ (PT)	+	22
B. quercicus group									
B. quercicus	IIIb	PT	—	—	+ (AP)	—	—	+	22
B. cognatus group									
B. cognatus	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. compactilis	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. speciosus	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. debilis group									
B. debilis	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. kelloggi	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. retiformis	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
TROPICAL AND SUBTROPICAL NORTH AMERICA									
B. valliceps group									
B. valliceps	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22

B. mazatlanensis	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	?
B. gemmifer	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	?
B. luetkeni	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. cavifrons	IIIa	CPT	—	+	+ (AP)	—	+ (PT)	+	?
B. coniferus	IIIa	CPT	—	+	+ (AP)	—	+ (PT)	+	22
B. ibarrai	IIIa	CPT	—	(+)	+ (AP)	—	+ (PT)	+	?
B. coccifer group									
B. coccifer	IIIa	CPT	—	(+)	+ (AP)	—	+ (PT)	+	22
B. cycladen	IIIa ?	CPT	—		+ (AP)	—	+ (PT)	+	?
B. canaliferus group									
B. canaliferus	II	SFCPT	+	+	+ (PT & CPT ?)	—	+ (FCPT)	+	22
B. occidentalis group									
B. occidentalis	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. marmoreus group									
B. marmoreus	II	SFCPT	+	+	+ (PT & CPT ?)	—	+ (FCPT)	+	22
B. bocourti group									
B. bocourti	—	—	—	+	—	—	—	—	22
B. periglenes group									
B. periglenes	—	—	—	+	—	—	—	—	?
TROPICAL AND SUBTROPICAL SOUTH AMERICA									
B. crucifer group									
B. crucifer	I & II	CPT or FCPT	+	+	+ (PT)	+ (PT)	+ (CPT)	+	22
B. marinus group									
B. marinus	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. arenarum	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. paracnemis	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. ictericus	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
B. guttatus group									
B. blombergi	I & II	FCPT	+	+	+ (PT)	+ (PT or CPT)	—	+	22
B. haematiticus	'III'	CPT	—	(+)	+ (AP)		+ (PT)	+	22
B. typhonius group									
B. typhonius								+	22
B. sternosignatus	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	?
B. granulosus group									
B. granulosus	II	FCPT	+	+	+ (PT)	—	+ (CPT)	+	22
TEMPERATE SOUTH AMERICA									
B. spinulosus group									
B. spinulosus	—	—	—	+	—	—	—	+	22
B. atacamensis	—	—	—	+	—	—	—	+	22

CONTINENT Species complex or non-*Bufo* genus Species group Species	*Martin call type*	*Physical complexity of entire call*	*Homologous call characters*					*Tympanum*	*Diploid number*
			PP	*AV*	*TIIAP*	*TIAP*	*TIVAP*		
B. chilensis	—	—	—	+	—	—	—	+	22
B. variegatus	—	—	—	+	—	—	—	+	22
TROPICAL OR SUBTROPICAL SOUTH AMERICA									
Atelopus ignescens				+					22
A. varius				+					22
Odontophrynus occidentalis	II	FCPT?	+	+	+ (PT)	?	+ (CPT)	+	22
O. americanus	I	CPT	+	+	—	+ (PT)	—	+	44 (4x)
O. americanus ?	I	CPT	+	+	—	+ (PT)	—	+	22
Melanophryniscus stelzneri	"III"	CPT	—	—	+ (AP)	—	+ (CPT)	—	22