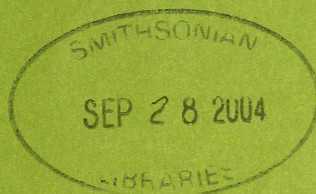# AMPHIBIAN DIVERSITY IN BOLIVIA:
A STUDY WITH SPECIAL REFERENCE
TO MONTANE FOREST REGIONS

by

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INTRODUCTION

Biodiversity

Life and its extraordinary diversity is the unique wealth which distinguishes the earth from all other planets. Biological diversity in all its aspects represents the foundation of human existence and mankind is a critical element of this diversity. We have just become aware of the real dimension of the earth's diversity in recent years and at the same time it is increasingly evident that due to the rapid growth of the world's human population, this diversity is undergoing a dramatic change.

The growing recognition and knowledge of the importance of biodiversity has become part of the public awareness of the dual role of biodiversity: as an economic resource, and as an essential condition for the survival of individuals and biotic communities. It is becoming evident that the loss of biodiversity has serious ecological and economical consequences. As a result, biodiversity is now seen as a critical component of global environmental change.

Biodiversity is not equally distributed on the earth's surface. The most diverse ecosystems are found in tropical countries and certain subtropical areas while the industrialized countries harbor comparatively low biological diversity. This enormous contrast between megadeveloped countries and megadiversity countries reinforces us to devote greater intention to establish efficient projects in the fields of research, conservation, and development. One of the most significant international agreements about conservation, exploration, and sustained use of biodiversity is the Convention on Biological Diversity (CBD) of Rio de Janeiro, 1992. This convention regulates the use of biological resources through a fair and well-balanced procedure of benefit sharing and was signed by almost all nations of the world.

Terminology

Often the term biological diversity or biodiversity is confused with species diversity. Biodiversity is far more inclusive and describes diversity in all aspects of biology; that is the morphological, physiological, ethological, ecological, and genetic diversity in populations, species, or higher taxonomic categories.

Usually, biodiversity is defined considering three different hierarchic levels (e.g., Solbrig 1991, 1994): (1) ecosystem diversity is the result of the diversity of abiotic factors which are available as different combinations of potential resources. Living organisms are related to different kinds and combinations of resources to use them for their reproduction. There are unalterable interactions between these abiotic factors and living organisms. These interactions as well as all ecological processes are elements of ecosystem diversity; (2) species diversity is a substantial part of ecosystem diversity. Species diversity is the result of the evolutionary trend to develop an increasing diversity of combinations of genes on the one hand

and to 'freeze' this different combinations occasionally in distinct units, the species, on the other hand. These units are more or less limited in their ability to exchange genes with other units. Every unit (species) is characterized by the use of a particular combination of resources (ecological niche); (3) intraspecific diversity reflects the tendency of life to diversify. The spectrum of intraspecific diversity includes minimal differences in the genome to differences resulting in the development of races and subspecies. If these differences result in speciation processes, often depends on external (and mostly random) influences like e.g. geographical isolation.

Measuring diversity is discussed controversially. Many authors only consider species numbers (which are easy to determine) within a particular space as index for diversity. In addition, a variety of diversity indices has been developed, connecting species numbers with abundance (e.g., Pianka 1977, Spellerberg 1991). However, the combination of species numbers and abundance as only two qualities out of numerous others connected with species appears somewhat arbitrary to describe the complex patterns of biodiversity. At least, these indices do not answer the basic questions of biodiversity research: "Why are there so many organisms and how do they manage to coexist?" and "Why are there differences in numbers of coexisting species at different places?" For researchers investigating biogeography and biodiversity, species which are small, rare or less abundant may have the same importance than abundant larger species (see Brown 1988). Moreover, comparison and description of biodiversity will not become more exact because of indices, since not all species contributing to the diversity of a particular region or area are discovered and described.

However, this work mainly focuses on species diversity as a value for describing diversity patterns. It is used here in the sense of numbers of coexisting species in a certain space. An important concept differentiates species diversity into three categories (Cody 1986): alpha, beta, and gamma diversity. Alpha diversity equals the number of species existing at one place, beta diversity describes the species-turnover along an ecological gradient, and gamma diversity describes the rate of species substitutions within ecologically similar habitats which are separated by a certain geographical distance. Alpha diversity reflects the maximum density of species, wheras beta diversity gives a value for habitat specialization and ecological plasticity of species. Gamma diversity is strongly depending on the ability of taxa to evolve and their tendency to endemism.

Significance of Research on Species Diversity

Research on systematics and taxonomy, largely ignored in an era of genetics and biochemistry (e.g., Butler et al. 1998), is experiencing a comeback under the modern designation 'biodiversity research'. This answers to an urgent need, for a few years ago it became apparent that only a small percentage of the earth's diversity

in species is scientifically known. Since 1758 - the official beginning of scientific nomenclature - some 1.8 million species have been described. Today, the actual species number inhabiting the earth has been estimated to include anywhere from 10 to 100 million species (e.g., May 1992). At the same time, it becomes increasingly evident that the near future will bring species extinction on a scale such as it has occurred only a handful of times in the earth's history. In other words, innumerable species will become extinct before we will ever have had the opportunity to study and know them.

The species that remain hidden from scientific and general knowledge are by no means only inconspicuous insects or worms. Major groups of vertebrates are still unknown. For example, the recent discoveries of new bovid species in the forests of Vietnam (Dung et al. 1993, Peter & Feiler 1994) demonstrate the defectiveness of our knowledge in a spectacular way.

Bolivia – a megadiversity country

The term megadiversity country was first developed by Mittermeier (1988) in order to stress the importance of those few countries which harbor a major portion of the world's biological diversity. Of course, animal and plant species are not aware of geopolitical borders but the megadiversity approach acknowledges that conservation is managed at country level (Groombridge 1990). However, Bolivia is still neglected in recent publications concerning megadiversity countries. Moraes & Beck (1992) were the first to propose Bolivia to be included in the list. Bolivia is still one of the least investigated countries of South America and scientists unfamiliar with it tend to underestimate its diversity. This diversity is manifested at all levels, from its abiotic conditions, called 'geodiversity' by Barthlott et al. (1996), to the hierarchic biological systems which exist within its borders. The fact that Bolivia actually is a megadiversity country was stressed by several authors in a book edited by Barthlott & Winiger (1998) which resulted from a congress on biodiversity with main focus on Bolivia.

Ecosystem Diversity

The ecosystem constitutes an important hierarchic level of biological systems. Only few countries in the world can match Bolivia's ecosystem diversity (see Fig.4). There is probably no other tropical country which has access to as many biogeographical regions and biomes as Bolivia. In his scheme of tropical vegetation, Lauer (1986) classifies zonal vegetation according to hydrothermical units. Almost all of them, from desert to rainforest, from hot lowlands to glaciers, can be found in Bolivia. Furthermore, there is a complex differentiation between zonal and azonal ecosystems. For example, Ribera (1992) lists more than 40 different ecoregions for Bolivia.

Species Diversity

Species are a second important level of biological systems and although it is not possible to estimate species numbers for many groups of Bolivian organisms, Bolivia undoubtedly contains extraordinary high levels of species diversity. This high degree of species diversity is due to Bolivia's abiotic diversity in space and time. All the historical, geological, orographical and climatic processes are responsible for the richness at species level we can find today on Bolivian territory. All factors and mechanisms which stimulate and accelerate speciation or guarantee the maintenance of high species diversity, such as habitat heterogeneity, extinction-buffering long-term stability, isolation and local medium disturbances are active in Bolivia (Ibisch 1998). Moreover, its geographical location facilitates the immigration of very different biogeographical elements (see also discussion).

Genetic Resource Diversity

All organisms which are actual or potential providers of resources for human life are genetic resources. The diversity of Bolivia's genetic resources can be assumed to be tremendous. Genetic resources include stable foods and medicines, construction material and clothing. Bolivia has dozens of cultivated and wild plant species which are of enormous importance for global food security (Cárdenas 1989). As an example, one of the most important stable foods worldwide, the potato, originated in the high Andes of Bolivia and Peru. Currently, 38 species of potato with hundreds of local varieties are cultivated by local farmers. In the Departamento Santa Cruz alone, Vázquez & Coimbra (1996) identified 130 edible fruits of wild plants, at least ten of them with high export potential.

Ethno-Cultural Diversity

Beside these kinds of diversity, Bolivia is especially rich in ethno-cultural diversity which in a broader sense is also part of the biological diversity. Today, vast portions of the Andean region are occupied by Aymará and Quechua people. Ethnodiversity in the Bolivian lowlands is much greater, especially in humid areas which are biologically more diverse. About 30 different cultures that developed special adaptations to their different natural resources can still be found in the Bolivian lowlands (Libermann 1995).

Amphibians

Amphibians inhabit a variety of life zones. With the exception of oceans they can be found from deserts to the subpolar region, from sea level to snow line, every imaginable type of freshwater, from the ground up to the highest treetop. Amphibians seem to have once again reached a level of diversity comparable to their first "golden age", the Carboniferus and the Permian. Equipped with lungs

and limbs, they were the first vertebrates to leave the water in the Devonian some 350 to 360 million years ago to conquer the land masses previously uncolonized by vertebrates. During this process they developed an enormous diversity in forms and species, including representatives of several meters in length and with very little resemblance to present-day amphibians. The fossil evidence of Paleozoic amphibians ends with the Trirassic, but amphibians did not become entirely extinct. The first frog-like creature (*Triadobatrachus massinoti*) appeared in the Triassic in Madagascar, still sporting a short tail, but already displaying first signs of a saltatory mode of life. In the Jurassic, diverse recent frog families already existed such as tongueless frogs (Pipidae) and disk-tongued frogs (Discoglossidae). Salamanders and caecilians followed in the Cretaceous. From that time on, amphibians experienced a second golden age that lasts into the present days.

Species Diversity

Amphibians need freshwater. Thus, it comes as no surprise that the moist environment of the tropics is home to their greatest diversity. High temperatures and the constant access to water in form of precipitation create ideal conditions, and the number of amphibian species increases the nearer one gets to the equator. But actually the situation is far more complex and should not be seen just against the background of current climate conditions. Instead, past climate oscillations and orographic changes must also be considered, since they created environments that were hostile to amphibian survival or, on the other hand, caused the extinction of many species.

Today, more than 5100 extant amphibian species have been described (Glaw et al. 1998a) and the number increases at a yearly rate of approximately 70 to 100 newly discovered species (Glaw & Köhler 1998). The rate in discovering new amphibian species has never been as great as it is now. Since 1994, the number of known recent amphibians is greater than that of mammals and the biggest burst in new species descriptions is not yet reached (Glaw & Köhler 1998). With approximately 4500 valid species, frogs (Anura) are by far the most species-rich amphibian group, only one tenth (450 species) are salamanders (Urodela) and a mere 165 species count among caecilians (Gymnophiona).

By far, most of the new species described in the recent years originate from the Neotropical region (68%; Glaw & Köhler 1998, Glaw et al. 1998b). Of course, current species descriptions do not necessarily reflect the true status of existing species diversity, because different levels of research intensity have to be considered. Research may be more intensely focused on Latin America than on Africa and Asia. Nevertheless, current studies show that there is still no end to be seen in the discovery of new amphibians in tropical South America. Therefore it is probable that amphibian species diversity actually is concentrated in the Neotropics (Köhler et al. 1998a).
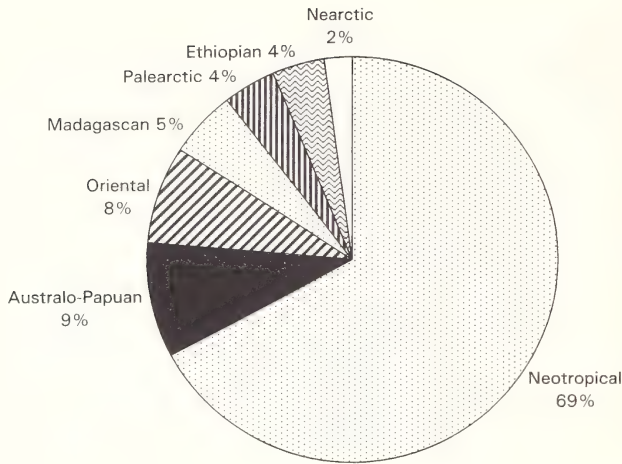
Fig.1: Percentages of amphibian species described from the beginning of 1986 to the end of 1995 in different biogeographical regions (after Glaw & Köhler 1998).

Despite the recognizable increase of investigation efforts during the last decades of this century, recent surveys indicate that actual species diversity in amphibians is still underestimated in nearly every tropical forest. Due to the use of modern techniques such as biochemical and genetic analysis as well as the almost obligatory analysis of species-specific advertisement calls in anurans, the real degree of species numbers becomes more and more evident (see also Hanken 1999). Still another important factor is the research in previously not or only poorly investigated areas. For example, Pethiyagoda & Manamendra-Arachchi (1998) suggested the actual number of frog species inhabiting Sri Lanka to be more than 250 instead of the 54 species recognized in the current literature. Similar cases can be found in other regions such as for example Madagascar (Glaw & Vences 1994, Glaw 1999), Vietnam (e.g., Inger et al. 1999), or Bolivia (De la Riva et al. 2000).

Natural History

Few vertebrates, with the exception of fishes, are as dependent on environmental moisture – usually in the form of precipitation – as amphibians. The geographic range, ecology, behavior, and natural history of amphibians is strongly influenced by the distribution and abundance of freshwater. As a result, the spontaneous and often synchronized breeding of several species of frogs with the first rainfalls is a well-known phenomenon, especially in areas where rainfall is strongly seasonal. On the other hand, the multitude of other ecological factors which interact to affect amphibian activity and life history is poorly understood (McDiarmid 1994a).

Amphibians may occur in terrestrial, aquatic, arboricol, or fossorial habitats, or in a combination of those. In most cases, only little is known about the species' nat-

ural history. Concerning the reproduction, a major part of the anuran species has external fertilization of the eggs and an aquatic development of tadpoles which represent a completely different life form. After a period of growth larvae undergo metamorphosis and move back to a terrestrial environment where they develop into mature adults. Others undergo direct development, that means, they lack an independent larval stage. The eggs hatch into nonfeeding larvae or small froglets. A few forms are ovoviviparous or viviparous combined with internal fertilization. However, within this generalized modes of reproduction several varieties in reproductive efforts evolved which can be interpreted as adaptations to different environmental conditions. These include different modes of parental care like for example attendance to egg clutches or juveniles, feeding of tadpoles, and back pack carrying of eggs, larvae, or froglets, as well as production of foam nests or development of the larvae inside the stomach or vocal sac of one of the parents. An overview about reproductive modes and parental care in anurans was given by several authors (e.g., Crump 1974, McDiarmid 1978, Duellman & Trueb 1986, Hödl 1990).

Caecilians (Gymnophiona) are aquatic or fossorial and thus difficult to sample. Due to their secretive habits, very little is known about their life history and ecology. Male caecilians have a protrusible copulatory organ, the phallodeum, and presumably fertilization is internal in all species. Most caecilians seem to be viviparous, although some are ovoviviparous.

Salamanders (Caudata) are mainly distributed in the Holarctic region, but a major radiation of plethodontid salamanders with direct development has evolved in the Neotropics. Salamanders display a variety of courtship patterns and reproductive modes. Most groups have internal fertilization without copulation, but few large species have external fertilization. Eggs of aquatic species are laid singly, in strings, or in clumps in ponds or streams, sometimes beneath stones or attached to vegetation. These species have aquatic larvae which usually metamorphose and move back to a terrestrial environment. As adults they return to aquatic environments for reproduction. Most plethodontid salamanders are terrestrial or arboricol and deposit egg clumps in moist sites in leaf litter, bromeliads, beneath rocks and logs, and have direct development of the young. Visual and chemical signals appear to be more important for communication than in anurans.

In anurans, the most important medium to communicate seems to be acoustic. It has been demonstrated that frog calls have different kinds of functions such as advertising, territorial, or distressing (e.g., Blair 1958, Duellman & Trueb 1986, Hödl & Gollman 1986). Today, the analysis of mating or advertisement calls is almost obligatory in some groups as a character to distinguish species which might be morphologically very similar. Advertisement calls work as a very effective pre-zygotic isolating mechanism. However, it became evident that other forms of communication of visual or even seismic character might play important roles as well (e.g., Harding 1982, Lewis & Narins 1985, Narins 1990, Cardoso & Heyer 1995).

The amount of different life forms, behaviors, and reproductive modes evolved in amphibians as well as the variety of habitats used by them is hardly to be exceeded by any other vertebrate group. This makes it a challenge for every researcher studying the biology of amphibians.

Global Amphibian Decline?

The phenomenon of a worldwide decline of amphibian populations has been the subject of several articles published in scientific journals as well as in commercial newspapers. Since it became evident that several populations in different parts of the earth were declining, a discussion about possible reasons began, whether this decline mirrors natural fluctuations in population size or might be caused by human impact (e.g., Pechmann et al. 1991, Blaustein et al. 1994). If they were due to human impact, the question if local or global factors are responsible often remained open (Blaustein & Wake 1990). The possibility of a global phenomenon was seriously discussed, because several populations, especially in Central America and Andean South America, obviously declined although they inhabit apparently undisturbed habitats (e.g., Crump et al. 1992, La Marca & Lötters 1997). Many theories appeared to explain this phenomenon, including the influence of increased ultraviolet radiation, acid precipitation, fragmentation of habitats, overcollecting, chemical pollution as a result of volcanic activity, and pathogens (e.g., Morell 1999).

Recent findings in southern Central America are alarming. Lips (1997) observed declines of anuran populations in Panama in previously very diverse communities, including findings of dying individuals. Her observations strongly argue for a disease probably caused by a virus.

Possibly, amphibians react more sensitive in response to environmental changes than other vertebrates because of their permeable skin and an aquatic stage in their life cycle. This would make them important indicator organisms, but well-managed monitoring projects are needed to throw more light on the factors influencing fluctuations in population size.

Investigation of Bolivian amphibians – a historical view

The very first reference referring to Bolivian amphibians is the description of *Hylaplesia picta* (= *Epipedobates pictus*) by Bibron (in Tschudi) in the year 1838, with the type locality Santa Cruz de la Sierra. The second reference is the description of *Leiuperus marmoratus* (= *Pleurodema marmoratum*) from the Departamento Potosí by Dúmeril & Bibron (1841). Some years later, in 1847, the French explorer and naturalist Alcides d'Orbigny published some herpetological results in his volume V of "Voyage dans l'Amerique Méridionale". In his work, which at this time contained very important botanical, zoological, and anthropological information, d'Orbigny presented some data and illustrations of amphibians collected on Bolivian territory.

As a matter of fact, the first known regions of Bolivia were the early settled valleys of the highlands, namely the vicinities of the cities of La Paz and Cochabamba. Early investigations in these areas resulted in several species descriptions late in the century (Boettger 1891, Boulenger 1882, 1887, 1891, 1898, 1902, Steindachner 1892, Werner 1899, 1901). All these publications were of basic taxonomic contents and mainly included taxa from the mentioned valleys and the adjacent Altiplano. A majority of the species described in these publications was collected by P. O. Simons.

Only when the vast oriental areas of the Bolivian lowlands became accessible to some explorers, people got an approximate imagination of Bolivia's fauna. During the first half of this century, various papers contributed to the knowledge of Bolivian amphibians (e.g., Andersson 1906, 1932, Barbour & Noble 1920, De Grys 1938, Dunn 1942, 1949, Eisentraut 1932, Gaige 1929, Mertens 1929, Müller 1924, Müller & Hellmich 1936, Nieden 1923, Parker 1927b, 1928, 1934, 1940, Procter 1921), mainly publishing results of larger expeditions. Among the most important expeditions covering Bolivian lowlands were the "Swedish Chaco-Cordillera Expedition" (1901–1902) under direction of Earland Nordenskiöld (see Andersson 1906), the American "Mulford Exploration of the Amazon Basin" (1921–1922), accompanied by the herpetologist Everet N. Pearson, and the "Deutsche Gran Chaco-Expedition" by Franz Krieg at the end of the 1920's (results published by Müller & Hellmich 1936). However, at these times investigations were mostly restricted to regions around religious missions founded by Jesuits in the eighteenth century.

Between 1910 and 1950 the German family Steinbach collected many amphibians and other animals at different Bolivian localities, but mainly at Buenavista, Departamento Santa Cruz (type locality of *Hamptophryne boliviana*, *Pseudopaludicola boliviana*, and *Scinax parkeri*). The collected specimens are deposited in various collections (see Ergueta 1991b).

In the 1950s and 60s, research activity concerning amphibians was relatively low and several of the publications dealt only in part with Bolivian populations (e.g., Barrio 1965, Bokermann 1964, Cochran 1955, Cochran & Goin 1970, Duellman 1956, Funkhouser 1957, Gallardo 1961a, b, 1965, Lutz 1973, Rivero 1961, Vellard 1951, 1957, 1960). Apart from these works with a different geographic emphasis, some publications were exclusively on Bolivian anurans (Cei 1968, Donoso-Barros 1969a, b, 1970, Gans 1960, Shreve 1959). Among these papers are several descriptions of new species and subspecies which today are treated as junior synonyms of previously described taxa.

The 1970s were somehow more fruitful in contributing to the knowledge of Bolivia's amphibian fauna. Bolivian specimens have been included in revisions of taxonomic groups or particular regions, mainly published by North American herpetologists (e.g., Duellman 1971, 1972a, 1973, 1974a, b, Duellman & Fritts 1972, Edwards 1974, Lynch 1975, 1976, Heyer 1970, 1973, 1977, 1978, 1979,

Silverstone 1976, Trueb & Duellman 1971, Vellard 1970). Subsequently, Charles M. Fugler published some results of his investigations in the northern Departamento Beni (Fugler 1983, 1984, 1985, 1986, 1988) and few other authors provided new taxonomic information (Cannatella 1980, 1983, Lynch & McDiarmid 1987, Wake 1984). In the same period, Gorham (1974) published his list of world amphibians, including data on Bolivian species.

However, the first compiled list of amphibian species known to occur in Bolivia was provided by Harding (1983). Although at this time, Harding's (1983) list represented an important contribution, it contained mistakes and omissions. The next account of Bolivian amphibians was included in "Amphibian species of the world" edited by Frost (1985), and in the additions and corrections to this work by Duellman (1993). The first comprehensive checklist was provided by Ignacio De la Riva (1990a). His list contained 112 amphibian species, distribution data, comments on the status of several taxa, first records for the country, a list of species he predicted to occur in Bolivia, as well as for the first time color pictures of many of the species. De la Riva's (1990a) work was an useful basis for subsequent studies and somehow the starting point of an "investigation boom" concerning Bolivian amphibians.

In the 1990s, many more publications appeared dealing with Bolivia's amphibian fauna. The main part of these articles was contributed by De la Riva (1990b, 1992a, b, 1993a, b, c, 1994a, b, 1995a, b, c, d, 1996, 1998, 1999a, b, c, d, 2000,
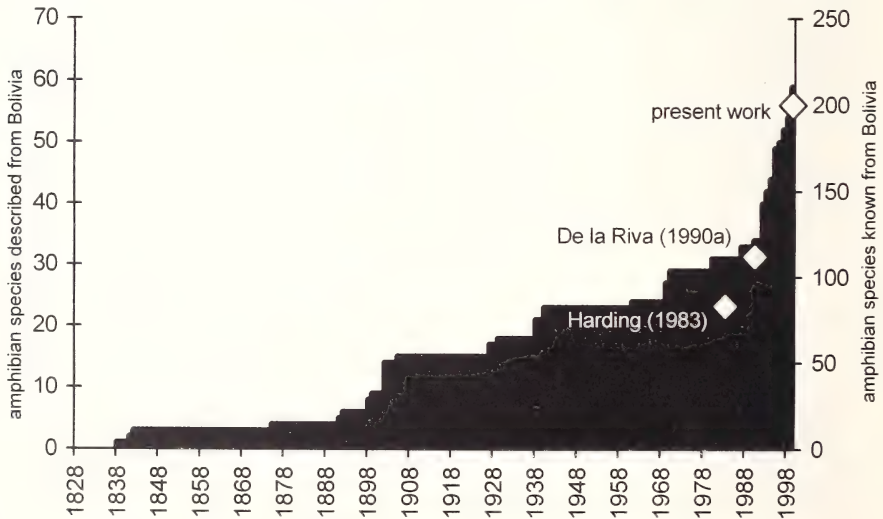
Fig.2: Figure demonstrating the increase of investigation efforts in Bolivia: Numbers of amphibian species described from Bolivian territory since 1828 (species currently considered as synonyms included), and (♦) total number of valid amphibian species known from Bolivia (Harding 1983: 83 species; De la Riva 1990a: 112 species; present work: 200 species).

De la Riva & Gonzales 1998, De la Riva & Köhler 1998, De la Riva & Lynch 1997) who focused his Ph.D. thesis on an amphibian community in the northern part of the Departamento Santa Cruz (De la Riva 1993d). His publications included the descriptions of nine new frog species as well as several first records for the country. De la Riva also was the first who, together with Rafael Márquez and Jaime Bosch, published data of the advertisement calls of many Bolivian frogs (Bosch et al. 1996, De la Riva et al. 1994, 1995, 1996a, b, c, 1997, Márquez et al. 1993, 1995, 1996).

Other publications in the recent years include the descriptions of new species (Harvey 1996, Harvey & Ergueta 1998, Harvey & Smith, 1993, 1994, Harvey & Keck 1995, Köhler 2000a, b, Köhler & Jungfer 1995, Köhler & Lötters 1999a, 2000, Köhler et al. 1998c, Lötters & Köhler 2000a, Lavilla & Ergueta 1995a, b, 1999, Reichle & Köhler 1997, Reynolds & Foster 1992), new distribution data (e.g., Köhler 1995b, 1997a, b, Köhler & Lötters 1999b, Köhler & Reichle 1998, Lötters & Köhler 2000b, Reichle & Köhler 1996a, b, Reichle et al. 1997), contributions on ecology and/or community structure (Ergueta 1991a, 1993, Harvey 1998, Hoogmoed 1993, Ibisch & Böhme 1993, Köhler et al. 1995a, b, Köhler & Böhme 1996, Reichle 1997a, b, c, Reichle & Köhler 1998), as well as an overview about Bolivia's amphibian species diversity (Köhler et al. 1998b). The populations of two Bolivian species, *Telmatobius culeus* and *T. albiventris* (the latter name was placed as a junior synonym of the former by Vellard 1992), were considered to be of vulnerable or endangered status and therefore are listed in the "Libro rojo de los vertebratos de Bolivia" (Ergueta & Harvey 1996).

As a result of these most recent publications, the taxonomic status of many nominal species was clarified, many taxa were added on Bolivia's list, and a lot more is known now about distribution and biology than few years before. The increase of studies on Bolivian amphibians is illustrated by the remarkable fact that 31 out of 55 (= 56%) valid amphibian species described from Bolivian territory since 1838 were described in the last ten years (see Fig.2). However, many more species are still to be discovered and their ecology and distribution has to be studied.

Objectives of the study

Seeing the introducing words about the present state of knowledge of Bolivian amphibians, it is obvious that a study on their diversity, distribution, and biology can be nothing else than preliminary. This is especially true when there are well defined limits in research time, funding, and personnel resources like in this study. New amphibian species are continuously discovered in Bolivia and the checklist could be updated monthly. However, a comprehensive revision of the Bolivian amphibian fauna is not the purpose of this work. Due to the limitations mentioned above, this would need much more financial and personnel efforts than available herein. For example, examining all the amphibian specimens harbored by collec-

tions distributed all over the world was beyond the possibilities of this thesis. As a result, this study includes erroneous and insufficient information, and many omissions. Nevertheless, it appears interesting enough to provide an analysis of diversity and distribution patterns at the present state. Although or because new data arise permanently, it seems to be important to draw an integrative and summarizing picture early to identify tendencies and relationships as well as deficits. This will at least draw attention to unanswered questions and stimulate further research.

The main objective is to provide a preliminary documentation of the amphibian diversity of Bolivia, not only at the regional level but also at a local level. The intention is also to figure the quantitative distribution of diversity and to discuss factors implied. In this study, it is tried to describe amphibian diversity and distribution from a more or less synthetic point of view leading to a more entirely understanding of patterns. Generally, amphibian diversity and distribution is related to altitude and latitude and dependent from the amount of precipitation and the degree of temperatures. Therefore, ecoregions were defined as one possible scale to analyze spatial patterns, leading to the questions "How is amphibian diversity and distribution linked to ecoregions?" and "Where can we find the highest degrees in diversity and endemism?" However, ecoregions represent a rather rough scale not adequate to answer the question "How does the degree of diversity change within short distances?" Elevational gradients within the diverse montane forests of Bolivia were chosen as a principal study area to receive insights to the different levels of species diversity. Another purpose is to characterize community structures and to provide new biological data of the investigated species, like for example advertisement calls and habitat use, since they are also part of biodiversity and necessary to understand ecological relationships. Eventually, possible reasons explaining the identified patterns are discussed with biogeographical and historical background.

Why a Diversity Study in Bolivia?

Bolivia still is the least explored Neotropical country with respect to amphibians (and most other groups of organisms). Despite the remarkable increase of investigations in the past ten years, the picture to be drawn is only fragmentary. A further important reason is that almost all of the relevant South American eco-geographical regions are unified on Bolivian territory. Bolivia is an ideal region to investigate the change of diversity patterns along ecological gradients. Finally, it appears significant to conduct biodiversity and biogeographical studies at the level of political countries, although they mostly represent artificial and randomly limited areas. Biodiversity research always has also a political dimension. Nowadays, genetic diversity is regarded as a resource of the country and also conservation policy occurs at the country level.

Review of similar studies in the Neotropics

Summarizing, there is no similar study to that presented herein hitherto, focusing on general biogeographical patterns within the political borders of one country as well as on diversity patterns within different montane forest areas. By far, most of the studies published on Neotropical amphibians deal with alpha taxonomy or various aspects of a particular species (distribution, physiology, behavior, etc.). Others are about phylogenetic relationships within different taxonomic categories (e.g., Hillis & de Sá 1988, Graybeal 1997, Vences et al. 2000). As far as I know, similar studies on diversity patterns, including investigations along altitudinal transects, are now taking place in central Peru, carried out independently by E. Lehr and L. O. Rodríguez (pers. comm.), but the results are not published yet. However, some other categories of publications include at least aspects similar to the contents of this work.

The most similar study is probably the one on the distribution of frogs of the genus *Eleutherodactylus* in the Cordillera Occidental, western Colombia (Ruiz-Carranza et al. 1997, Lynch 1998). In two separate publications the authors briefly described ten sampled transects and Lynch (1998) summarized and discussed the findings of distributions of species and diversity of communities. Although only a single genus was considered, the study provides data for 76 species exclusively distributed in montane forests (Lynch 1998) which represents a greater number of species than involved in the analysis herein. Lynch & Duellman (1997) summarized the distributions of *Eleutherodactylus* species on the Andean slopes of Ecuador.

In addition, there are few studies dealing with amphibian distribution along a particular altitudinal transect. Heyer (1967) investigated sites at different elevations in the Cordillera de Tilarán, Costa Rica. Cadle & Patton (1988) published results for vertebrate distributions at the eastern versant of the Andes in southern Peru, also including valuable data for amphibian species. Johnson (1989) focused on biogeographic patterns in southern Mexico, providing information on altitudinal ranges for certain groups. In an unpublished thesis, Franzen (1994) investigated the herpetofauna in the Guanacaste National Park, Costa Rica, including amphibian distribution on the slopes of the volcanoes Orosi and Cacao. All these papers provide at least some data usable for superficial comparisons with findings in the present study.

Another category of publications is the one dealing with general herpetofaunal distribution patterns in South American. In a book edited by Duellman (1979a), several authors discussed the origin and history of patterns known at that time (e.g., Gallardo 1979, Hoogmoed 1979, Lynch 1979). Subsequently, the same was subject in publications for example by Duellman (1982), Heyer & Maxson (1982a, b), Heyer (1988), and Kress et al. (1998). All of them reflect upon patterns on a large geographical scale, comprising distributions almost all over the sub-

continent as a basis for discussing general mechanisms of speciation and dispersal (see discussion).

Other studies mainly focused on amphibian (or herpetofaunal) communities of particular areas with limited expanse. Among these are also long term ones providing valuable data and insight to Neotropical amphibian community structures and distribution patterns. In the following, only some of the most important ones are listed: Martin (1955) – Mexican cloud forest; Stebbins & Hendrickson (1959) – Colombia; Crump (1971) – Belém, Brazil; Duellman (1978c) – Santa Caecilia, Ecuador; Toft & Duellman (1979) – Río Llullapichis, Peru; Schlüter (1984, 1987a, b) – Panguana, Peru; Heyer et al. (1990) – Boracéia, Brazil; Rodríguez (1992) – Cocha Cashu, Peru; Duellman & Mendelson (1995) – northern Loreto, Peru. Analogous studies were published for Asian (e.g., Brown & Alcala 1961, Lloyd et al. 1968, Inger 1969, Inger & Colwell 1977) and African communities (e.g., Barbault 1974, 1976, Rödel 1996). However, comparisons of the data resulting from research at single sites revealed interesting patterns with respect to distribution, community composition, habitat use, and reproductive modes (e.g., Duellman 1988, 1989, 1990).

STUDY AREA

Bolivia

General Information

The state of Bolivia reached its independence from Spain on August 6, 1825. In the following, Bolivia lost more than half of its territory as a consequence of wars (1879–1935) with all its neighboring countries (Argentina, Brazil, Chile, Paraguay, and Peru). At present days, Bolivia's surface is 1 098 581 km^2 and therefore it represents the fifth largest country on the South American continent (Montes de Oca 1989). Politically, it is divided into nine departments and more than hundred provinces. Capital is the town Sucre in the Departamento Chuquisaca, but La Paz is the governmental seat as well as the largest city in the country, with more than 1.2 million inhabitants, followed by Santa Cruz de la Sierra and Cochabamba. Bolivia is inhabited by more than 7 million people, with a mean population density of approximately 6 persons/km^2. The majority of the human population (70–80%) inhabits the Andean regions, an area constituting 38% of Bolivia's surface (Montes de Oca 1989). Official languages are Spanish, Aymara, and Quechua. Bolivia contains the highest portion of indigenous people of all South American countries and it is considered to represent the second poorest country on the continent.

Human settlement on the territory of present-day Bolivia started ten to twelve thousand years ago after the last glacial period of the Pleistocene. Approximately 100 years BC, the culture of Tiwanaku erected its center in the Andean highlands near the lake Titicaca. In the thirteenth century, the Tiwanaku culture was fol-

lowed by smaller groups of Aymara tribes existing parallel; subsequently the Quechua speaking Inca overcame the whole territory (15th and 16th century). In some regions, the Inca reached their power shortly before the Spanish conquerors arrived, but they did not manage to include most of the Bolivian lowland tribes in their empire. Later in the 16th century, with the colonization by the Spanish, Bolivia became an important factor in the worldwide growth of economy. Especially the silver mines of the Cerro Rico in Potosí contributed essentially to the richness of the Spanish empire. As a consequence of the silver exploitation, Potosí became the largest city of the world, larger than Paris or London at that

Fig.3: Bolivia's position to its neighboring countries and its political division into nine Departamentos with their corresponding capital cities.

time. Since the day of independence, Bolivia was ruled by nearly 70 presidents. There were many armed risings and terror regimes, but since 1982 Bolivia is developing in a relatively stable and democratic way.

Today, Bolivia's economy is mainly based on mining, oil and gas production, cultivation of industrial crops (e.g., soy beans, rice, cotton), cattle, and timber extraction (e.g., Ibisch 1998). Another important factor not to be depreciate is the production of coca and/or cocaine. At a rough estimation, 30% of Bolivia's gross domestic product comes from the production of drugs (see Müller 1999). Main developmental problems are the impoverishment of the rural population, the migration pressure on cities and unsettled tropical rainforest regions, as well as the destruction of natural environments (for further information see Ibisch 1998).

Geography

The country is situated between 09°38' and 22°53' southern latitude and 57°25' and 69°38' western longitude. Highest mountains are in the western Cordillera the Sajama (6542 m a.s.l.) and the Pomerape (6222 m a.s.l.) and in the eastern Cordillera the Illampu (6412 m a.s.l.) and Illimani (6402 m a.s.l.). The Chiquitanía mountains reach 1.300 m a.s.l. Some pre-Cambrian outcrops (inselbergs) of the Brazilian shield might reach 500 m altitude. Bolivia also is the place to find the most important watershed on the continent. Approximately 66% of the country's surface belong to the Amazon river system, with the large rivers Beni, Guaporé, Madre de Dios, and Mamoré. Other 21% of Bolivia's surface are part of the La Plata river system (rivers Pilcomayo, Bermejo, Paraguay, Paraná), and the rest is part of the Altiplano water system.

Generally, Bolivia can be divided into the following physiogeographic regions which are characterized by different geomorphological and historical conditions: (1) the Altiplano which is limited by the (2) western Cordillera, and the (3) eastern Cordillera. The (4) sub-Andean regions including the inter-Andean valleys are a transition zone to the (5) eastern lowlands. In the east, the lowlands meet the (6) Brazilian shield. This contact zone is interrupted by the (7) Chiquitanía mountain chains (Montes de Oca 1989).

The final uplift of the Andes took place five to three million years ago. This event was accompanied by drastic changes in climatic conditions. In the quaternary, geomorphological processes were strongly influenced by the cycles of glacial and inter-glacial periods, resulting in changes of temperatures and humidity which accounted for different amounts of glacier covering of the Andean region. For an overview of Bolivia's geomorphological history and its geoecology see Hanagarth (1993) and Hanagarth & Szwagrzak (1998).

Climate

According to the definition of the tropics by Lauer (1975), Bolivia is a tropical country without thermal seasons. As a result of the Andean uplift, Bolivia contains

warm and hot lowland tropics as well as cool and cold highland tropics. Additionally, the hygric differentiation is very complex and results in a high diversity of tropical ecosystems from very humid to arid. Due to its location in the center of the South American continent, Bolivia is the only country that has equivalent portions of Amazonian rainforest vegetation, Cerrado formations, Chaco dry-forest, as well as the climatic highly diverse Andean region. It is the unique location within an area of different climatic and biogeographic transition and contact zones which accounts for Bolivia's diversity (Solomon 1989). With the help of pollen analysis, it was shown that the vegetation of the Andean highlands experienced drastic vertical dislocations during the Pleistocene (e.g., Graf 1994). At the climax of the last glacial period 18–19 000 years ago, puna vegetation was located 1000 m lower than today. Mean annual temperatures at that time were approximately 7°C lower, but the amount of annual precipitation was about 50% above the values of present days. Vast areas of the Bolivian Andes were covered by glaciers, the snow line was situated at 4600 m a.s.l. (today 5200 m a.s.l.), and the forest line at 2000–2500 m a.s.l. At the maximum of the last Pleistocene inter-glacial period, mean temperatures were approximately 2°C higher than today. Since 5000 years, the phenomenon of "El Niño" is existent. "El Niño" periodically causes extreme climatic conditions resulting in less precipitation in the Andes of Bolivia during the rainy season ("El Niño-Southern-Oscillation").

During the last ice-age, temperatures in the Bolivian lowlands were 3–4°C lower than today and the amount of precipitation was reduced. Humid rainforests had a more restricted distribution, but probably were not replaced by completely forest-free formations like postulated in the theory of Pleistocene refugia (e.g., Haffer 1969, Brown 1982, Bush 1994, Vanzolini & Williams 1981). In a more recent theory, the main presumption is that regions with extremely stable ecological conditions remained in times of drastic climatic changes ("Ecologically Extremely Stable Areas - EESAs"; Fjeldså 1995, Fjeldså et al. 1999). These regions do not have to be forests, they only have to guarantee the survival of pretentious species (Fjeldså 1995).

At present days, Bolivia's climate is very diverse and depending on different degrees of altitude and humidity (Lauer 1986). The mean temperature decreases with increasing altitude (0.5–0.6°C/100 m). The temperature dependent altitudinal zones have been classified into *Tierra caliente*, *T. templada*, *T. fría*, *T. helada* and *T. nevada* (e.g., Lauer & Erlenbach 1987). Within the Bolivian Chaco close to the Argentinean border the hottest spot of the continent is located, with temperatures reaching 48°C (see Spichiger & Ramella 1989). Periodically, cold southern winds from Antarctic regions ("surazos") have important climatic influences. They are most common in the dry season in the middle of the year and might result in a drop of temperature below 3°C. These temperature droppings reach the northern savannas of the Beni (Hanagarth 1993).

The convective tropical climate results in a decrease of steam contents in the air with increasing altitude. Due to cool downs, the steam content increases stepwise. In the eastern versants of the Andes, two important condensation levels can be observed. The first is below 2000 m a.s.l. and the second above 2700 m a.s.l. At the second level, a broad bank of fog (or clouds) is usually present. A maximum of precipitation can be found in lower montane rainforests of the Yungas de Cochabamba region at approximately 1500 m a.s.l. Annual precipitation in that region can be expected to be more than 6000 mm. The Yungas of La Paz are some-what less humid (ca. 3000 mm estimated). The western part of Bolivia is dry due to the influence of the cold Pacific Humbold stream (like western Chile and Peru). Generally, the situation concerning amounts of precipitation is very complex within the Andean region, mainly influenced by high mountain chains forming watersheds.

Precipitation in the northern Bolivian lowlands (1700–2000 mm) increases from the northeast to the southwest, parallel to the Andean slopes (Killeen 1998). In contrast to the dryness in the Andean highlands, the above mentioned El Niño-Southern-Oscillation causes unusual high amounts of rainfall in the northeastern lowlands of Bolivia (Hanagarth 1993). The western lowlands are remarkably drier, with minima in precipitation in the central Chaco (< 400 mm).

The El Niño phenomenon probably did also affect the present study. The rainy season 1997/98 was strongly influenced by the presence of an El Niño effect. As a result, the first heavy rains in western Bolivia started late (middle of December) and the absolute amount of rainfall was lower than in non-El Niño years. At the same time, precipitation in the Yungas region probably increased.

Vegetation – ecoregions

Supposedly, in past times more than 600 000 km² of Bolivia were covered by forests. After data provided by the Worldbank (1994) Bolivia had 556 000 km² of forest in 1980 and 493 000 km² in 1990. This is about half of the countries' sur-face, placing it in the ranks of the ten most forest rich countries of the world (rank five or six among tropical countries; Ibisch 1998). Annual deforestation is about 6200 km² which equals 1–2% of the remaining forests. The estimation of forest extent in historical times in the Andes is difficult. According to Kessler & Driesch (1994), 90% of the Andean forests (mainly *Polylepis* spp.) have been destroyed.

The floristic diversity of Bolivia is high. Eighteen to twenty-thousand plant species might occur on Bolivian territory (Moraes & Beck 1992, Ibisch 1996, Beck 1998), among them about 2700 species of trees (Killeen et al. 1993). Generally, the Bolivian flora is still insufficiently known which is illustrated by the large number of new species described in recent times. For example, today more than 1300 species in the most species-rich family, the Orchidaceae, are known from Bolivia (Vásquez 1996) and still more are discovered every year. The
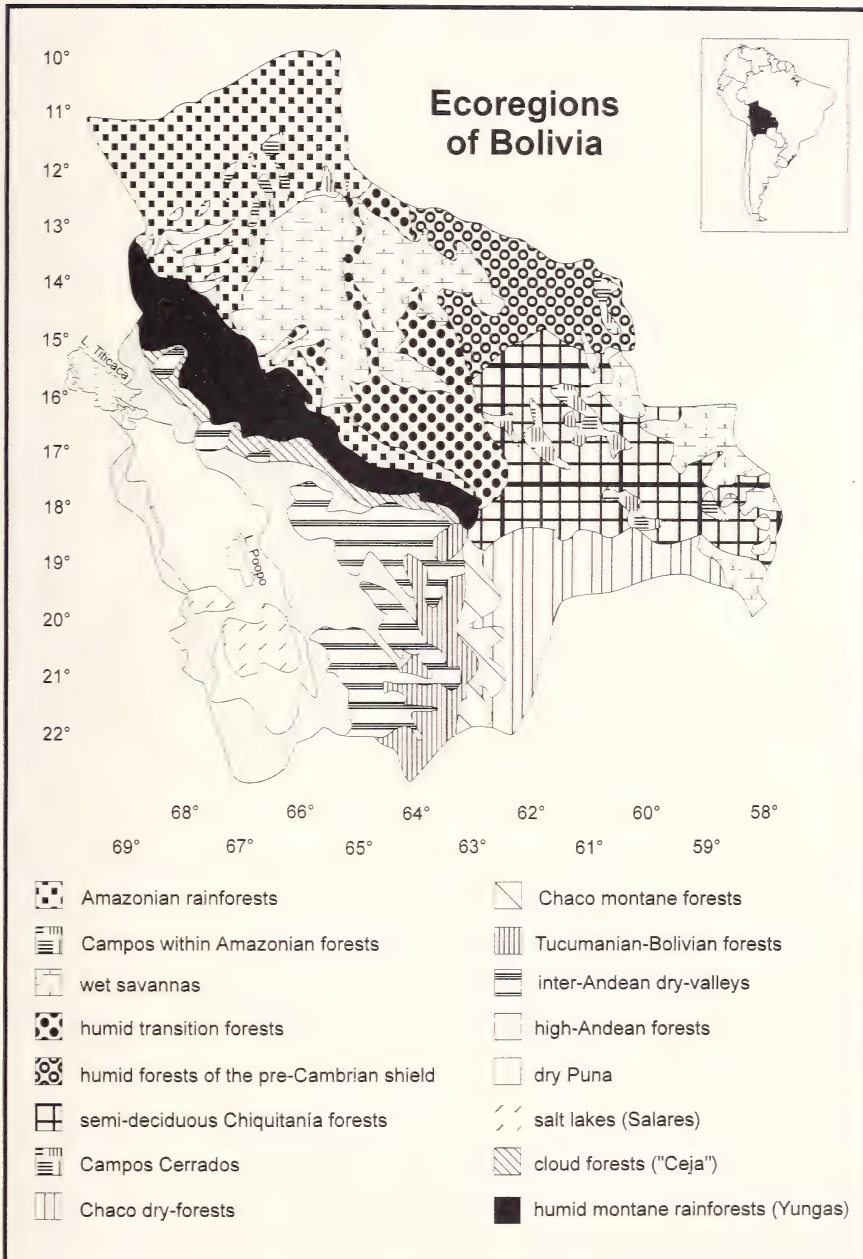
Fig.4: Schematic map of Bolivia showing its defined ecoregions.

number of known Bolivian orchids was only 322 in 1922 (Schlechter 1922) and about 500 were listed by Foster (1958). Several plant groups have their center of diversity in Bolivia (e.g., Cactaceae, Amaranthaceae, *Cleistocactus*, *Puya*, *Fosterella*; see Ibisch 1998).

Bolivia's high diversity of different ecosystems is due to its geographical location. Bolivia is an Amazonian, Andean, Chaco, and Cerrado country. An useful overview of the vegetation of Bolivia and its ecoregions was provided by Beck et al. (1993). More recently, Ibisch (1996) characterized the ecoregions of Bolivia in detail, compiling own and literature data. The following brief characterization of Bolivian ecoregions is mainly based on the data given by Ibisch (1996). Information about conservation areas was taken from Ergueta & Gomez (1997).

Chaco dry-forest

Located in the Departamentos Santa Cruz, Chuquisaca, and Tarija; also in western Paraguay and northern Argentina; 300–600 m a.s.l.; mean annual temperature 25–26°C; maximum temperature 48°C at the Argentinean border; minimum temperature 1°C; mean annual precipitation 400–900 mm; about 1000 mm precipitation at the Andean foothills and in the northern transition zone to the Pantanal; 6–8 arid months; low dry-forest of 10–15 m height with various succulent plants; 50–100 tree species; important plant genera *Ziziphus*, *Geoffrea*, *Ruprechtia*, *Stetsonia*, *Cereus*; biogeographical relationships to the inter-Andean dry-valleys; land use: timber extraction, cattle; conservation areas: recently funded Parque Nacional y Area Natural de Manejo Integrado Kaa-Iya (see Taber et al. 1997).

Chaco montane forest

Located in the Departamentos Santa Cruz, Chuquisaca, and Tarija; also in northern Argentina; 600–1500 m a.s.l.; mean annual temperatures 18–22°C; mean annual precipitation 1000–2000 mm; 6–7 arid months; deciduous forest of medium height (< 25 m); important tree species: *Schinopsis haenkeana*, *Astronium urundeuva*, *Lithraea ternifolia*, *Zanthoxylum coco*; 100–200 tree species; relationships to Caatinga formations; land use: cattle, oil hauling; no areas with conservation status.

Inter-Andean dry-valleys

Located in the Departamentos La Paz, Cochabamba, Chuquisaca, Santa Cruz, Tarija; similar dry-valleys in Argentina and Peru; 1500–3000 m a.s.l.; mean annual temperature 12–16°C; maxima above 30°C, minima below 0°C; mean annual precipitation 500–700 mm; 6–8 arid months; (semi-)deciduous dry-forests of medium height (10–20 m); important plant species: *Prosopis* spp., *Schinus molle*, *Acacia* spp., *Tipuana tipu*, *Schinopsis haenkeana*, *Erythrina falcata*, *Kageneckia*

lanceolata; 100–200 tree species; almost all natural forests destroyed; area of high human population density; problems with soil erosion; conservation areas: only parts of the Parque Nacional Carrasco include small areas.

High-Andean forests

Located in the Departamentos La Paz, Cochabamba, Oruro, Chuquisaca, Potosí, Tarija; forest type continues in Argentina, parts of northern Chile, and Peru; 2500–4600 m a.s.l. (*Polylepis* growth up to 5200 m a.s.l. around the Sajama); considered the highest forests of the world; mean annual temperature below 10°C; temperatures below 0°C relatively common; mean annual precipitation 500–700 mm; 6–8 arid months; low to medium high evergreen montane forests (5–15 m); most important tree species: *Polylepis* spp., *Baccharis* spp., *Berberis* spp., *Escallonia* spp., *Senna* spp.; 10–50 tree species; large parts destroyed; land use: extraction of fire-wood, grazing; conservation areas: Parque Nacional Sajama, Parque Nacional Llica, Reserva Nacional Eduardo Avaroa, Reserva Nacional Ulla Ulla.

Semi-deciduous Chiquitanía forests

Located in the Departamento Santa Cruz in the Provincias Velasco, Ñuflo de Chavez, Sandoval, and Chiquitos; unique ecoregion in South America; transition zone between Amazonian rainforests and Chaco dry-forest; relationships to the Brazilian Cerrados; 300–1200 m a.s.l.; mean annual temperatures 18–23°C; mean annual precipitation 1000–1500 mm; 3–5 arid months; forest of medium height (15–25 m), large parts evergreen; important trees: *Cordia alliodora, Terminalia argentea, Astronium urundeuva, Schinopsis brasiliensis*; 200–400 tree species; land use: farming, cattle, timber extraction, slash and burn culture; nearly no conservation status, only the small Parque Nacional Historico Santa Cruz la Vieja.

Humid forests of the pre-Cambrian shield (and Campos Cerrados)

Located in the Departamento Santa Cruz in the Provincias Ñuflo de Chavez and Velasco, and parts of the Departamento Beni; also present in Brazil; 200–1000 m a.s.l.; mean annual temperatures 18–25°C; mean annual precipitation 1500–1800 mm; 2–4 arid months; evergreen forest of 15–30 m height; azonal vegetation on inselbergs and sandstone ridges; important trees: *Swietenia macrophylla, Terminalia oblonga, Schizolobium amazonicum, Gallesia integrifolia, Ocotea guianensis*; 400–650 tree species; few floristic relationships to the Chaco; land use: timber extraction, slash and burn cultures, gold mining, rubber collection (historically); conservation areas: Reserva Nacional Ríos Blancos y Negros, Parque Nacional Noel Kempff Mercado (protects humid forests as well as savannas on the Huanchaca plateau).

Wet savannas

Located in the Departamentos Beni, Santa Cruz, and northern La Paz; 130–250 m
a.s.l.; mean annual temperature around 26°C; mean annual precipitation
1000–2000 mm; 2–6 arid months; swamps and grass savannas with few small
groups of trees; important tree species: *Guazuma ulmifolia, Genipa americana,
Rheedia achachairu, Scheela priceps*; 200–400 tree species; the southern Beni
savannas are closely related with the Pantanal, the northern part is more closely
related to Campo Cerrado formations (Hanagarth & Beck 1996); land use: cattle;
conservation area: Reserva Biosfera Estación Biológica del Beni.

Humid lowland transition forests

Located in the Departamentos Beni, Santa Cruz, and Cochabamba; forest type
unique to Bolivia; 150–250 m a.s.l.; mean annual temperature around 25°C; mean
annual precipitation 1200–1800 mm; 2–4 arid months; evergreen rainforests of
25–30 m height; azonal gallery forests along rivers and wet savannas; important
tree species: *Hura crepitans, Swietenia macrophylla, Terminalia oblonga, Irartea
deltoidea, Bactris gasipaes*; 650–800 tree species; close relationships to the moist
forests of the pre-Cambrian shield; land use: timber extraction, slash and burn cul-
tures, coca plantation; no conservation areas.

Tucumanian-Bolivian montane forests

Located in the Departamentos Santa Cruz (Prov. Florida, Caballero, Vallegrande),
Chuquisaca, and Tarija; eastern Andean slopes south of Santa Cruz de la Sierra;
continue south to the subtropical montane forests of Argentina; 800–3000 m a.s.l.;
mean annual temperature 13–23°C; mean annual precipitation 1000–2000 mm;
3–5 arid months; montane forest of medium height (< 20 m); important tree
species: *Blepharocalyx salicifolius, Myrcianthes pseudomato, Cinnamomum por-
phyria, Cedrela lilloi, Juglans australis, Sambucus australis, Podocarpus parla-
torei, Alnus acuminata*; 200–400 tree species; many endemic species for the
ecoregion (Argentina and Bolivia); land use: timber extraction, agriculture, oil
hauling; conservation areas: Reserva Nacional de Fauna y Flora Tariquía.

Amazonian rainforests

Located in the Departamentos Pando, Beni, La Paz, as well as forests of the
Andean foot in the Departamentos Cochabamba and Santa Cruz (reaching
Provincia Ichilo); continue in Peru and Brazil; 100–500 m a.s.l.; mean annual tem-
perature 25–27°C; mean annual precipitation 1800–2200 mm; 0–3 arid months;
high evergreen rainforest (30–45 m); important tree species of the terra firme for-
est: *Bertholletia excelsa, Hevea brasiliensis, Couratari guianensis, Manilkara
bidentata, Enterolobium contortisiliquum, Mezilauris itauba, Phenakospermim*

guianensis; trees of the varzea forest: *Calophyllum brasiliense, Ceiba pentandra, Ficus* spp.; more than 800 tree species; typical Amazonian species are lacking in the forests of the Andean foot; land use: timber extraction, rubber, paranut collecting, coca plantation, oil hauling; conservation areas: Reserva Nacional Amazónica Manuripi-Heath, Parque Nacional Madidi, Parque Nacional Isiboro-Sécure, Parque Nacional Pilón Lajas, Parque Nacional Carrasco, Parque Nacional Amboró.

Humid montane rainforests – Yungas

Located in the Departamentos La Paz, Cochabamba, and Santa Cruz; continue to Peru; 500–2500 m a.s.l.; divided in upper montane rainforests (1500–2500 m) and lower montane rainforests (500–1500 m); mean annual temperature 15–24°C; minima below 0°C above 2300 m a.s.l.; mean annual precipitation 2500 to more than 6000 mm; Kessler (1999) suggested a yearly precipitation of 8000 mm in some parts of the Yungas de Cochabamba; maximum rainfall between 1500 and 1800 m a.s.l.; 0–2 arid months; characterized by steep slopes and deep valleys; evergreen montane rainforest of medium height (15–30 m); important plant genera: *Guatteria, Cyathea, Acalypha, Aniba, Nectandra, Persea, Inga, Trichila, Ficus, Solanum, Oreopanax, Brunellia, Hedyosmum, Clethra, Weinmannia, Clusia, Ocotea*; extremely rich in epiphytic plants; 400–650 tree species; land use: coca and Locoto plantations; conservation areas: Parque Nacional Amboró, Parque Nacional Carrasco, Parque Nacional Cotapata, Parque Nacional Pilón Lajas, Parque Nacional Isiboro-Sécure.

Cloud forests – "Ceja"

Also called *"ceja de la montaña"* which means eyebrow of the mountains; located in the Departamentos La Paz, Cochabamba, and Santa Cruz; continue in Peru; 2500–3500 m a.s.l.; at the perhumid northeastern versants of the Bolivian Andes, above 3200–3500 location of tree line; mean annual temperature 10–14°C; mean annual precipitation 2500–3500 mm; 0–2 arid months; low evergreen cloud forest (5–15 m); important tree species: *Thibaudia crenulata, Gaiadendron punctatum, Persea ruizii, Oreopanax pentalandianus, Freziera* spp., *Weinmannia* spp., *Polylepis* spp., *Escallonia* spp.; 50–100 tree species; land use: fire wood extraction, potato and Locoto plantations; conservation areas: Parque Nacional Amboró, Parque Nacional Carrasco, Parque Nacional Cotapata.

Fauna

The fauna of Bolivia comprises Amazonian, Andean, Chacoan, as well as Cerrado elements. Every of Bolivia's ecological life zones is inhabited by a typical fauna. There are many transition zones where elements of different origin meet to form special and unique communities.

In respect to vertebrates, Bolivia seems to be especially rich in fish and bird species (Ergueta & de Morales 1996). According to Armonia (1995), 1385 bird species are known from Bolivian territory which represent 43% of all South American avifauna (Rocha & Quiroga 1996). Remsen & Parker (1995) assumed that as many as 1088 species of birds could potentially exist within the conservation area of Parque Nacional Madidi (10 000 km²). If this assumption is correct, the area has the potential to become the planet's richest park for birds and probably for other terrestrial biota as well (Remsen & Parker 1995). Particularly, the eastern slopes of the tropical Andean region is rich in endemic bird species (Fjeldså & Rahbek 1998). Detailed data on the number of fish species are lacking, but the species number was estimated to be around 500 occurring in Bolivia (Sarmiento & Barrera 1996).

Table 1: Knowledge of Bolivian species diversity in selected groups (* = estimates).

	Number of Known Species	Reference
Mammals	327	Anderson (1997)
Birds	1385	Rocha & Quiroga (1996)
Reptiles	229	Dirksen (1995)
Fish	>500*	Sarmiento & Barrera (1996)
Vascular Plants	18 000–19 000*	Moraes & Beck (1992)
Orchidaceae	1330	Vásquez (1996)

Today, 327 species of mammals are known to occur in Bolivia (Anderson 1997) which represent about one third of all South American mammal fauna (Hutterer 1998). Several taxa are endemic to Bolivia, including two primates (*Callicebus modestus* and *Callicebus ollalae*), two marsupials (*Marmosops dorothea* and *Monodelphis kunsi*), and several rodents. The Andean highlands have a very special mammal fauna including rare species like the vicuña (*Vicugna vicugna*) and the Andean cat (*Felis jacobita*). The humid Yunga forests are still home to the Andean bear (Jucumari, *Tremarctos ornatus*), *Mazama chunyi*, and many endemic rodent species (Tarifa 1996). The Amazonian lowland regions of Bolivia harbor a typical fauna including pygmy anteaters, sloth, primates, cats, tapirs, deer, giant otter, and opossums. The pink river dolphin (Boutu, *Inia geoffrensis*) occurs in the Madre de Dios, Beni, and Mamoré river systems. The Beni savannas are an important habitat for the swamp deer (*Odocoileus dichotomus*) and the rare maned wolf (*Chrysocyon brachyurus*). Mammal diversity at some sites in the dry Chaco forests is comparable with that at Amazonian sites. The Chaco mammal fauna includes important and endangered species as for example the giant amardillo (*Priodontes maximus*), giant anteater (*Myrmecophaga tridactyla*), Chacoan peccary (*Catagonus wagneri*), and the Chacoan Tuco-Tuco (*Ctenomys conoveri*).

About 220-230 species of reptiles were recorded from Bolivian territory (Dirksen 1995, Pacheco & Aparicio 1996). Undoubtedly, this number is far from complete

because only very few inventory studies took place concerning reptiles. Four species of crocodiles (*Caiman latirostris, Caiman yacare, Melanosuchus niger, Palaeosuchus trigonatus*) and 13 turtle species are known from Bolivia. The largest group is represented by snakes with approximately 125 species (Fugler & Cabot 1995). Recently, Dirksen & De la Riva (1999) reported 102 species of lizards from the country.

Until today, no estimates on the species number of the little known group of invertebrates can, be given. Data and collections are far from complete and well managed investigation projects are necessary to seize Bolivia's invertebrate fauna.

Nature conservation

Bolivia's natural richness is protected by 29 conservation areas (listed by Ergueta & Gomez 1997) covering approximately 14% of the countries surface. These areas have different categories of conservation status, for example "Parques Nacionales", "Reservas", "Reservas de la Biosfera", "Refugios de Vida Silvestre", and "Areas Naturales de Manejo Integrado". Despite of few private organized reserves, the Dirección General de la Biodiversidad (DGB), La Paz, is the responsible governmental institution for conservation matters. Only part of these areas really enjoy a managed and controlled protection. The other part only exists on the paper and there are no fundings to fulfill conservation managements. Additionally, in several areas the boundaries are not properly defined. For these reasons, many of the protected regions suffer from human population pressure, slash and burn cultivation, illegal hunting, timber extraction, or gold mining.

In recent times, more and more funding for conservation efforts were received from external, non-Bolivian sources and large international organizations like Conservation International and the World Wildlife Fund for Nature (WWF) began to recognize the value of Bolivia's diverse biota and started initial projects.

Until today, vast areas of almost undisturbed ecosystems are still present, and unlike many other countries, Bolivia still has the opportunity to decide how to use and manage its natural resources.

Investigated Sites

Own investigations on Bolivia's amphibian diversity and distribution were conducted in the years 1994, and 1997–1999, in total comprising eleven months of presence in the country. The itinerar (Fig.5) shows the areas covered by investigation efforts. As obvious from this figure, the largest part of the investigations was focused on the humid montane forests in the Yungas de Cochabamba and Santa Cruz regions. Nevertheless, data on amphibians were obtained whenever travelling through the country and repeatedly interesting findings were even made when having stopped the car for a break to relax. Although the main focus of the study was on the Systematic Sampling Survey (SSS), all these collected data are pieces of the present work.
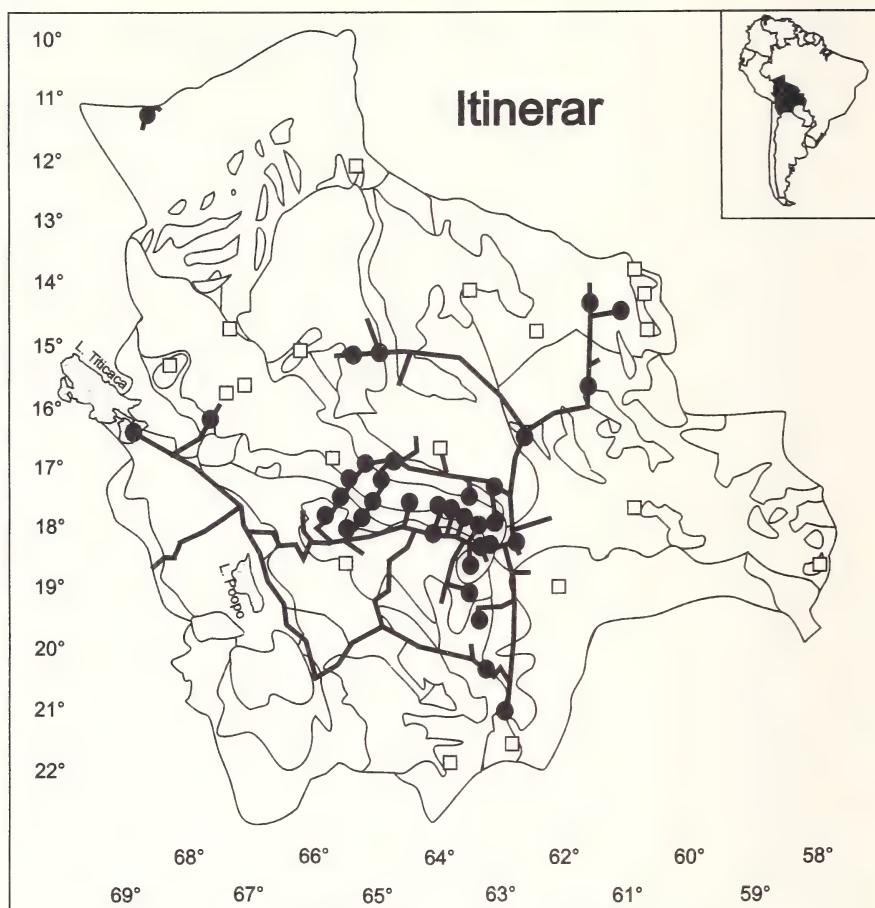
Fig.5: Itinerar. Spots indicate sites which were investigated at least four person days. Open squares indicate sites investigated by other herpetologists. Data from these studies were included in the distribution analysis.

The regions covered by own studies are roughly the following: moist forest of the pre-Cambrian shield in the northeren Departamento Santa Cruz including granitic rock outcrops (inselbergs) and floating meadows (October 1994); semi-humid Chiquitanía forests in northern Departamento Santa Cruz (October 1994); southern Beni savannas and humid transition forests west of Trinidad (November 1994); Chiquitanía and Chaco formations in the vicinity of Santa Cruz de la Sierra (November 1997/98 – February 1998/99); Chaco montane forests around Camiri (December 1997); inter-Andean temperate-valleys in eastern Departamento Chuquisaca (December 1997); inter-Andean dry-valleys between Samaipata and

Comarapa, Departamento Santa Cruz (November 1994, December 1997, January and November–December 1998); inter-Andean temperate-valley of Vallegrande (January 1998); high-Andean areas around Tiahuanacu and Lake Titicaca (December 1994); dry-puna in the Departamentos Oruro and Potosí (December 1994, January 1999); the inter-Andean valley of Cochabamba and adjacent high-Andean zones (December 1994, January–February 1999); seasonal Amazonian lowland forests around Cobija, Departamento Pando (January 1998); Amazonian lowland forests at the Andean foot in the Departamentos Cochabamba and Santa Cruz (December 1994, November 1997, February 1998, January 1999). For montane forest sites considered more detailed in this study see below.

Moreover, data obtained by colleagues in almost all regions of Bolivia, as well as data from museum specimens, mainly deposited in Bolivian collections, became part of this study (indicated by open squares in Fig.5).

The sites within montane forest regions investigated more thoroughly during this study are listed and briefly characterized below. Unfortunately, for almost all the sites detailed data on climate are lacking. So, the annual precipitation given for a site is only an estimation.

"Old" Chapare road. – Departamento Cochabamba, Provincia Chapare; this term comprises several sites within the Parque Nacional Carrasco, all located along the "old" road connecting lowland Paractito with Andean Cochabamba. The road lies within a region which is among those with the highest amount of rainfall in Bolivia. Kessler (1999) suggests the yearly amount to be around 8000 mm in some parts of the Parque Nacional Carrasco. It runs on the slopes of the Río San Mateo valley close to the border of Provincia Tiraque and is in reasonable good condition but not passable above approximately 2250 m a.s.l. due to a large landslide. Although the road is generally out of use for regular traffic (a new road running more or less parallel west of the "old" road was constructed in the 1970s), it is the only access to a still managed bauxit mine and it is probably also used for the transportation of coca leaves. Only the villages Paracti and El Palmar are to pass when travelling the road. The region is characterized by extremely steep slopes, with slope inclination frequently ranging between 40° and 85° (Ibisch 1996). The sites to be characterized in the following have no available local name and therefore their elevation is used as specification.

(1) 500 m a.s.l. – 7 km on road S from Paractito; 17°04' S, 65°29' W; investigated 3–4 February 1998; 12–14 December 1998, 2–3 January 1999; Amazonian rainforest at the Andean foot; slightly disturbed (coca plantations); many small to large streams, roadside ditches, no ponds; annual precipitation supposedly 2500–3500 mm.

(2) 700 m a.s.l. – 14 km on road S from Paractito, close to the valley of El Palmar; 17°06' S, 65°30' W; investigated 6–7 February 1998 and 20–21 December 1998;
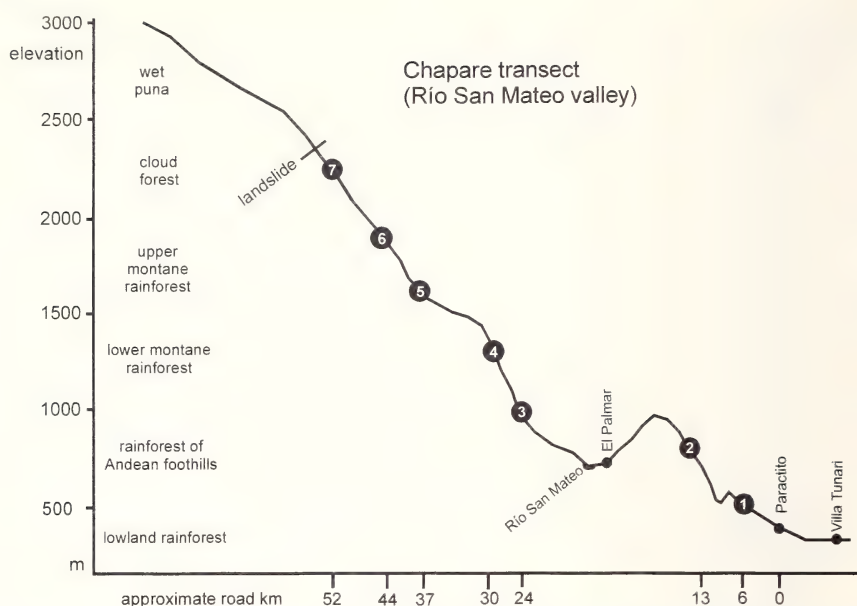
Fig.6: Schematic profile of the Chapare transect, roughly showing the study sites on an elevational gradient.

lower montane rainforest; disturbed by coca plantations; many small to large streams, roadside ditches, few artificial ponds; annual precipitation supposedly 2500–3500 mm.

(3) 950 m a.s.l. (Fig.7) – 24 km on road S from Paractito; 17°06' S, 65°34' W; investigated 4 February 1998 and 19 December 1998; lower montane rainforest; almost undisturbed; many small to large streams, roadside ditches, no ponds; annual precipitation supposedly 3000–4000 mm.

(4) 1250 m a.s.l. – 30 km on road S from Paractito; 17°07 ' S, 65°34' W; investigated 5 February 1998, 18 December 1998, and 3 January 1999; montane rain

Fig.7: "Old" Chapare road at 950 m a.s.l., flooded after heavy down-pour; 4 Feb. 1998.

Fig.8: "Old" Chapare road, montane rainforest at 1650 m a.s.l.

forests; undisturbed; steep slopes; many small to large streams, roadside ditches, no ponds; annual precipitation supposedly 3500–4500 mm.

(5) 1650 m a.s.l. (Fig.8) – 37 km on road S from Paractito; 17°07' S, 65°35' W; investigated 16–17 December 1998 and 3 January 1999; montane rainforests; undisturbed; steep slopes; many small to medium-sized streams, roadside ditches, no ponds; annual precipitation supposedly 4500–5000 mm.

(6) 1850 m a.s.l. – 44 km on road S from Paractito, 17°08' S, 65°36' W, investigated 15 December 1998 and 28 January 1999; upper montane rainforests; undisturbed; steep slopes; many small to medium-sized streams, roadside ditches, no ponds; annual precipitation supposedly 3500–4500 mm.

(7) 2150 m a.s.l. (Fig.9) – 52 km on road S from Paractito, 17°09' S, 65°37' W, investigated 14 December 1998 and 28–30 January 1999; upper montane rain

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Fig.9: "Old" Chapare road, border from upper montane rainforest to cloud forest, 2150 m a.s.l.

forests; slightly disturbed through mining activities; steep slopes; many small to medium-sized streams, roadside ditches, no ponds; annual precipitation supposedly 3500–4500 mm.

S of Cuevas (Fig.10). – Departamento Santa Cruz, Provincia Florida; few km by road S of Cuevas; 1300–1400 m a.s.l.; 18°14' S, 63°41' W; investigated 30–31 December 1997; semi-deciduous forest; partly disturbed; relationship to the Tucumanian-Bolivian montane forests; few small streams, ephemeral puddles present; 800–1000 mm annual precipitation; area within the influence of "surazos".

El Fuerte (Samaipata). – Departamento Santa Cruz, Provincia Florida; 5 km by road E of Samaipata; 1650–1950 m a.s.l.; 18°10' S, 63°50' W; investigated November 1994, 21 December 1997, 27 January 1998, and 8 February 1998; semi-deciduous forest, dry-valley vegetation, as well as elements from humid montane forests; large parts disturbed; small and medium-sized streams present in the area, many ephemeral water bodies of different sizes; 700–1000 mm annual precipitation; for a detailed description of the area see Köhler et al. (1995b) and Ibisch et al. (1996).

Fig.10: Bellavista, south of Cuevas, 1300–1400 m a.s.l.

Empalme (La Siberia). – Departamento Santa Cruz, Provincia Caballero; 31 km by road W of Comarapa; close to the Santa Cruz–Cochabamba border; 2450–2650 m a.s.l.; 17°51' S, 64°42' W; investigated 20 December 1997 and 23–25 November 1998; cloud forest ("Ceja"), parly disturbed; many small streams, numerous roadside ditches; annual precipitation expected to be around 2500–3800 mm; temperatures presumably not dropping below 0°C; usually strong wind from north-east.

SE of Guadálupe. – Departamento Santa Cruz, Provincia Vallegrande; 29 km by road SE of Guadalupe; 1650 m a.s.l.; 18°39' S, 63°59' W; investigated 7–8 January 1998; situated within Tucumanian-Bolivian montane forest, partly disturbed; many ephemeral ponds and puddles, one large stream; annual precipitation expected to be around 1500 mm; stronger relationships to the montane rainforests of the Yungas than to the Chaco montane forests; area within the influence of "surazos".

Fig.11: La Hoyada, 1800 m a.s.l.; montane rainforest with Locoto plantations in the foreground

Incachaca. – Departamento Cochabamba, Provincia Chapare; 2250–2350 m
a.s.l.; 17°15' S, 65°49' W; investigated 7–9 February 1998; upper montane rain-
forest partly influenced by "Ceja" climate; large parts disturbed; some parts cov-
ered by artificial conifer forest; many large and medium-sized streams, artificial
ponds; annual precipitation expected to be around 2500–3500 mm.

Karahuasi. – Departamento Cochabamba, Provincia Carrasco; 1800–2200 m
a.s.l.; 17°44' S, 64°44' W; north of Empalme; at the western limits of the Parque
Nacional Amboró and eastern limits of Parque Nacional Carrasco; investigated
3–4 January 1998, and 22–26 November 1998; upper montane rainforest; at lower
elevations disturbed through Locoto plantations; relatively steep slopes; all kinds
of water bodies available; annual precipitation expected to be 2500–4000 mm.

La Hoyada (Fig.11). – Departamento Santa Cruz, Provincia Florida; 1650–1900
m a.s.l.; 17°54' S, 63°08' W; north of Aguaclara, at the southern limits of the
Parque Nacional Amboró; investigated 16–18 November 1998; disturbed humid
montane forest, partially logged and cultivated areas, Locoto plantations; many
small rivers and creeks, some artificial ponds; valley partly situated on the south-
western flanks of the Cordillera Oriental; area within the influence of "surazos";
annual precipitation expected to be 2000–2500 mm.

La Yunga (Fig.12). – Departamento Santa Cruz, Provincia Florida; 2250–2350 m
a.s.l.; 18°04' S, 63°55' W; north of Mairana, at the southern limits of Parque
Nacional Amboró; investigated 31 December 1997 to 1 January 1998; upper mon-
tane rainforest and adjacent cloud forest; disturbed in the upper parts; small
streams but nearly no lentic water; annual precipitation expected to be 2500–3500
mm; influenced by "surazos".

Macuñucu. – Departamento Santa Cruz, Provincia Ichilo; 500 m a.s.l.; 17°44' S,
63°36' W; campsite within the Parque Nacional Amboró; investigated 1–3
December 1998; semi-humid lowland rainforests; many streams of all sizes; few
swampy areas; relationships to Amazonia as well as to transition forests; annual
precipitation expected to be around 1000–1500 mm; influenced by "surazos".

Fig.12: "La Yunga" (de
Mairana), 2300 m a.s.l.;
understory of cloud for-
est.

Mataracú. – Departamento Santa Cruz, Provincia Ichilo; 500 m a.s.l.; 17°33' S, 63°52' W; campsite within the Parque Nacional Amboró; investigated 15–19 November 1997 and 16–17 January 1999; humid Amazonian forest at the Andean foot; undisturbed; many small and medium-sized streams, swamps, small ephemeral ponds; annual precipitation around 1800–2300 mm; seasonal climate.

Paracti, Río Roncito. – Departamento Cochabamba, Provincia Chapare; these localities are close to each other on the road connecting Villa Tunari and Cochabamba (see Reynolds & Foster 1992 for details); 1600–1950 m a.s.l.; 17°11' S, 65°47' W; investigated 9–10 February 1998 and 13–14 January 1999; montane rainforest; partly disturbed along the roads; influenced by heavy traffic; small and medium-sized streams, roadside ditches; annual precipitation expected to be around 2500–4000 mm.

Fig.13: Approximately 40 km west of Río Seco, view from 1000 m a.s.l. to the eastern Chacoan lowlands.

Remates. – Departamento Santa Cruz, Provincia Caballero; 2000–2300 m a.s.l.; 17°53' S, 64°21' W; at the southern limits of the Parque Nacional Amboró, north of San Juan del Potrero; investigated 2–3 January 1998; upper montane rainforest and adjacent cloud forest; small and medium-sized streams, ponds and ephemeral puddles present; annual precipitation expected to be around 2500–3500 mm; influenced by "surazos".

W of Rió Seco (Fig.13). – Departamento Santa Cruz, Provincia Cordillera; approximately 30 km (airline) west of Río Seco; 950–1200 m a.s.l.; 18°35' S, 63°32' W; investigated 6–10 December 1997; Chaco montane forest; largely disturbed through cattle; sandstone formations; islands of forest remnants; small and medium-sized seasonal rivers, few ponds; annual precipitation expected to be 1000–1200 mm; influenced by "surazos".

Sehuencas. – Departamento Cochabamba, Provincia Carrasco; 2100–2300 m a.s.l.; 17°29' S, 65°17' W; within the Parque Nacional Carrasco; north of Montepunco; investigated 29 November to 6 December 1994 and 19–20 December 1997; upper montane rainforests; steep slopes; many small and larger streams, many puddles and roadside ditches; annual precipitation expected to be 3000–5000 mm; a detailed description of the area was given by Köhler et al. (1995a) and Ibisch (1996).

W of Vaca Guzman. – Departamento Chuquisaca, Provincia Luis Calvo; 13 km by road W of Vaca Guzman; 1340 m a.s.l.; 19°50' S, 63°49' W; investigated 15–17 December 1997; large artificial lagoon, surrounded by disturbed Tucumanian-Bolivian montane forest formations; annual precipitation expected to be 1200–1500 mm; influenced by "surazos".

MATERIAL AND METHODS

Field Work

Sampling Methods

Several techniques are available for compiling species lists or information on species richness for a site. The common field techniques are methods of general collecting, as historically practiced by herpetologists. Usually, they involve searching and collecting of specimens in all appropriate microhabitats during both, day and night and result in moderate habitat modification, such as turning rocks and fallen logs or removal of epiphytes. These general collecting techniques have been used for both long-term and short-term sampling projects, and according to Scott (1994), they are probably the most efficient way to estimate the species richness in an area within constrained time. No other collecting method is as productive in amassing species for a list and in obtaining series of specimens (Scott 1994).

The purpose in this study was to obtain as many species of amphibians as possible from a certain site to compare its relative species richness with those from other investigated sites. Because various sites had to be sampled, the available time for research was strongly limited at each site. To approach the necessary species inventories of the chosen sites, short-term, number-constrained sampling method called Systematic Sampling Survey (SSS) were used (see Scott 1994). This method has been used with birds (Terborgh 1989) and was suggested to be appropriate for tropical amphibian faunas inhabiting forest litter by Scott (1976, 1994). The Systematic Sampling Survey can be used to compare and rank habitats and sites according to relative species richness. This SSS sampling method depends on the validity of the following assumption: more species are present in a limited sample of a species-rich fauna than are present in a similarly sized sample from a less rich fauna (see Hurlbert 1971).

The SSS method requires equivalent preselected numbers of specimens (number-constrained) sampled at different sites. According to Scott (1994), samples of approximately 100 specimens may be adequate to rank a series of diverse faunas with respect to species richness. If the site has not been adequately sampled in the investigators' view, efforts can be concentrated on the collection of additional species (not specimens).

During this study, amphibians were searched and collected at the chosen sites by at least two experienced investigators (up to five). Usually, the major habitat types at one site were identified and briefly surveyed during the day. Thereby, it was most important to find possible amphibian breeding sites (e.g., water bodies with egg masses or tadpoles) which were investigated more thoroughly at night. The specimens were mainly encountered by visual sightings and recognition of calling males. During the day, rocks, fallen logs, and bolsters of moss were turned to discover hidden specimens. Small fishing nets were used to obtain tadpoles from their aquatic environment. It was tried to search all suitable habitat types present at one site.

Each site was sampled until approximately 100 specimens (a supposedly sufficient number according to Scott 1994) were collected or encountered. If it was not possible to obtain the number of specimens required after a prolonged time of searching (e.g., due to dry weather conditions), the site was investigated for a second period. Therefore, the sampling time at each site varied considerably, from few hours to several days. During searching, some individuals were identified by their advertisement call and were not seen and collected. Usually, only a representative part of the collected specimens was prepared as vouchers.

Limitations: The results from short-term sampling are highly depending on collecting and environmental variables. Possibly, one of the most important variables in sampling amphibian species is the weather during sampling. Using the SSS technique, unfortunate conditions lead to a prolonged sampling time to receive comparable data. Furthermore, SSS enables the investigator to reduce bias

in collecting efforts (in contrast to passive techniques such as pitfall arrays which depend on trap location and species susceptibility). On the other hand secretive, fossorial, canopy-dwelling, and deep-water species are more difficult to inventory and may require specialized searching methods. In practice, there is usually no time (and/or money) to use specialized techniques to investigate a special habitat type. Therefore, a principally different habitat distribution of frog species among different sites will reduce the comparability of the received data.

Finally, with SSS the actual number of species occurring in a defined area will not be estimated accurately. It only enables an investigator to rank sites and habitats according to their relative species richness. For this reason, own results were combined with literature data to conduct the Parsimony Analysis of Endemism (see below).

Moreover, sampled sites apparently were not always of the same size. Therefore, the comparisons according to species richness have to be taken with some precaution, because they are not reflecting absolute values.

Biological Data

Although the primary goal of the investigation was to obtain data on the amphibian diversity in Bolivian montane forests, many observations were made on the species' biology in the field. These included for example the kind of microhabitats used by a species, the calling activity of males, the time of reproduction, the character and size of egg clutches, the kind off egg laying sites, observations on escape and/or defense behavior, predation, and miscellaneous other things. Most of these observations provide valuable new information to the knowledge of certain Bolivian species and it would be somehow irresponsible to withhold such data from any herpetologist. Moreover, these biological data can give at least some insight to the complex ecological relationships within an amphibian community.

As a standard, at least following biological observations were noted for every specimen collected: kind of microhabitat used, substrate, general activity, calling activity in males, minimum distance to other calling males of the same species, reproductive state of females, as well as any other remarkable behavior observed.

Additionally, it was tried to record the vocalization of every species encountered calling (for methods see below). The advertisement call often significantly helped to identify the species. Moreover, analysis of the recordings subsequently to the field trip may reveal the presence of additional anuran species which were unable to be collected.

Associated Data

Besides the collecting of specimens and the observation on the species' biology, certain abiotic parameters were measured. Geographic position was obtained using a Magellan 3000 XL GPS receiver. Elevation above sea level was measured

with a Thommen altimeter. Air and water temperatures were obtained with a Greisinger GTH 215 digital thermometer (precision 0.1°C). Climatic conditions (e.g., dry, light rain, heavy rain, fog, rained before sampling, wind, etc.) during sampling time were noted, although the absolute amount of precipitation was not measured due to the limited time at each site. Additionally, color slides were taken from the sampled habitats to better remind the general conditions.

All data obtained, whether biological or abiotic, were noted in a field book or on a field catalogue sheet similar to that figured by Inger (1994:62).

Preparation of voucher specimens

After collecting, amphibian specimens were carried in transparent plastic bags. Color slides and notes on coloration in life were taken from living specimens before preparing them as voucher specimens. The specimens were killed in Chloretone solution that was prepared in dissolving a small amount of hydrous chlorobutanol crystals in 0.5 liter of water. This solution was freshly prepared every three weeks when gradually loosing its strength (compare McDiarmid 1994b). Species showed noticeable differences responding to the Chloretone solution. Some died rather quickly (within 2 minutes), others took longer (up to 10 minutes).

After death, the completely relaxed specimens were fixed with 96% ethanol in a plastic tray with white paper towels on its bottom soaked with ethanol. Each specimen was positioned in the tray in a way that facilitate measurements and examination of key characters. In frogs, the limbs were drawn in next to the body and flexed into a natural position; fingers and toes were straightened and spread to display tubercles and webbing. Since the ethanol does not penetrate the body of larger specimens sufficiently within a short time, additional 96% ethanol was injected into their body cavity through the anus. The fixation time depended on the specimens' size and on the species (e.g., individuals of the *Hyla pulchella* species group needed significantly more time for fixation). Usually, small specimens were fixed within a few minutes and then had to be removed from the 96% ethanol quickly to avoid desiccation. Large specimens remained in the covered fixation tray for several hours.

When fixed, a tag with a field number (JKSL) was attached to each specimen. Each number corresponds to the data for the respective specimen noted in a field book. Among these data are information about the exact locality, date, time, collector, habitat, weather conditions, calling activity, coloration in life, and miscellaneous observations.

The fixed and tagged specimens were transferred to jars with 70% ethanol for final preservation. Usually, smaller, more fragile specimens were put into separate small jars to avoid damages, whereas more robust specimens of one locality were preserved and transported together in a larger jar.

Tadpoles were killed, fixed, and preserved putting them into 5–8% formalin immediately after collecting (see McDiarmid 1994b). Due to a larger content of water, larvae require a stronger fixative than adults and ethanol is seemingly not adequate. Each tadpole sample from one locality received a JKSL field number that was put together with the sample into the jar.

Taxonomy

Species identifications

Comparison with museum specimens and literature data

Correct and accurate species identification is the required basis for every study on amphibian diversity, distribution, and biology. The identification of specimens included in this study was partly based on the comparison of morphological key characters with the data provided in the literature, mainly original species descriptions or subsequent revisions of species groups. Additionally, collected specimens were compared with material already deposited in scientific collections, especially with type specimens. Measurements of specimens (for comparisons) were taken to the nearest 0.1 mm using dial calipers. The following account contains all institutions from which material was examined for the purpose of proper species identifications as well as institutions where specimens collected during this study were deposited subsequently.

BMNH   Natural History Museum, London
CBF   Colección Boliviana de Fauna, La Paz
CM   Carnegie Museum, Pittsburgh
KM   Musaei Zoologici Uniwersytetu Jagiellonskiego, Kraków
KU   Kansas University, Natural History Museum, Lawrence
MNCN   Museo Nacional de Ciencias Naturales, Madrid
MNHN   Muséum national d'Histoire naturelle, Paris
MZUSP   Museu de Zoologia da Universidade de São Paulo
NHMG   Naturhistoriska Museet Göteborg
NKA   Museo de Historia Natural "Noel Kempff Mercado" (amphibian collection), Santa Cruz de la Sierra
NMW   Naturhistorisches Museum Wien
NRM   Naturhistoriska Riksmuseet, Stockholm
SMF   Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt/Main
SMNS   Staatliches Museum für Naturkunde, Stuttgart
USNM   National Museum of Natural History, Smithsonian Institution, Washington
ZFMK   Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn
ZMB   Zoologisches Museum Berlin
ZSM   Zoologische Staatssammlung München

Following type specimens have been examined during the present study: *Atelopus tricolor* (ZFMK 28103, lectotype), *Bufo acutirostris* (ZSM 1147/0, holotype), *Bufo amboroensis* (NKA 953, holotype), *Bufo echinodes* (USNM 257799, holotype), *Bufo fissipes* (BMNH 1947.2.20.64, holotype), *Bufo inca* (USNM 49557, holotype), *Bufo justinianoi* (NKA 950, holotype), *Bufo pleuropterus* (KM 1030, holotype), *Bufo simus* (NMW 16521, syntype), *Bufo stanlaii* (CBF 3346, ZFMK 60464, 67096–97, USNM 257796–98, ZSM 144/1999, holotype and paratypes), *Centrolenella bejaranoi* (KU 182369–71, holotype and paratypes), *Centrolenella bergeri* (KU 182363–68, holotype and paratypes), *Centrolenella phenax* (KU 162263–64, holotype and paratype), *Centrolenella pluvialis* (KU 173224–27, holotype and paratypes), *Dendrobates eucnemis* (NMW 19190 [1,2,4], syntypes), *Protherapis bolivianus* (BMNH 1947.2.13.89, –91, lectotype and paralectotype), *Hyla aperomea* (KU 181812, holotype), *Hyla armata* (BMNH 1947.2.13.60, syntype), *Hyla callipleura* (BMNH 1947.2.13.64–74, lectotype and paralectotypes), *Hyla carinata* (NRM 1874, syntypes), *Hyla leali* (KU 92058–59, paratypes), *Hyla minima* (NMW 19436, holotype), *Hyla ocapia* (NRM 1873, syntypes), *Hyla prasina* (ZMB 4675, holotype), *Hyla riveroi* (CM 37433, holotype), *Hyla zebra* (MNHN 4817, syntypes), *Nototrema bolivianum* (NMW 16490, holotype), *Adenomera griseigularis* (ZFMK 31800, holotype), *Eleutherodactylus ashkapara* (CBF 3344, ZFMK 70318, holotype and paratype), *Eleutherodactylus danae* (KU 162307, holotype), *Eleutherodactylus dundeei* (USNM 507897–99, paratypes), *Eleutherodactylus lindae* (KU 162305, holotype), *Eleutherodactylus llojsintuta* (CBF 3300–01, NKA 3475–76, ZFMK 66387–89, holotype and paratypes), *Eleutherodactylus mendax* (KU 173234–35, holotype and paratype), *Eleutherodactylus olivaceus* (CBF 3329–30, ZFMK 67132–33, holotype and paratypes), *Eleutherodactylus pluvicanorus* (NKA 1100–04, ZFMK 60186–91, holotype and paratypes), *Eleutherodactylus rhabdolaemus* (KU 175082–83, paratypes), *Eleutherodactylus samaipatae* (ZFMK 59600, holotype), *Eleutherodactylus zongoensis* (CBF 2503, holotype), *Eleutherodactylus* species A (CBF 3341, ZFMK 60402, holotype and paratype), *Hylodes cruralis* (BMNH 1947.2.15.70, holotype), *Hylodes fenestratus* (NMW 19940 [1,2], syntypes), *Hylodes gollmeri bisignata* (NMW 16502, holotype), *Hylodes granulosus* (BMNH 1947.2.15.72, holotype), *Hylodes peruvianus* (NHMG 490, holotype), *Hylodes platydactylus* (BMNH 1947.2.15.91–92, –94, lectotype and paralectotypes), *Ischnocnema sanctaecrucis* (NKA 1198, holotype), *Phrynopus kempffi* (NKA 480, paratype), *Phrynopus pinguis* (CBF 1906–08, 1911–12, holotype and paratypes), *Phyllonastes carrascoicola* (ZFMK 59569–73, holotype and paratypes), *Phyllonastes ritarasquinae* (CBF 3350, holotype), *Telmatobius huayra* (CBF 1223, holotype), *Telmatobius jahuira* (CBF 1675–76, holotype and paratype), *Telmatobius verrucosus* (NMW 22922, holotype), *Telmatobius yuracare* (NKA 511–13, paratypes), *Caecilia marcusi* (ZSM 79/1982, 83/1982, holotype and paratypes).

Additionally, topotypic material of following species has been examined: *Bufo castaneoticus, Bufo quechua, Epipedobates pictus, Hyla charazani, Scinax castroviejoi, Telmatobius edaphonastes,* and *Hamptophryne boliviana.*

Comparison of Advertisement Calls

Another important resource for distinguishing species was the analysis of advertisement calls. It has been demonstrated that mating calls are an effective prezygotic isolation mechanism in anurans (e.g., Blair 1958, 1962, Duellman 1967, Fouquette 1960, Littlejohn 1965, Penna 1997). Every species has its own distinct call which differs from calls of other species. This is especially true for co-existing species where barriers in time and space are only insufficiently developed (Hödl & Schaller 1978). In the present study, recorded advertisement calls were compared with already published data and/or with own recordings from other localities and species.

Nomenclature

Generally, terminology and taxonomic classification follows Frost (1985) and Duellman (1993). In cases where the taxonomic status of a specimen or a population deserves comments, these are given in the taxonomic account. Some scientific species names used herein are incomplete, containing only the generic name with the addition "species A, B, ...". This refers to populations which have already been identified as distinct species but no species name is available. Most of these new species will be named in the near future and in some cases the description is already in press. If so, this is mentioned in the taxonomic account. A "cf." in front of the species name means that the specific identification is only preliminary and possibly the populations actually correspond to a closely related but different species.

Bioacoustics

Recording

Unless otherwise mentioned, frog calls were recorded in the field using a Sony WM-D6C professional walkman or an Aiwa HS-F150 cassette recorder, respectively, a Sennheiser Me-80 directional microphone, and TDK-MA60 cassettes. No filters or noise reduction systems were used during recording. Gain settings were adjusted manually to ensure that calls were recorded at optimal levels, avoiding clipping or distortion. The distance between microphone and recorded individual varied from few centimeters to several meters and depended on the accessibility of the habitat and call motivation of the individual. Disturbance of calling males caused by the procedure of recording was tried to reduce to a minimum. During recording the air and/or water temperature were measured as close as possible to

the calling specimens. The following associated data were spoken on the tape previous or subsequent to the call recording: date, time of recording, locality, specific identification of recorded individual (if possible), calling site habitat, distance to calling individual to be recorded, general weather conditions, other species calling in background, and air and/or water temperature. The greatest part of these data as well as the corresponding field number of the voucher specimen were later noted in a field book and in part also on the tape box.

Sampling, analysis, and presentation

Recordings were sampled with a rate of 22.05 kHz and 16-bit resolution using IBM compatible computers. Analysis of the calls was conducted with the sound analysis software Cool Edit 96 (Syntrillium Software Corporation). The choices of the recordings selected for analysis were based on the certainty of the identification of the recorded individual as well as on criteria of sound quality. Frequency information was obtained through fast Fourier transformation (FFT, width 1024 points). Temporal information was measured in oscillograms. In some recordings, frequency sections not containing call structures were filtered to remove background noise. Settings for frequency and time ranges and resolutions were chosen according to the essential structural parameters to be measured. A representative audiospectrogram (FFT width 256 points) and oscillogram of a 'typical' call is presented in the species account chapter. The figured time segment was chosen to provide as much information as possible on the principal structure of the call.

Call descriptions

Terminology in call descriptions generally follows Heyer et al. (1990). However, note and pulse repetition rates were calculated within calls or within notes, respectively, following method "B" of Scoville & Gottlieb (1978). They were not reckoned up with call repetition rates like done by other authors (e.g., Márquez et al. 1993, 1995). The experience showed that different call repetition rates may be the result of differences in individual calling motivation, whereas calculation of repetition rates within calls (or notes) resulted in a character which is very species specific and independent from individual motivation. In the call descriptions, the range of numerical parameters is followed by the mean and one standard deviation in parentheses. To facilitate the understanding, brief definitions of the used terms follow.

A u d i o s p e c t r o g r a m : A visual representation of a call displaying the frequency of the sound over time.
C a l l : An acoustic unit of frog vocalization, may be composed of either identical or different notes; separated from other calls by a period longer than the call; can function alone as an independent vocalization.

Call group: Calls may be organized into groups which are separated by long periods of silence; spacing of calls in groups is regular or changing in a predictable pattern.

Call (repetition) rate: Number of calls repeated in a defined period of time. The value is provided as calls per minute.

Dominant frequency peak: The frequency of the call (or note) at which most sound energy is concentrated.

Frequency modulation: Changes in frequency of a sound over time.

Frequency range: The frequencies of the call at which at least some sound energy is recognizable. Often, the actual frequency range is difficult to measure, because its representation in an audiospectrogram is dependent from the spectral settings of the used software program, or the call's frequency range is overlapped by background noise in the frequency analysis.

Harmonic: Many sounds have their energy concentrated in several separated, evenly spaced frequencies called harmonics. These frequencies are multiples of the lowest or first harmonic. In pulsed calls, some frequency bands might reflect amplitude modulation generated by the laryngial glottis and is not to be confused with the carrier frequency and its harmonics generated by the vocal cords (see Bradbury & Vehrencamp 1998).

Note: Calls are often broken into smaller subunits by 100% amplitude modulation with only short intervals between them relative to length of note. A call which is amplitude modulated to 100% is said to be made up of notes; one which is modulated at less than 100% is said to be pulsed.

Note (repetition) rate: Number of notes repeated in a defined period of time within a call. The value is provided as notes per second.

Oscillogram: A visual representation of a call displaying the amplitude of the sound as it changes over time.

Pulse: The smallest named subunit of a call (or a note), produced by amplitude modulation of less than 100%. A note which is modulated to whatever depth is said to be pulsed. A call in which the primary modulation is not 100% is said to have only one note which is pulsed.

Pulse (repetition) rate: Number of pulses repeated in a defined period of time within a note. The value is provided as pulses per second.

Inclusion of literature data

When investigating a certain area within limited time, it is mostly not possible to find all the species that actually occur there. Especially the inhomogenous climatic conditions during sampling time may be responsible for obviously incomplete sampling results. Moreover, as mentioned above the used SSS technique is not adequate to estimate the actual number of species occurring in a defined area

accurately. For this reason, it was necessary to combine own findings with distribution data already published in papers concerning Bolivian amphibians to conduct the Parsimony Analysis of Endemism (PAE) described below. In some cases, species have not been recollected since their description, but there is no reason to believe that they got extinct. In many cases, there are vouchered records in the literature from sites or elevations which were not accessible during the present study. The information was included in the analysis of general distribution patterns, if the records were regarded to be reliable.

Parsimony analysis of endemism

Although identifying areas of endemism is widely recognized as critical in all methods of biogeographic analysis (e.g., Harold & Mooi 1994), few methods of determining patterns of endemism exist. Phenetic clustering methods have been used to analyze species similarities between sites, but this technique is plagued with problems, with different similarity indices and clustering methods producing different dendrograms. Recently, parsimony analysis, developed for phylogenetic studies, has been used to determine hierarchical patterns of endemism. This method, Parsimony Analysis of Endemism (PAE), was first described by Rosen (1988) and Rosen & Smith (1988), and was later adopted for herpetofaunal analysis (e.g., Raxworthy & Nussbaum 1996, 1997, Harvey 1998). Under ideal conditions (i.e., when faunas are known completely) this technique produces dendrograms that link sites on the basis of shared species. Species endemic to one or more areas are treated as apomorphies.

PAE resembles cladistic phylogenetic analysis, except that the operational taxonomic units are geographic areas rather than taxa, and the characters used in PAE are species distributions. The character state for each species distribution is either present or absent. Shared presence of species provides evidence of biogeographic affinity between different sites, and is used to produce a hierarchical pattern of endemism. PAE reversals either represent species that have gone extinct or were missed during surveys.

Dendrograms resulting from PAE might demonstrate historical relationships among the faunas. However, linkage between sites might simply reflect shared environmental conditions that result in colonization by similar faunas.

Parsimony analysis of endemism was done using PAUP* (Phylogenetic Analysis Using Parsimony) version 4.0 (Swofford 1998). Heuristic searches were performed using the TBR (tree bisection reconnection) branch swapping algorithm. When more than one most parsimonious tree were found, a strict consensus of all trees was calculated. Trees were rooted using a hypothetical outgroup area devoid of all species (see Rosen & Smith 1988). All characters were analyzed unordered, without differential character weighting. No upper limit was imposed on the maximum number of trees saved. To get an indication of the robustness of the pro-

duced topologies, bootstrap analyses were performed (Felsenstein 1985) as implemented in PAUP*. This method builds trees based on the same number of characters as the maximum parsimony analysis, but the characters are chosen randomly, and characters are not eliminated from the pool of characters. Thus, some characters will be used more than once for tree calculation, while others will not be used. A total of 500 of these tree pseudoreplicates was calculated. The percentage in which a certain clade is present in these pseudoreplicates is the bootstrap value.

Data for the PAE (and NJAE) analysis of sites were taken from the following sources: Balta, Peru (Duellman & Thomas 1996); Cocha Cashu, Peru (Rodríguez & Cadle 1990, Rodríguez 1992); Cuzco Amazonico, Peru (Duellman & Salas 1991); Pakitza, Peru (Morales & McDiarmid 1996); Panguana, Peru (Schlüter 1984, Aichinger 1985); southeastern Peru (Cadle & Patton 1988 and misc. publ.); Puerto Almacén, Bolivia (De la Riva 1993d); Manaus, Brazil (Zimmerman & Rodríguez 1990); Los Colorados, Argentina (Lavilla et al. 1995). Used data sets may be obtained from the author.

Neighbor joining analysis of endemism

Neighbor Joining (NJ) analysis is a second method used in phylogenetic studies to produce dendrograms of relationships. NJ analysis first calculates a distance matrix between data sets and then searches for the tree which connects all sets with the minimum amount of branch length. Starting from the initial distance matrix, the program produces a further matrix which contains the distance between nodes. The two nodes with the closest distance are connected in the tree and are replaced by a new node which corresponds to their putative last common ancestor. This cluster is thus considered as one unit only in the further analysis. The program now searches again for the nodes with closest distance, etc., until all data sets in the tree are connected.

Here, the method was adopted to analyze patterns of endemism. Analogue to the PAE, this method is here called Neighbor Joining Analysis of Endemism (NJAE). The NJAE was conducted using exactly the same data sets and options as in the PAE. NJAE was based on total character difference. The NJAE method produced exactly the same dendrograms as PAE, but partly resulted in different bootstrap values. In the results chapter, usually only one dendrogram is presented giving both bootstrap values, that for PAE and NJAE.

Limitation of data

Like already stated, data resulting from field surveys in general, and especially from short term ones, are usually not complete. It has been demonstrated in long term studies that abundance of amphibian species in tropical forests show rather chaotic patterns (Duellman 1995). According to Pearman et al. (1995), accumulation of species num-

bers is reached best by the usage of a combination of different sampling methods. Even then, the species diversity at a site can not be discovered completely. As is obvious from the sampling methods described above, there was not the opportunity to use (or test) different and time consuming methods for sampling. All obtained data and the conclusions drawn from it have therefore to be regarded as preliminary. Including literature data, as done in the analysis (PAE, NJAE), provides a slightly more realistic picture of actual patterns. However, comparably few publications deal with Bolivian amphibians and the available data to fill up existing gaps are less than sufficient. Therefore it is almost sure that future findings will restrict the results and conclusions presented herein.

In practice, and like any other method for discovering patterns among regional faunas, PAE is influenced by sampling errors. The degree to which incomplete data affect the results of PAE are not yet quantitatively assessed. Nevertheless, PAE provides testable biogeographic hypotheses of faunal relationships.

RESULTS

Preliminary checklist and distributions

In the following, an updated checklist of the amphibians of Bolivia is provided. Many of the included data resulted from own studies presented herein. Although most of the species are also listed in De la Riva et al. (2000), some differences exist which are due to my personal point of view and/or data that were not included in the mentioned publication. In addition to the account of species, data on the distribution within the political borders of Bolivia's Departamentos as well as within the ecoregions suitable for the species are provided. Moreover, it is stated, if the species is considered to be endemic for Bolivia or not. An asterisk (*) following the year of description indicates that the type locality of the species is in Bolivia. The checklist is followed by some annotations, because certain records deserve comments.

Abbreviations used in the table are as follows. (1) Abbreviations of Departamentos: LP – La Paz; CB – Cochabamba; SC – Santa Cruz; BE – Beni; PA – Pando; PO – Potosí; OR – Oruro; CH – Chuquisaca; TA – Tarija. (2) Abbreviations of suitable ecoregions: AM – Amazonian rainforests; Cej – "Ceja" (cloud forest); Chi – Chiquitanía forests (includes the Cerrado formations); CL – Chaco lowland forests; CM – Chaco montane forests; HiA – high-Andean vegetation; HTf – humid transition forests; IAV – inter-Andean dry-valleys; PCS – forests of the pre-Cambrian shield; TB – Tucumanian-Bolivian forests; WSa – wet savannas; YU – Yungas – montane rainforests. (3) Others: e – occurrence expectable; X – occurrence documented by voucher specimens and/or published data.

Species	End.	Departamento									Ecoregion(s)
		LP	CB	SC	BE	PA	PO	OR	CH	TA	
Bufonidae											
Atelopus tricolor Boulenger, 1902		X	X								YU
Bufo amboroensis Harvey & Smith, 1993*	●	e	X	X							YU
Bufo arenarum Hensel, 1867			X	X					X	e	CL, CM, IAV, TB
Bufo castaneoticus Caldwell, 1991		e			e	X					AM
Bufo fissipes Boulenger, 1903		X	X		X						AM, YU
Bufo granulosus Spix, 1824		X	X	X	X	X			e	X	AM, CL, CM, HTf, PCS, WSa
Bufo guttatus Schneider, 1799		X		X	e	X					AM, HTf, PCS
Bufo justinianoi Harvey & Smith, 1994*	●	X	X	X	X						YU
Bufo marinus (Linnaeus, 1758)		X	X	X	X	X					AM, HTf, PCS
Bufo paracnemis Lutz, 1925				X	X				X	X	Chi, CL, CM, TB, WSa
Bufo poeppigii Tschudi, 1845		X	X	X							AM, YU
Bufo quechua Gallardo, 1961*	●	e	X	X							Cej, YU
Bufo rumbolli Carrizo, 1992										X	IAV, TB
Bufo spinulosus Wiegmann, 1834		X	X				X	X	X		HiA, IAV
Bufo stanlaii Lötters & Köhler, 2000	●		X	X							YU
Bufo typhonius complex		X	X	X	X	X			X		AM, Chi, HTf, IAV, PCS, YU, WSa
Bufo veraguensis Schmidt, 1857		X	X	X							IAV, TB, YU
Dendrophryniscus minutus (Melin, 1941)		e	X		e						AM
Melanophryniscus rubriventris (Vellard, 1947)			X	e					X	X	IAV, TB
Centrolenidae											
Cochranella bejaranoi (Cannatella, 1980)*	●	X	X	X					X		TB, YU
Cochranella nola Harvey, 1996*	●		e	X					e		TB, YU
Cochranella pluvialis (Cannatella & Duellman, 1982)		X	e								YU

Species	End.	Departamento									Ecoregion(s)
		LP	CB	SC	BE	PA	PO	OR	CH	TA	
Hyalinobatrachium bergeri (Cannatella, 1980)*		X	X	X							AM, YU
Dendrobatidae											
Allobates femoralis (Boulenger, 1884)		X	e		e	X					AM
Colostethus brunneus (Cope, 1887)				X							AM, HTf, PCS
Colostethus mcdiarmidi Reynolds & Foster, 1992*	●	X	X								YU
Colostethus trilineatus Boulenger, 1884		X	X	X	X	X					AM, HTf, PCS
Colostethus sp. A						X					AM
Epipedobates bolivianus (Boulenger, 1902)*	●	X	e								YU
Epipedobates hahneli (Boulenger, 1883)		X			e	X					AM
Epipedobates pictus (Bibron in Tschudi, 1838)*		X	X	X	X	e					AM, Chi, HTf, PCS, YU
Epipedobates trivittatus (Spix, 1824)		e				X					AM
Hylidae											
Gastrotheca lauzuricae De la Riva, 1992*	●		X	e							Cej, YU
Gastrotheca marsupiata (Duméril & Bibron, 1841)		X	X				X	X	X		HiA, IAV
Gastrotheca splendens (Schmidt, 1857)	●		e	X							YU
Gastrotheca testudinea (Jiménez de la Espada, 1871)		X	X	e							AM, YU
Gastrotheca sp. A	●	e	X	X	X						Cej, YU
Hyla acreana Bokermann, 1964		e	X	X	X	X					AM, Chi, HTf, PCS
Hyla albonigra Nieden, 1923*	●		X	e				X	X	e	HiA, IAV
Hyla albopunctata Spix, 1824				X							Chi, PCS
Hyla andina Müller, 1924		X	X	X					X	X	Cej, HiA, IAV, TB, YU
Hyla armata Boulenger, 1902*		X	X	X							YU
Hyla balzani Boulenger, 1898*		X	e								YU
Hyla bifurca Andersson, 1945		e	e	X	X	X					AM, HTf, PCS

Species	End.	LP	CB	SC	BE	PA	PO	OR	CH	TA	Ecoregion(s)
Hyla boans (Linnaeus, 1758)		X	e	X	X	e					AM, HTf, PCS
Hyla calcarata Troschel, 1848		X			e	X					AM, HTf, PCS
Hyla cf. callipleura Boulenger, 1902*	●		X	e							YU
Hyla charazani Vellard, 1970*	●	X									Cej, IAV
Hyla chlorostea Reynolds & Foster, 1992*	●		X								YU
Hyla fasciata Günther, 1859		e		X	X	X					AM, HTf, PCS
Hyla geographica Spix, 1824		X	X	X	X	e					AM, HTf, PCS, WSa
Hyla granosa Boulenger, 1882		e			e	X					AM, HTf
Hyla koechlini Duellman & Trueb, 1989		X	e	X	X	e					AM, HTf
Hyla lanciformis (Cope, 1870)		X	X	X	X	X					AM, HTf, PCS, WSa
Hyla leali Bokermann, 1964		e	X	X	X	e					AM, HTf, PCS, WSa
Hyla leucophyllata (Beireis, 1783)		e	e	X	X	X					AM, HTf, PCS, WSa
Hyla marianitae Carrizo, 1992			X	X					X	e	IAV, TB, YU
Hyla marmorata (Laurenti, 1768)		X		X	e	X					AM, HTf, PCS
Hyla punctata (Schneider, 1799)		X	e	X	X	X					AM, Chi, CL, HTf, PCS, WSa
Hyla raniceps (Cope, 1862)				X	X						Chi, CL, PCS, WSa
Hyla rhodopepla Günther, 1859		X	X	X	e	e					AM, YU
Hyla riveroi Cochran & Goin, 1970		X	X	X	X	X					AM, HTf, PCS
Hyla rubicundula Reinhardt & Lütken, 1862					e	e					Chi
Hyla sarayacuensis Shreve, 1935		X			e						AM
Hyla melanargyrea Cope, 1887				X	e						Chi, PCS
Hyla minuta Peters, 1872		e	e	X	X	X			X	X	AM, Chi, HTf, IAV, PCS, TB, YU
Hyla nana Boulenger, 1889				X	X				e		Chi, CL, HTf, WSa

Species	End.	Departamento									Ecoregion(s)
		LP	CB	SC	BE	PA	PO	OR	CH	TA	
Hyla parviceps Boulenger, 1882		e	e	X	e	X					AM, HTf, PCS
Hyla schubarti Bokermann, 1963		X			e	X					AM, HTf, PCS
Hyla tritaeniata Bokermann, 1965				X	X						Chi, WSa
Hyla sp. A	●	e	X								AM, YU
Hyla sp. B		e		e	e	X					AM
Osteocephalus buckleyi (Boulenger, 1882)		e	X	X	X	e					AM, HTf
Osteocephalus leprieurii (Duméril & Bibron, 1841)		e		X	e	e					AM, HTf, PCS
Osteocephalus pearsoni (Gaige, 1929)*		X	e	e	X	e					AM, HTf
Osteocephalus taurinus Steindachner, 1862		X	X	X	X	e					AM, HTf, PCS
Osteocephalus sp. A				X	e						AM, HTf, PCS
Phrynohyas coriacea (Peters, 1867)		e		X	e	e					AM, HTf, PCS
Phrynohyas resinifictrix (Goeldi, 1907)		e			e	X					AM
Phrynohyas venulosa (Laurenti, 1768)		X	X	X	X	X			X	X	AM, Chi, CL, CM, HTf, IAV, PCS, TB
Phyllomedusa bicolor (Boddaert, 1772)		e		e	X	e					AM
Phyllomedusa boliviana Boulenger, 1902*		X	e	X					X	e	Chi, IAV, TB, YU
Phyllomedusa camba De la Riva, 2000*		X	e	X	X	X					AM, HTf, PCS
Phyllomedusa hypochondrialis (Daudin, 1800)				X	X						Chi, CL, PCS, WSa
Phyllomedusa palliata Peters, 1872		e	e	X	X	X					AM, HTf
Phyllomedusa sauvagii Boulenger, 1882				X					e	X	CL
Phyllomedusa tomopterna (Cope, 1868)		X	e		e	e					AM
Phyllomedusa vaillanti Boulenger, 1882		X	X	X	e	e					AM, HTf, PCS
Scarthyla ostinodactyla Duellman & de Sá, 1988		e									AM
Scinax acuminatus (Cope, 1862)				X					e	e	Chi, CL

Species	End.	Departamento									Ecoregion(s)
		LP	CB	SC	BE	PA	PO	OR	CH	TA	
Scinax castroviejoi De la Riva, 1993*			X	X					X	e	TB, YU
Scinax chiquitanus (De la Riva, 1990)*		e	e	X	X	X					AM, HTf, PCS
Scinax fuscovarius (Lutz, 1925)			X	X	X				X	e	IAV, Chi, CL, CM, HTf, PCS, TB, WSa
Scinax garbei (Miranda-Ribeiro, 1926)		e	X	X	X	X					AM, HTf, PCS
Scinax nasicus (Cope, 1862)				X	X				e	e	Chi, CL, PCS
Scinax nebulosus (Spix, 1824)				X	e						AM, HTf, PCS, WSa
Scinax parkeri (Gaige, 1929)*				X	X						AM, HTf, PCS, WSa
Scinax ruber (Laurenti, 1768)		X	X	X	X	X					AM, HTf, PCS, WSa
Scinax squalirostris (Lutz, 1925)		X	e	e	e						AM, HTf, PCS, WSa
Sphaenorhynchus lacteus (Daudin, 1802)		e	e	X	X	X					AM, HTf, PCS, WSa
Leptodactylidae											
Adenomera andreae Müller, 1923		e	X	X	X	X					AM, HTf, PCS
Adenomera diptyx (Boettger, 1885)				X					e		Chi, CL, PCS
Adenomera hylaedactyla (Cope, 1868)		X	X	X	X	X					AM, Chi, HTf, PCS, WSa
Ceratophrys cornuta (Linnaeus, 1758)		e	X	X	X	e					AM, HTf, PCS
Ceratophrys cranwelli Barrio, 1980				X					e	X	Chi, CL
Chacophrys pierottii (Vellard, 1948)				X					e	X	CL
Eleutherodactylus ashkapara Köhler, 2000*	●	e	X	e							YU
Eleutherodactylus bisignatus (Werner, 1899)*	●	X	e								YU
Eleutherodactylus cruralis (Boulenger, 1902)*		X	X	X							AM, YU
Eleutherodactylus danae Duellman, 1978		e	X								YU
Eleutherodactylus discoidalis (Peracca, 1895)			X	X					X	X	TB, YU
Eleutherodactylus dundeei Heyer & Muñoz, 1999				X							Chi, PCS

Species	End.	LP	CB	SC	BE	PA	PO	OR	CH	TA	Ecoregion(s)
Eleutherodactylus fenestratus (Steindachner, 1864)		X	X	X	X	X					AM, YU
Eleutherodactylus fraudator Lynch & McDiarmid, 1987*	●		X	X							Cej, YU
Eleutherodactylus llojsintuta Köhler & Lötters, 1999*	●	e	X	X							YU
Eleutherodactylus mercedesae Lynch & McDiarmid, 1987*	●	X	X	e							YU
Eleutherodactylus olivaceus Köhler et al., 1998*		e	X	X							AM, YU
Eleutherodactylus platydactylus (Boulenger, 1903)		X	X	X							Cej, YU
Eleutherodactylus pluvicanorus De la Riva & Lynch, 1997*	●	e	X	X							Cej, YU
Eleutherodactylus rhabdolaemus Duellman, 1978		X	X	X							Cej, YU
Eleutherodactylus samaipatae Köhler & Jungfer, 1995*			e	X					e	X	IAV, TB
Eleutherodactylus toftae Duellman, 1978		e	X	e							AM
Eleutherodactylus ventrimarmoratus (Boulenger, 1912)		e	e		e	X					AM, YU
Eleutherodactylus zongoensis Reichle & Köhler, 1997*	●	X	e	X							YU
Eleutherodactylus sp. A	●								e		TB, YU
Ischnocnema quixensis (Jiménez de la Espada, 1872)		e	X			X					AM
Ischnocnema sanctaecrucis Harvey & Keck, 1995*	●	e	X	X							YU
Lepidobatrachus laevis Budgett, 1899				X					e	X	CL
Leptodactylus bolivianus Boulenger, 1898*		X	X	X	X	X					AM, HTf, PCS
Leptodactylus bufonius Boulenger, 1894				X	X				X	X	CL
Leptodactylus chaquensis Cei, 1950			X	X	X				X	X	Chi, CL, CM, PCS, TB, WSa
Leptodactylus didymus Heyer et al., 1996		e		e	e	X					AM
Leptodactylus elenae Heyer, 1978		X	e	X	X				e	e	Chi, CL, HTf, PCS, WSa
Leptodactylus fuscus (Schneider, 1799)			X	X	X	X			X	X	Chi, CL, HTf, PCS, WSa
Leptodactylus gracilis Duméril & Bibron, 1841				X					X	e	IAV, TB

Species	End.	Departamento									Ecoregion(s)
		LP	CB	SC	BE	PA	PO	OR	CH	TA	
Leptodactylus griseigularis (Henle, 1981)		X	X	e							AM, YU
Leptodactylus knudseni Heyer, 1972		e	X	X	X						AM, HTf, PCS
Leptodactylus labyrinthicus (Spix, 1824)			X	X	X	e			e		Chi, CM, HTf, PCS, TB
Leptodactylus laticeps Boulenger, 1918				X					e	X	CL
Leptodactylus latinasus Jiménez de la Espada, 1875				X					e	X	CL
Leptodactylus leptodactyloides (Andersson, 1945)		X	e	X	X	X					AM, Chi, HTf, PCS, TB, WSa
Leptodactylus macrosternum Miranda-Ribeiro, 1926		X	e	e	X	X					AM, HTf, PCS, WSa
Leptodactylus mystaceus (Spix, 1824)		e	e	X	X	e					AM, Chi, HTf, PCS
Leptodactylus mystacinus (Burmeister, 1861)				X					e	e	CL
Leptodactylus ocellatus (Linnaeus, 1758)				X							WSa
Leptodactylus pentadactylus (Laurenti, 1768)		X			e	X					AM
Leptodactylus petersii (Steindachner, 1864)		e	e	X	X	X					AM
Leptodactylus podicipinus (Cope, 1862)		X	e	X	X	X					AM, Chi, CL, HTf, PCS, WSa
Leptodactylus rhodomystax Boulenger, 1884		e		e	X	e					AM
Leptodactylus rhodonotus (Günther, 1869)		X	X	X							AM, YU
Leptodactylus syphax Bokermann, 1969				X							Chi
Lithodytes lineatus (Schneider, 1799)		e	X	X	X	e					AM, HTf, PCS
Odontophrynus americanus (Duméril & Bibron, 1841)			X	X					X	e	Chi, CL, CM, TB
Odontophrynus lavillai Cei, 1985				X					e	e	Chi, CL
Phrynopus kempffi De la Riva, 1992*	●		X	X							Cej
Phrynopus laplacai (Cei, 1968)*	●	X									Cej
Phrynopus pinguis Harvey & Ergueta, 1998*	●	X									Cej
Phrynopus sp. A	●	e	X								Cej, YU

Species	End.	Departamento									Ecoregion(s)
		LP	CB	SC	BE	PA	PO	OR	CH	TA	
Phrynopus sp. B	●	X									Cej, YU
Phrynopus sp. C	●	X									Cej, YU
Phyllonastes carrascoicola De la Riva & Köhler, 1998*	●		X	X							YU
Phyllonastes ritarasquinae Köhler, 2000*	●	e	X								YU
Phyllonastes sp. A	●	X									YU
Physalaemus albonotatus (Steindachner, 1863)				X	e				X	e	Chi, CM, PCS
Physalaemus biligonigerus (Cope, 1861)				X					X	X	Chi, CL, CM, TB
Physalaemus cuqui Lobo, 1993				X					e	X	CL, CM
Physalaemus cuvieri Fitzinger, 1826				X							Chi, CL, PCS
Physalaemus nattereri (Steindachner, 1863)				X							Chi
Physalaemus petersi (Jiménez de la Espada, 1872)		X	X	X	X	e					AM, HTf, PCS
Pleurodema cinereum Cope, 1877		X	X	X				X	X	X	Cej, HiA, IAV, TB
Pleurodema guayapae Barrio, 1964				X					e	e	CL
Pleurodema marmoratum (Duméril & Bibron, 1841)*		X	X				X	X			HiA
Pseudopaludicola boliviana Parker, 1927*		X	e	X	X						AM, HTf, PCS, WSa
Pseudopaludicola mystacalis (Cope, 1887)					X						Chi, WSa
Telmatobius bolivianus Parker, 1940*	●	X									Cej, YU
Telmatobius culeus (Garman, 1875)*	●	X									HiA
Telmatobius edaphonastes De la Riva, 1995*	●		X	X							Cej, YU
Telmatobius huayra Lavilla & Ergueta, 1995*	●						X				HiA
Telmatobius ifornoi Lavilla & Ergueta, 1999*	●	X									Cej, YU
Telmatobius jahuira Lavilla & Ergueta, 1995*	●	X									Cej, YU
Telmatobius marmoratus (Duméril & Bibron, 1841)		X	X				X	X	X		Cej, HiA, IAV
Telmatobius simonsi Parker, 1940*	●	X	X						X	e	IAV

Species	End.	Departamento									Ecoregion(s)
		LP	CB	SC	BE	PA	PO	OR	CH	TA	
Telmatobius verrucosus Werner, 1899*	●	X									Cej, YU
Telmatobius yuracare De la Riva, 1994*	●		X	X							Cej, YU
Telmatobius sp. A	●		X	X							Cej, YU
Vanzolinius discodactylus (Boulenger, 1883)		e			e	X					AM
Microhylidae											
Chiasmocleis albopunctata (Boettger, 1885)				X					e		Chi, CL, CM, PCS
Chiasmocleis ventrimaculata (Andersson, 1945)		e	X	e	X	e					AM, HTf, WSa
Dermatonotus muelleri (Boettger, 1885)				X					e	X	CL
Elachistocleis bicolor (Valenciennes, 1838)		e	e	X	X	X			e	e	AM, Chi, CL, CM, HTf, PCS, TB, WSa
Elachistocleis ovalis (Schneider, 1799)		X	e	X	X	e			e	e	Cej, Chi, CL, CM, HTf, IAV, PCS, TB
Hamptophryne boliviana (Parker, 1927)*		e	e	X	X	X					AM, HTf, PCS
Pipidae											
Pipa pipa (Linnaeus, 1758)		e	e	X	X	e					AM, HTf, PCS
Pseudidae											
Lysapsus limellus Cope, 1862		X	e	X	X	e					Chi, HTf, PCS, WSa
Pseudis paradoxa (Linnaeus, 1758)		e	e	X	X	e			e	e	AM, CL, Chi, HTf, PCS, WSa
Ranidae											
Rana palmipes Spix, 1824		X	X	X	X	e					AM
Plethodontidae											
Bolitoglossa sp. A	●		X	X							AM, YU
Caeciliidae											
Caecilia marcusi Wake, 1984*	●	e	X		X	e					AM, HTf
Siphonops annulatus (Mikan, 1820)		X	e		X						AM, HTf, PCS
Siphonops paulensis Boettger, 1892				X	e						Chi, HTf, PCS

Annotations to the checklist

In the following, annotations on the updated list of Bolivian amphibians are provided. The comments refer only to species not mentioned in the account of montane forest species considered more detailed in this study (see species accounts).

Additions to the list

The record of **Bufo rumbolli** Carrizo, 1992 is based on specimens from the Departamento Tarija deposited in the CBF.

Eleutherodactylus dundeei Heyer & Muñoz, 1999 was tentatively included for the Bolivian territory based on morphological similarities which were obvious when comparing paratypes of E. dundeei with specimens from lower elevations of Parque Nacional Amboró, Departamento Santa Cruz, Bolivia, and the identical advertisement call characteristics of Amboró populations and E. dundeei from the type locality Chapada dos Guimarães, Mato Grosso, Brazil. Advertisement calls of Bolivian specimens were recorded on 2 December 1998 at Macuñucu, P.N. Amboró, Provincia Ichilo, Departamento Santa Cruz, 550 m a.s.l. Calls consisted of 6–7 pulsatile notes, repeated at a rate of 13 notes per second; call duration varied from 495–605 ms (mean 552.3 ± 54.4); note duration varied from 46–81 ms,
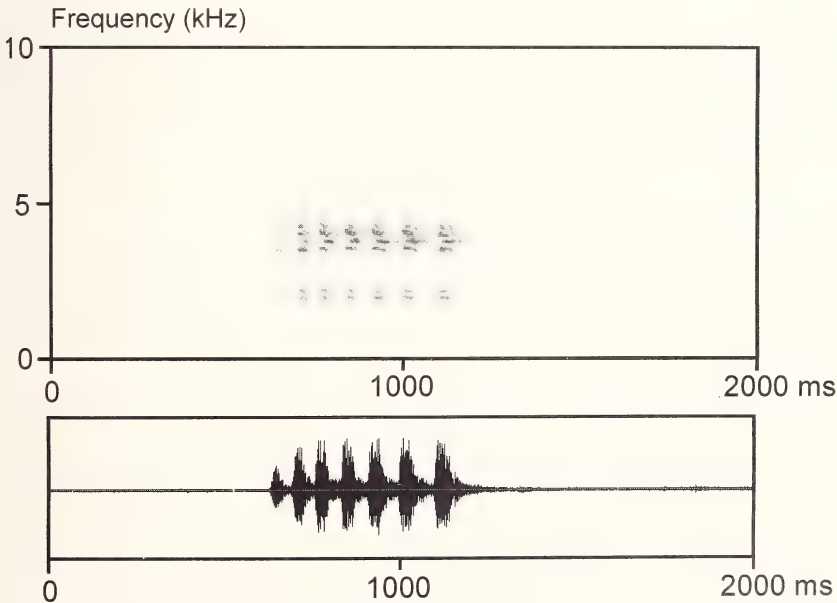
Fig.14: – Audiospectrogram and oscillogram of the advertisement call of *Eleutherodactylus dundeei* from Macuñucu, P.N. Amboró, 550 m a.s.l. Recording obtained on 2 December 1998. Air temperature 26.0°C.

the first note of the call always being the shortest; call energy was distributed between 1500 and 6500 Hz, with a dominant frequency peak at 3610 Hz (frequency bands result from the pulsatile character of the call); calls were emitted at a rate of approximately two calls per minute. Four calls of one individual were analyzed; air temperature was 26.0°C at time of recording. These data coincide very well with those provided by Heyer & Muñoz (1999) for a population from the type locality of *E. dundeei*. However, the known localities for *E. dundeei* are separated by an approximate distance of 850 km airline! The species is therefore expected to occur in suitable habitats of the intervening area like for example in the Serranía de Chiquitos. The known elevational range is about 300–650 m a.s.l. To my opinion, specimens of *Eleutherodactylus dundeei* have at least partly been misidentified as *E. peruvianus* by De la Riva (1994b). Examination of the holotype of *E. peruvianus* clearly revealed that it is not conspecific with the specimens occurring in Parque Nacional Amboró from which the call is described above.

Leptodactylus ocellatus (Linnaeus, 1758) was long time confused with *L. chaquensis* and many old Bolivian records of *L. ocellatus* (e.g., Aparicio 1992, De la Riva et al. 1992) actually correspond to the *L. chaquensis-L. macrosternum* species pair. Recently, the first voucher specimens of *L. ocellatus* were collected in the Bolivian part of the Pantanal wet lands (De la Riva & Maldonado 1999). These records probably represent the northern and westernmost records for the species.

The presence of ***Physalaemus cuqui*** Lobo, 1993 in southern Bolivia is based on examination of specimens from the Departamento Tarija (in the CBF) and the Chaco, Departamento Santa Cruz (in the NKA). Recently, Lavilla & Scrocchi (1999) reported the species from Reserva Tariquía.

Deletions from the list

Harvey (1997) tentatively recorded ***Bufo gallardoi*** Carrizo, 1992 from El Palmar, Departamento Chuquisaca. The species is not included here, because its taxonomic status is somewhat obscure and the Bolivian records are not considered reliable.

The record of ***Hyla walfordi*** Bokermann, 1962 (De la Riva et al. 1997) was based on misidentified specimens of *H. tritaeniata*.

Eleutherodactylus peruvianus (Melin, 1941) was excluded from the checklist, because examination of the holotype (NHMG 490) revealed that none of the Bolivian specimens identified as *E. peruvianus* coincide with the holotype. To avoid further confusion, I here provide a brief description of the *E. peruvianus* holotype generally following the terminology and characters of Lynch & Duellman (1997).

Description. – An adult female characterized by (1) skin of dorsum shagreen, that of venter smooth; dorsolateral folds prominent; (2) tympanic membrane

distinct, ovoid; tympanic annulus clearly visible beneath skin, slightly less than half the eye length; (3) snout long, sub-acuminate in dorsal view, rounded in lateral profile; canthus rostralis sharp in cross section; (4) upper eyelid narrower than IOD; (5) vomerine teeth prominent, triangular in outline, narrowly separated, behind choanae; (6) vocal slit condition unknown; (7) first finger much longer than second; tips of outer two fingers truncate with large pads, tip of first two fingers more rounded, much less expanded; (8) fingers bearing narrow lateral fringes; (9) ulnar tubercle prominent; (10) heel lacking tubercle; outer edge of tarsus smooth; tarsal fold present but short; (11) inner metatarsal tubercle elongated and elevated, outer round, about the size of inner; supernumarary plantar tubercles absent; (12) toes with moderately marked lateral fringes; basal webbing; fifth toe longer than third, not reaching distal subarticular tubercle of fourth toe; toe tips truncate to rounded, expanded, slightly smaller than those on outer fingers; (13) in preservative, dorsum cream with four brown chevrons and brown markings, few irregular distributed dark brown spots; brown interorbital bar; dark supratympanic stripe, extending to angle of jaws; upper half of tympanic membrane medially dark brown, lower half cream; venter cream; throat cream with fine brown mottling; groin brown with dark brown spotting; dark brown canthal stripe, fading to upper lip; dorsal surfaces of limbs barred; dark brown blotches on anterior surfaces of limbs; posterior surface of hind limbs brown with fine cream spotting; sole of foot and tarsus dark brown; dark brown cloacal blotch; (14) moderate-sized, SVL 41.5 mm.

Measurements (in mm). – SVL 41.5; tibia length 29.2; head width 17.9; head length 18.7; upper eyelid width 4.1; IOD 5.8; tympanum length 2.6; eye length 6.2; E–N 6.0; foot length approximately 36–37.

Especially, the distinct dorsolateral folds in combination with finger lengths and coloration distinguishes *E. peruvianus* from all *Eleutherodactylus* currently known from Bolivia. However, I do not exclude the possibility that *E. peruvianus* occurs in Bolivia, but hitherto I am not aware of any vouchered record.

The record of **Phrynopus peruvianus** (Noble, 1921) (see Köhler 1995b) was based on a misidentified juvenile of *Pleurodema marmoratum*.

Telmatobius albiventris Parker, 1940 was considered to be a junior synonym of *T. culeus* by Vellard (1992). This suggestion is herein followed and *T. albiventris* is excluded from the checklist (see also De la Riva et al. 2000).

Species complexes

Fourteen subspecies have been described in the species **Bufo granulosus** Spix. 1824 (Gallardo 1965). Some of these subspecies were elevated to species rank subsequently (e.g., *Bufo dorbignyi, B. fernandezae, B. pygmaeus*; Frost 1985, Cei

1987). At least four subspecies, i.e. *Bufo g. goeldi*, *B. g. major*, *B. g. mini*, and *B. g. mirandaribeiroi*, were mentioned for Bolivia (Köhler et al. 1997). It is very likely that actually more distinct species are involved and sympatric distribution was suggested for the two Bolivian subspecies *B. g. major* and *B. g. mini* (Frost 1985, Lavilla 1992), indicating that both are separate species. During studies in 1994, the author found *B. g. mirandaribeiroi* close to *B. granulosus* specimens which might represent *B. g. mini* in the northern Departamento Santa Cruz (Köhler 1995a). However, data on distribution and variation of the mentioned forms is too sparse and it is refrained here from elevating any of the subspecies to species rank.

Toads in the **Bufo typhonius** complex (= *Bufo margaritifer* complex) are the subject of various taxonomic discussions (e.g., Hoogmoed 1986, 1989, 1990). Probably, much more species than originally believed are involved under the name *B. typhonius* (Hass et al. 1995). Some forms for long time considered to represent synonyms have recently been recognized as distinct species (e.g., Caldwell 1991, La Marca & Mijares-Urrutia 1996), other morphs were described without assigning names (e.g., Duellman & Mendelson 1995, Köhler & Lötters 1999b). In Bolivia, Lötters & Köhler (2000) recognized at least four different forms or species. One of them, *Bufo castaneoticus*, was already recorded by Köhler & Lötters (1999b) who described an additional form (without assigning a name) from northernmost Bolivia. A third form seems to occur throughout a vast area in the Bolivian lowlands (see De la Riva et al. 1996a, Köhler et al. 1997, Lötters & Köhler 2000) and a fourth form is that occurring in montane forests described as *B. stanlaii* by Lötters & Köhler (2000). Summarizing, there remain at least two different forms (probably more) in the *B. typhonius* complex (one of which shows similarities with the description of *B. acutirostris*) with unclear taxonomic status, occurring in the tropical lowlands of Bolivia.

Telmatobius marmoratus (Duméril & Bibron, 1841) is a polytypic species with currently nine recognized subspecies (De la Riva et al. 2000). The validity of these subspecies and the real specific diversity in the *T. marmoratus* complex is being reviewed by I. De la Riva.

Resurrection from synonymy

Hylodes gollmeri var. *bisignata* Werner, 1899 was considered a junior synonym of *E. fenestratus* by Lynch (1980) and Lynch & Duellman (1997). Werner (1899) himself gave no information on the type locality, but Häupl & Tiedemann (1978) stated "Chaco, Bolivia" as the locality for *H. gollmeri bisignata*. Therefore, Heyer & Muñoz (1999) suspected *E. bisignatus* to be distinct from *E. fenestratus*, because both taxa obviously are occurring in completely different ecoregions, the dry Chaco and the humid Amazon, respectively. Actually, a correct statement about the origin of *E. bisignatus* is more difficult to access. The dry lowland

Chaco forests of Bolivia appear quite inappropriate for frogs with direct development and none of the recent collections in the area (e.g., Gonzales 1998) confirmed the presence of an *Eleutherodactylus* species. There exists another locality named Chaco in the Unduavi valley, Yungas de La Paz, 16°21' S, 67°49' W, at approximately 1850 m a.s.l. (I. De la Riva pers. comm.). Since Werner (1899) described *Telmatobius verrucosus* from this locality, it is very probable that *E. bisignatus* also comes from the same general area. The statement of Gorham (1966) that the type locality of *E. bisignatus* is in western Ecuador is obviously in error. This view is strongly supported by the recent collection of specimens at Valle del Zongo, Provincia Murillo, Departamento La Paz, 1250 m a.s.l., which agree perfectly with the type specimen of *E. bisignatus* (NMW 16502; Fig.15). Moreover, the examination of the *E. bisignatus* holotype revealed considerable differences to *E. fenestratus*. As a consequence, I here regard *Eleutherodactylus bisignatus* (Werner, 1899) a valid species.

In the following, I provide a diagnosis based on the type specimen and two additional ones from Valle del Zongo (ZFMK 72524–525). Terminology and description of characters follow Lynch & Duellman (1997).

Eleutherodactylus bisignatus (Werner, 1899) bona species

H o l o t y p e : NMW 16502; "Chaco, Bolivia" (according to Häupl & Tiedemann 1978). This locality is possibly within the Yungas de La Paz region from where Werner (1899) probably also described *Telmatobius verrucosus* (see Gorham 1966).

D i a g n o s i s : A species of the *Eleutherodactylus conspicillatus* group (sensu Lynch & Duellman 1997) distinguished from other *Eleutherodactylus* by the following combination of characters: (1) skin on dorsum finely shagreen, dorsolateral folds absent, skin of venter smooth, discoidal folds well to groin; (2) tympanic membrane distinct, round; tympanic annulus visible distinct, its diameter about one third of the eye length; (3) snout acuminate in dorsal view, rounded in lateral profile; canthus rostralis rounded in cross-section, straight or slightly sinuous in ventral view; loreal region gradually sloping; lips flared; (4) upper eyelid lacking tubercles, equal in width than IOD; (5) vomerine odontophores triangular, prominent, narrowly separated, median behind choanae; (6) males with vocal slits and large vocal sac; males with nonspinous nuptial pads; (7) first finger longer than second; tips of outer two fingers rounded, with large pads, tips of inner two fingers rounded, only slightly expanded; (8) fingers with weakly defined lateral fringes; (9) no ulnar tubercles; (10) no tubercles on heel and tarsus, distinct tarsal fold; (11) inner metatarsal tubercle oval and elevated, three times the size of rounded outer; supernumerary plantar tubercles absent; (12) toes with lateral fringes; webbing absent; fifth toe longer than third, not reaching distal subarticular tubercle of fourth toe; toe tips rounded, expanded, only slightly smaller than those of outer fingers; (13) dorsum tan to brown, with indistinct diffuse darker markings; brown canthal and supratympanic stripe; a pair of dark dorsolateral
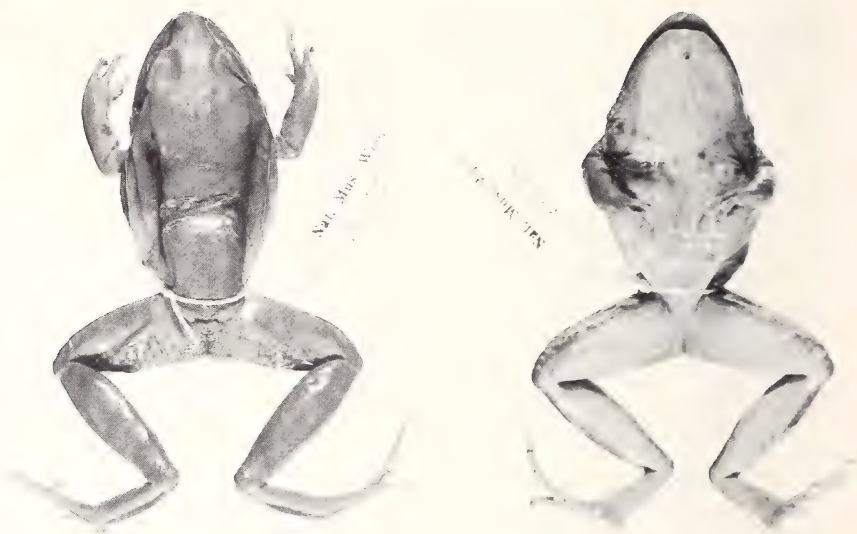
Fig.15: Dorsal and ventral view of preserved holotype of *Hylodes gollmeri bisignata* (NMW 16502; = *Eleutherodactylus bisignatus*).

blotches in scapular region; venter cream with diffuse brown speckling, throat with brown flecks; (14) adults moderate-sized, SVL of male 32.6 mm, two females 45.7 and 50.3 mm.

Eleutherodactylus bisignatus is most similar to *E. fenestratus* and *E. samaipatae*, from which it differs mainly by shorter fingers, more robust forearms, a narrower dorsal plane in front of the orbits, and a loreal region sloping gradually to the flared lips. In addition, *E. samaipatae* differs from *E. bisignatus* by paler color and longer legs. *Eleutherodactylus dundeei* differs in the same manner as do *E. fenestratus* and *E. samaipatae*, and occurs in a completely different habitat. *Eleutherodactylus peruvianus*, a species that may occur in the distribution area of *E. bisignatus*, differs by the presence of distinct dorsolateral folds, sharp canthus rostralis, and coloration. Other species in the *E. conspicillatus* group occurring in adjacent Peru include *E. skydmainos* and *E. buccinator*. The latter species differs from *E. bisignatus* by distinct dorsolateral folds, a X-shaped middorsal mark, and

Plate I: **a)** *Atelopus tricolor* Boulenger, 1902, female, Provincia Chapare, 1350 m; **b)** *Bufo arenarum* Hensel, 1867, male, W of Vaca Guzman, 1360 m; **c)** *Bufo fissipes* Boulenger, 1903, subadult, Provincia Chapare, 1400 m; **d)** *Bufo justinianoi* Harvey & Smith, 1994, male, Provincia Chapare, 2100 m; **e)** *Bufo paracnemis* Lutz, 1925, male, N of Sta. Rosa de la Roca, 400 m; **f)** *Bufo poeppigii* Tschudi, 1845, couple, Karahuasi, 1800 m; **g)** *Bufo quechua* Gallardo, 1961, couple, Incachaca, 2250 m; **h)** *Bufo stanlaii* Lötters & Köhler, 2000, female, road to San Onofre (Chapare), 1900 m.

Plate I

coloration. *Eleutherodactylus skydmainos* is distinguished by smaller size and a prominent interocular fold.

Distribution: Known only from Valle del Zongo, Provincia Murillo, Departamento La Paz, 1250 m a.s.l., 16° 04' S, 68° 01' W. As mentioned above, the provided data on the type locality are imprecise, but it is very probable that *E. bisignatus* occurs in the Unduavi valley and inhabits a wider range than currently known, at least in the Yungas de La Paz region.

Remarks: In a recent paper, Reichle (1999) revalidated this taxon without any argumentation obviously by mistake again as a subspecies of *E. gollmeri* (i.e., *E. gollmeri bisignatus*), a species in the *E. gollmeri* species group, subgenus *Craugastor* (Lynch & Duellman 1997).

Unnamed species

***Colostethus* sp. A**, a species seemingly related to *C. trilineatus*, was reported and briefly described from northern Bolivia by Köhler & Lötters (1999b). Gonzales et al. (1999), who also recorded *Colostethus brunneus* from Bolivia, discussed its taxonomic status which finally remains unsolved.

***Hyla* sp. B**, already reported by Köhler & Lötters (1999b), is a species from Amazonian Bolivia seemingly related to *H. leali*. It is being described by Köhler & Lötters (in press).

***Osteocephalus* sp. A** is a new species from northern Departamento Santa Cruz related to *O. leprieurii*, being described by E. Smith, M. Harvey, and S. Reichle. It might turn out that Bolivian populations currently assigned to *O. leprieurii* actually correspond to this new species (S. Reichle pers. comm.).

***Phrynopus* sp. A** refers to an undescribed species from cloud forests of the Departamento Cochabamba which is being described by M. Harvey.

***Phrynopus* sp. B and C** correspond to new species discovered in the Yungas de La Paz region which will be described by I. De la Riva and S. Reichle.

A new minute leptodactylid frog, seemingly related to *Phyllonastes*, has been discovered in the Yungas de La Paz region. This taxon, here tentatively listed as ***Phyllonastes* sp. A**, will supposedly be described in a new genus by Harvey & McDiarmid (in prep.).

Miscellaneous notes – taxonomic problems

The taxonomic status of ***Bufo pleuropterus*** Schmidt, 1857, currently considered a synonym of *B. typhonius*, remains unclear. Its type locality was given as "Grenzgebiet von Bolivia gegen Peru, in etwa 3000' Höhe" by Schmidt (1858). According to the loss of Bolivian territory in 1909 and the travel route of the collector, J. v. Warszewiez, the type locality is probably in present-day Peru.

According to the descriptions by Schmidt (1857, 1858) and the juvenile holotype (KM 1030), it may possibly represent a valid species. However, the drawing provided by Schmidt (1858: fig. 17) is somewhat misleading with respect to the snout shape. Actually, the snout of the type specimen is much less pointed in dorsal view.

Morphological variation in Bolivian **Gastrotheca marsupiata** (Duméril & Bibron, 1841) was reviewed by De la Riva (1992a) who distinguished high-Andean populations from those occurring in the montane rain forests of the Yungas. Köhler et al. (1995a) described the variation and biology of a population from Sehuencas and subsequently Köhler (1995a) suspected that the populations from humid montane forests represent an undescribed species. This assumption was based on differences in morphology, advertisement call, egg numbers, and data obtained from protein electrophoresis (conducted by N. Juraske and U. Sinsch). So, the name *G. marsupiata* herein is used in a restricted sense, referring only to populations in the Andean highlands (see also remarks on *Gastrotheca* sp. A in species account). Examination of the holotype of *Nototrema bolivianum* Steindachner, 1892 (NMW 16490) confirmed the decision by Duellman & Fritts (1972), placing it as a junior synonym of *G. marsupiata*.

Recent collections at the type locality of **Hyla charazani** Vellard, 1970 revealed that it is a valid species in the *Hyla armata* group (S. Reichle pers. comm.).

The record of **Phrynohyas resinifictrix** (Goeldi, 1907) is based on calls only; no voucher specimens are available (S. Reichle pers. comm.).

Phyllomedusa camba De la Riva, 2000 was known since Cannatella (1983) announced that part of the specimens identified as *P. boliviana* by Funkhouser (1957) actually correspond to an undescribed species. The species then was repeatedly reported from Bolivia, Brazil, and Peru without being named (e.g., Duellman & Salas 1991, De la Riva et al. 1995, Duellman & Thomas 1996, Köhler & Lötters 1999b).

According to Lescure et al. (1995) the correct spelling and year of description is **Phyllomedusa hypochondrialis** (Daudin, 1800).

Scinax squalirostris (Lutz, 1925) was recently discovered in a dry-valley in the Yungas de La Paz region (Apolo), a surprisingly unexpected place for this Cerrado distributed species (De la Riva et al. 2000).

The taxonomic identification of Amazonian populations presently called **Leptodactylus macrosternum** Miranda-Ribeiro, 1926 is unclear. It is clearly distinguished from *L. ocellatus* but with the present knowledge it is almost impossible to separate *L. chaquensis* from *L. macrosternum*. *Leptodactylus chaquensis* actually might represent a junior synonym of *L. macrosternum* (De la Riva & Maldonado 1999).

Frequency (kHz)
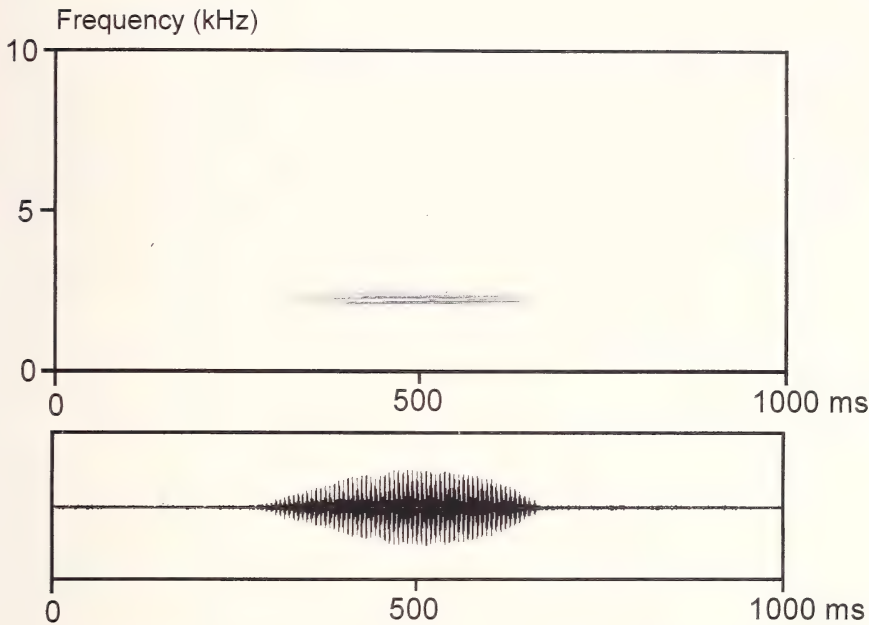
Fig.16: Audiospectrogram and oscillogram of the advertisement call of *Odontophrynus lavillai* from Santa Cruz de la Sierra, 350 m a.s.l. Recording obtained on 14 November 1997. Air temperature 20.0°C.

Odontophrynus lavillai Cei, 1985 was reported for Bolivia by De la Riva et al. (1996b). Cei (1985) mentioned differences in skin texture which distinguish *O. lavillai* from *O. americanus*. These differences in skin texture and coloration do not seem to be that distinct in Bolivian populations. However, recordings of advertisement calls support that two different species occur on Bolivian territory. In the following, the call of *O. lavillai* recorded on 14 November 1997 in the town of Santa Cruz de la Sierra, Provincia Andres Ibañez, Departamento Santa Cruz, 350 m a.s.l., is described. Calls consisted of single pulsed notes; note duration varied from 355–393 ms (mean 375.0 ± 16.2); pulse rate within calls was approximately 160 pulses per second; calls were repeated in regular intervals at a rate of approximately 19 calls per minute; call energy was distributed between 1800 and 2500 Hz, with a mean dominant frequency of 2050 Hz (frequency bands result from the pulsatile character of the call). Five calls of one individual were analyzed. Air temperature during recording was 20.0°C.

In comparison, advertisement calls of Bolivian ***Odontophrynus americanus*** differ from those of *O. lavillai* by a lower frequency, a lower pulse rate, longer note duration, and a higher call repetition rate. A description of *O. americanus* calls recorded on 9 January 1998 at Pampagrande, Provincia Florida, Departamento Santa Cruz, 1300 m a.s.l., is provided. Calls consisted of single pulsed notes; note

Frequency (kHz)
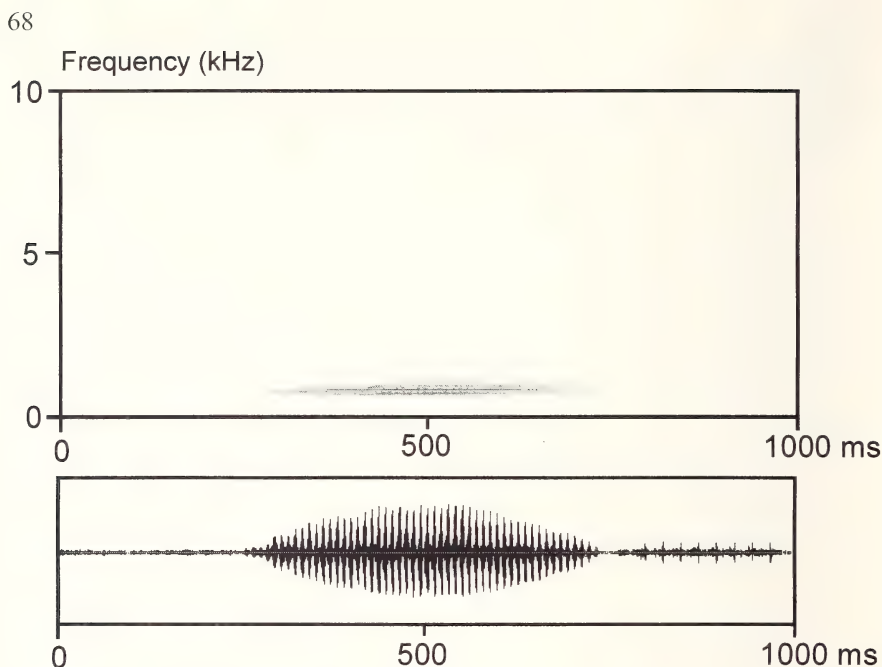
Fig.17: Audiospectrogram and oscillogram of the advertisement call of *Odontophrynus americanus* from Pampagrande, 1300 m a.s.l. Recording obtained on 9 January 1998. Air temperature 21.4°C.

duration varied from 432–574 ms (mean 468.3 ± 26.0); pulse rate within calls was approximately 107 pulses per second; calls were repeated in regular intervals at a rate of approximately 34 calls per minute; call energy was distributed between 500 and 1050 Hz, with a mean dominant frequency of 740 Hz (frequency bands result from the pulsatile character of the call). Seven calls of two individuals were analyzed. Air temperature during recording was 21.4°C. These data coincide relatively well with the data published by Márquez et al. (1995) for a population from Santa Cruz de la Sierra. Hitherto, the exact Bolivian distributions in the *O. americanus–O. lavillai* species pair remain unknown. Both species seem to occur in sympatry in several areas and the assignment of certain populations to one or the other species might be difficult.

In a recent paper on phylogeny in the genus *Physalaemus*, Cannatella et al. (1998) used the name **Physalaemus freibergi** (Donoso-Barros, 1969), currently considered a synonym of *P. petersi* (Jiménez de la Espada, 1872). However, a formal resurrection of this taxon was not intended (D. C. Cannatella pers. comm.).

Despite much taxonomic confusion regarding the Yungas *Telmatobius* (e.g., Vellard 1951, 1970), it now seems clear that **Telmatobius bolivianus** Parker, 1940 and **T. verrucosus** Werner, 1899 both have to be considered valid species (De la Riva et al. 2000).

Species predicted to occur in Bolivia

When De la Riva (1990a) published his checklist on Bolivian amphibians, he expected 47 species likely to occur on Bolivian territory. However, a record of *Eleutherodactylus discoidalis* for Bolivia by Peracca (1897) was overlooked in this list and therefore it was also listed as a species to be expected (De la Riva et al. 2000). Until today, 20 species out of the 46 predicted by De la Riva (1990a) have been recorded from Bolivia. Recent investigations on Neotropical herpeto-faunas led to the description of new amphibian taxa from sites in neighboring countries close to the Bolivian border, as well as to records of species formerly known only from more remote areas with respect to Bolivia. As a consequence, 61 amphibian species are herein considered to be likely distributed in Bolivia. The species are listed under five generalized domains, not reflecting the actual diversity of ecoregions and habitats.

A m a z o n i a : *Bufo glaberrimus, Colostethus peruvianus, Dendrobates biolat, D. quinquevittatus, D. vanzolinii , Epipedobates macero, E. simulans, Hyla allenorum, H. bokermanni, H. brevifrons, H. rossalleni, H. sarayacuensis, H. timbeba, H. xapuriensis, Scinax goinorum, S. ictericus, S. pedromedinai, Sphaenorhynchus carneus, Osteocephalus subtilis, Agalychnis craspedopus, Phyllomedusa atelopoides, Edalorhina perezi, Hydrolaetare schmidti, Leptodactylus dantasi, Eleutherodactylus altamazonicus, E. buccinator, E. imitatrix, E. skydmainos, E. zimmermanae, Phyllonastes myrmecoides, Phyzelaphryne miriamae, Altigius alios, Chiasmocleis shudikarensis, Ctenophryne geayi, Caecilia tentaculata,* and *Typhlonectes compressicauda.*

C h a c o   a n d   C e r r a d o : *Melanophryniscus stelzneri, Epipedobates braccatus, Hyla varelae, Lepidobatrachus llanensis, Physalaemus centralis, P. fuscomaculatus,* and *Chiasmocleis meheleyi.*

N o r t h e r n   C o r d i l l e r a   O r i e n t a l : *Atelopus erythropus, Cochranella phenax, C. spiculata, C. truebae, Hemiphractus johnsoni, Eleutherodactylus cosnipatae, E. lindae, E. mendax, E. ockendeni, E. peruvianus,* and *E. salaputium.*

S o u t h e r n   C o r d i l l e r a   O r i e n t a l : *Bufo gallardoi, B. gnustae, Gastrotheca chrysosticta,* and *Telmatobius oxycephalus.*

C o r d i l l e r a   O c c i d e n t a l : *Telmatobius halli, T. pefauri,* and *T. zapahuirensis.*

Species diversity and endemism in Bolivia

Taxonomic diversity

Summarizing the present state of knowledge, 200 valid amphibian species in 44 genera and 11 families were reported from Bolivia (Bufonidae: 4 genera, 19 species; Centrolenidae: 2 genera, 4 species; Dendrobatidae: 3 genera, 9 species; Hylidae: 8 genera, 68 species; Leptodactylidae: 16 genera, 86 species; Microhylidae: 4 genera, 6 species; Pipidae: 1 genus, 1 species; Pseudidae: 2 gen-

era, 2 species; Ranidae: 1 genus, 1 species; Plethodontidae: 1 genus, 1 species; Caeciliidae: 2 genera, 3 species). Forty-five of them are endemic to Bolivia which equals 22.5%. Of these endemic species, the major part (60%) belongs to the family Leptodactylidae followed by the Hylidae (18%) and Bufonidae (9%). Additional species were already discovered and are under description.

In spite of the enormous progress in the knowledge of Bolivian amphibians, it is obvious that the amphibian fauna of Bolivia still is a poorly known one compared to other South American countries. Species lists of neighboring countries appear more complete, although new species are discovered almost everywhere and every year. According to Glaw & Köhler (1998), 68% of all newly described amphibian species between 1986 and 1995 originate from the Neotropical region. For comparison with Bolivia, published species numbers for other countries are as follows: Brazil – 517 (Mittermeier et al. 1997); Colombia – 583 (Ruíz-Carranza et al. 1996); Ecuador – 375 (Coloma 1991); Peru – 315 (Rodríguez et al. 1993), 316 (Morales 1995); Venezuela – 200 (Péfaur 1992), more than 260 (La Marca 1997). These numbers demonstrate that research on amphibian diversity in Bolivia is still in an initial state. There is no reason to believe that Bolivia's amphibian fauna is less diverse than that of other Neotropical countries (when taking into account differences in the countries' surfaces), because Bolivia is especially rich in different biomes (see Study area: vegetation - ecoregions) harboring different amphibian faunas.

Spatial patterns of species diversity and endemism

The spatial patterns of species richness were tentatively analyzed by Köhler et al. (1998b) who cross-linked the distribution of 166 species with eight Bolivian ecoregions. The authors used a simplified scheme of ecoregions, because they regarded the available data on amphibian distributions as insufficient to conduct a more detailed analysis. Köhler et al. (1998b) found a general decrease of species richness the further one travels from the northern humid Amazonian lowland forests to the semi-humid and semiarid Chiquitanía forests and Campos Cerrados south to the dry Chaco. However, this north-south gradient was interrupted by the Beni savannas which are more closely related to the Cerrado formations (northern Beni savannas) and the wet lands of the Pantanal (southern Beni savannas), respectively, than to other Bolivian zones (Hanagarth & Beck 1996). High levels of amphibian diversity were found in the perhumid Yungas which harbor almost all endemic taxa. Approximately 68% of the species occurring in the Yungas are Bolivian endemics (Köhler et al. 1998b). The relatively small area of the perhumid Yungas was considered the most diverse ecoregion compared to the vast lowland regions. The Yungas exhibit a remarkable fragmentation of habitats, and as a result communities are not only species rich but their composition may vary greatly within short distances. The other ecoregions in the Andes (i.e., the Tucumanian-Bolivian montane forests, the inter-Andean dry valleys, and the puna) show comparatively low species diversity.

Here, I provide a new, more detailed analysis of spatial diversity patterns as well as patterns of endemism, considering 12 Bolivian ecoregions and 195 species. Although the data basis of this new analysis is much more detailed than the one used by Köhler et al. (1998b), it does not necessarily imply that really every species cross-linked with a certain ecoregion was actually collected there. On the contrary, I associated suitable ecoregions with each species. This was possible only through extrapolation of the distribution data available and is especially true for the lowland distributed species. For example, if one species was recorded from humid Amazonian forests as well as from the humid forests of the pre-Cambrian shield, its presence in the humid transition forests in-between was assumed, but not its presence in the Beni savannas, because they constitute completely different habitats. However, the ecoregions provided on the map (Fig.4) are not detailed enough to show for example forest patches within the Beni savannas, a habitat type suitable for Amazonian amphibians.

Species Richness and Political Endemism

The resulting values for relative species richness and political endemism are shown in Fig.18. Percentages of species richness refer to 195 species (i.e., 100%) currently known from Bolivian territory. The relative rates of Bolivian endemics in each region was determined using the absolute number of species occurring in the respective region as a baseline of 100%.

In general, the results obtained from the new analysis agree with the patterns found by Köhler et al. (1998b). However, there are some new aspects and certain differences which deserve comments. As expectable, the Amazonian rainforests are the richest region in species number, harboring 45.1% of the Bolivian amphibian fauna. The Amazonian rainforests are followed by the humid forests of the pre-Cambrian shield (35.4%) and the humid transition forests (34.9%), with nearly equal degree. The numbers decrease further when traveling to the Chiquitanía forests (22.1%; including Cerrado formations) and the dry Chaco lowland forests (17.9%). As equally reported by Köhler et al. (1998b), the wet savannas of the Beni are not compatible within this decreasing trend in the lowlands, going from the north-west to the south-east, harboring a less species-rich amphibian fauna (15.4%). Going to the montane or Andean regions, it becomes obvious that the per-humid Yungas are by far the most species-rich region within the Bolivian Andes (32.0%), followed by the cloud forests (11.8%) and the Tucumanian-Bolivian montane forests (11.3%). The drier areas, namely the Chaco montane forest, the high-Andean puna, and the inter-Andean dry-valleys, harbor significantly smaller numbers of species.

Regarding rates of political endemism, the cloud forests are inhabited by the largest relative number of endemic species (69.6%), followed by the Yungas montane forests with 54.0% endemic species. These both regions were combined to a single one by Köhler et al. (1998b), who also found the highest degree (68%) of

Relative Richness and Bolivian Endemism

45.1% (4.5%)

15.4% (0%)

35.4% (0%)

32.3% (54.0%)

11.8% (69.6%)

34.9% (0%)

22.1% (0%)

17.9% (0%)

7.2% (0%)

4.6% (22.2%)

8.2% (18.8%)

11.3% (13.6%)

L. Titicaca

Poopó

Amazonian rainforests		Chaco montane forests
Campos within Amazonian forests		Tucumanian-Bolivian forests
wet savannas		inter-Andean dry-valleys
humid transition forests		high-Andean forests
humid forests of the pre-Cambrian shield		dry Puna
semi-deciduous Chiquitanía forests		salt lakes (Salares)
Campos Cerrados		cloud forests ("Ceja")
Chaco dry-forests		humid montane rainforests (Yungas)

Fig.18: Map of Bolivia showing 12 ecoregions and relative amphibian species richness. Percentages of species richness in each region refer to 195 species (= 100%) known from Bolivian territory. The percentage of species endemic to Bolivia relative to the absolute species number occurring in the respective region is given in parentheses. For further information see text.

relative endemism in that region. When analyzing the distribution of species within these two regions more detailed, it can be demonstrated that most of the endemic species occur more or less exactly at the border between the upper montane rainforests and the cloud forests. The lower montane rainforests contain less endemic species. These results underline the very special role of the Yungas and cloud forest regions which in large parts represent very unique ecosystems. The high-Andean region harbors a remarkable rate of 22.2% endemic species, but this relatively high degree becomes a more realistic value when considering the percentage representing two out of a total of nine species occurring in high-Andean Bolivia. The inter-Andean valleys and the Tucumanian-Bolivian forests each harbor three endemic amphibian species (18.8% and 13.6%, respectively). Like the Andean highlands, these two regions continue to northern Argentina and therefore have this relatively low degree in endemic amphibian species. For the same reason, namely the extension of the ecoregion beyond Bolivia's borders, all lowland regions except the Amazonian rainforests do not contain a single species endemic to the country. The rate of 4.5% endemic species present in the Amazonian rainforest ecoregion refers to species occurring in the lower Andean foothills which were here considered to be part of the Amazonian ecoregion. Endemic species are lacking in the northern part of this region.

To estimate the endemism in an ecoregion relative to its species richness more precisely, I here suggest to use a regional Index of Endemism (IPE). An IPE value smaller than 1.0 means that the degree in endemism is under-represented relative to species richness in that ecoregion, an IPE value greater than 1.0 indicates over-representation of endemic species. The IPE constitutes as follows: number of endemic species occurring in one ecoregion (EE) as percentage of the total known endemic species for Bolivia (TE), through the number of species occurring in an ecoregion (ES) as percentage of the total number of species known for the country (TS).

$$IPE = EE \times TS / TE \times ES$$

$$or\ IPE = PE / PS$$

with PE: percentage of total known Bolivian endemics occurring in the ecoregion; and PS: percentage of total known Bolivian species occurring in the ecoregion. The resulting IPE values are summarized in table 2, identifying the cloud forests ("Ceja") and the montane rainforests (Yungas) as the richest zones in relative regional endemism by far, with the Yungas also being remarkably species-rich. The amphibian fauna in the high-Andean region displays an adequate degree of endemic species, although the high-Andean community is made up only by very few species. All other regions show an under-representation of endemic species, harboring relatively greater portions of widely distributed amphibian species.

Comparing these diversity patterns with those of Köhler et al. (1998b) reveals several differences. In the present analysis, most richness values, especially those from Amazonian rainforests, humid transition forests, humid forests of the pre-

Table 2: Percentages of known endemics per ecoregion relative to all endemic amphibian species known from Bolivia (PE), and percentage of all known Bolivian species known from one ecoregion (PS). An index of political endemism IPE (PE/PS) smaller than 1.0 indicates that endemic species are not adequately represented relative to species richness; an IPE greater than 1.0 indicates over-representation of endemic species. The sum of percentages is greater than 100%, because certain species occur in more than one ecoregion.

Ecoregion	Percentage of total known Bolivian endemics (%) PE	Percentage of total known Bolivian species (%) PS	Index of Political Endemism IPE (PE/PS)
cloud forests - "Ceja"	37.2	11.8	3.1
montane rainforests - Yungas	79.1	32.3	2.4
high-Andean forests and puna	4.7	4.6	**1.0**
inter-Andean dry-valleys	7.0	8.2	0.9
Tucumanian-Bolivian forests	7.0	11.3	0.6
Amazonian rainforests	9.3	45.1	0.2
wet savannas	0	15.4	0
humid transition forests	0	34.9	0
humid forests of the pre-Cambrian shield	0	35.4	0
Chiquitania forests and Campos Cerrados	0	22.1	0
Chaco lowland forests	0	17.9	0
Chaco montane forests	0	7.2	0

Cambrian shield, and Chaco lowland forests (boundaries of ecoregions in Köhler et al. 1998b differ from those chosen herein), are significantly higher than those in Köhler et al. (1998b). The reasons are twice: (1) new records of species previously unknown from Bolivia in the mentioned regions, and (2) the association of single species to more ecoregions suggested to be suitable. Recent fieldwork carried out in different parts of Bolivia showed that many species exhibit much wider ranges than formerly assumed. The relative species richness of the wet savannas is lower in the present study, because in this region no additional species records were made. The consideration of montane rainforests (Yungas) and cloud forests as separate ecoregions resulted in different degrees of endemism on the lower and upper Andean slopes. In spite of the increased absolute species number known from Bolivia, relative species richness in the Yungas is significantly higher in the present study. This fact is partly due to the discovery of new undescribed species in that region (most of these have to be considered endemics) which account for a significant part of the 29 additional species considered herein. Moreover, it has been demonstrated that several species occurring in the Amazonian forests of the Andean foot are able to enter the lower montane rainforests.

Ecoregion Endemism

When analyzing ecoregion endemism, not considering political borders, the patterns appear different compared to political endemism (Fig.19). The humid mon-

tane rainforests of the Yungas, extending into southeastern Peru, are especially rich in amphibian species endemic to the region (33.3%). Many species share this pattern of distribution, occurring along the eastern Andean slopes from central or southeastern Peru to central Bolivia. Several species of the Yungas rainforests also inhabit the "Ceja" cloud forests or the forests of the Andean foot, respectively. When taking into account species distributed in the Yungas and the peri-Andean forests (here included within Amazonian rainforests), the value for species endemic for both regions (Yungas and forests of the Andean foot) is 51.6%. When regarding the montane rainforests of the Yungas and the cloud forests as one region (as done by Köhler et al. 1998b), 55.7% of the species occurring there are restricted to this region. A remarkably high degree of regional endemism occurs in the high-Andean ecoregions (44.4%), although this rate is made up by very few species.

Due to the extension into Bolivia's neighboring countries and the lack of geographical barriers, political endemism in the lowland ecoregions is practically zero (with the exception of species inhabiting Amazonian forests at the Andean foot; see above). In contrast, a remarkable number of species is restricted to the dry Chaco forests of southeastern Bolivia, northern Argentina, and Paraguay, constituting one fourth (25.7%) of all amphibian species occurring in the Bolivian Chaco. This can be easily explained by a high level of species' specialization to this dry and extremely seasonal environment. The Amazonian rainforests also harbor a remarkable number of species restricted to the region. This is explainable by a generally high humidity associated with certain types of unique habitats and forest formations (e.g., primary rainforest containing large tree species), as well as by consequences of historical climatic conditions which are responsible for distributions restricted to southwestern Amazonia. The relatively low degree of endemic species in the Cerrado and Chiquitanía forest domains is made up by species like for example *Hyla melanargyrea* and *H. rubicundula* which are known only from eastern Bolivia and the Cerrado formations of Brazil. Other lowland ecoregions have to be considered transition zones and therefore harbor species of adjacent regions. Their degree of regional endemism is to be neglected.

Analyzing the drier montane regions, nearly no ecoregional endemism occurs. This is in contrast to plant endemism, found to be high for example in the Tucumanian-Bolivian montane forests (e.g., Ibisch 1996). This fact is explainable through the richness in transition zones between inter-Andean valleys, Tucumanian-Bolivian forests, and Chaco montane forests. As a result, species found to be primarily distributed in the Tucumanian-Bolivian forests also enter the inter-Andean valleys, and species of the Chaco montane forests may enter the Tucumanian-Bolivian forests. However, when looking at these three regions as a whole or summarizing at least the distribution of inter-Andean valleys in combination with Tucumanian-Bolivian forests, it becomes clear that in large parts the amphibian fauna is unique to these regions.
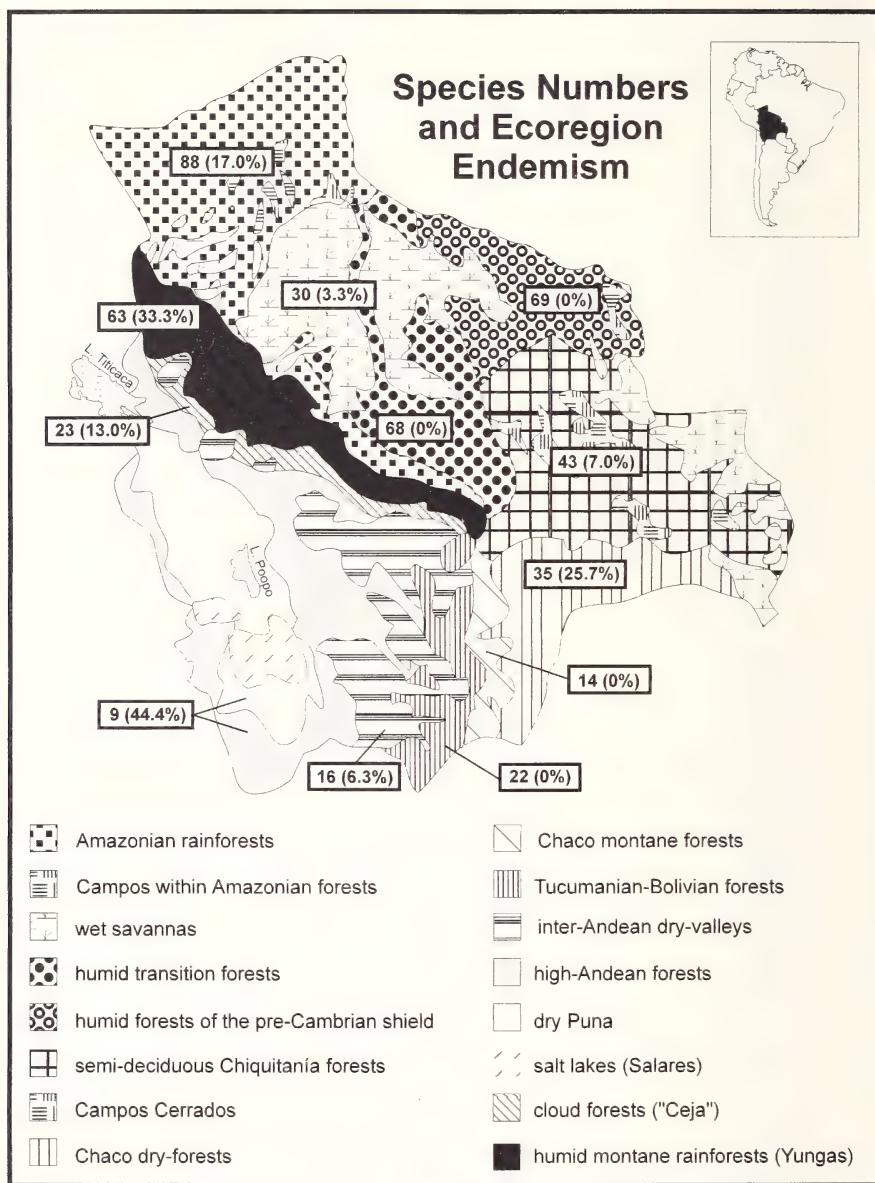
Fig.19: Map of Bolivia showing 12 ecoregions and corresponding absolute numbers of amphibian species. The percentage of species endemic to an ecoregion relative to the absolute species number occurring in the respective region is given in parentheses. For further information see text.

'Hotspots' of Diversity

The general analysis of spatial patterns provided above is not detailed enough to identify local hot spots of species richness and/or endemism. This is possible only through detailed local studies of amphibian faunas and their environments in combination with for example establishing Geographical Information Systems (GIS). However, the analysis presented herein can be used to show some principal trends and patterns.

The humid parts of the vast lowland regions harbor a highly diversified amphibian fauna, but the regions' structures are largely uniform and such is its amphibian diversity. In a more restricted sense, it would therefore not be true to talk of the Amazonian rainforest as a hot spot of diversity. When focusing on more restricted areas, it can be demonstrated that high levels of species richness and evenness can be found wherever different types of ecoregions meet to form a mosaic of different habitats. Such regions can be found in the lowlands where the occurrence of wet savannas, patches of different forest types, and Cerrado formations within short distances is responsible for extraordinarily high species numbers. Other areas with high diversity are situated within transition zones of montane ecoregions. One of such areas is the vicinity of the village Samaipata, Provincia Florida, Departamento Santa Cruz. There, montane rainforests, inter-Andean dry-valleys, and Tucumanian-Bolivian montane forests are very close to each other and form a mosaic of co-existing ecological communities (Ibisch et al. 1996). As a result, the Samaipata area harbors amphibians originating from the Chaco domain, due to the relationships of the inter-Andean dry-valleys to this ecoregion (e.g., *Leptodactylus gracilis*, *Elachistocleis* cf. *ovalis*), typical montane forest species (e.g., *Cochranella nola*, *Hyla marianitae*), high-Andean taxa (e.g., *Hyla andina*, *Pleurodema cinereum*), as well as species having a very wide range on the continent (e.g., *Hyla minuta*, *Phrynohyas venulosa*). When looking at the vicinity of Samaipata, within 10 to 15 km radius, approximately 40 species, or one-fifth of all known Bolivian species can be found. Another very species-rich area is the Madidi region, western Bolivia, Departamento La Paz. This region includes large parts of the Yungas de La Paz montane forests as well as humid peri-Andean forests. There is an interesting orographic area containing numerous "Serranias" of low and mid-elevation, arguing for diverse climate and ecological communities. Remsen & Parker (1995) suggested the Parque Nacional Madidi to represent the earth's richest conservation area for terrestrial biota. Undoubtedly, many amphibian species are still to discover in this area and I would agree with the statement that P.N. Madidi harbors the greatest number of amphibian species compared to other Bolivian parks. A fourth remarkable area is the eastern part of the lower Parque Nacional Amboró. There, different ecoregions interdigitate and we can find species-rich amphibian communities containing real Amazonian species (e.g., *Bufo marinus*, *Hyla acreana*, *H. boans*, *H. lanciformis*, *Phyllomedusa vaillanti*, *Physalaemus petersi*, *Hamptophryne boliviana*), species

mainly distributed in the Chaco-Cerrado domain or open wet savanna habitats (e.g., *Bufo granulosus, B. paracnemis, Hyla nana, H. punctata, H. raniceps, Adenomera diptyx, Eleutherodactylus dundeei, Leptodactylus chaquensis, L. elenae, Physalaemus albonotatus, P. biligonigerus, Pseudis paradoxa*), as well as species primarily ranging in the lower montane rainforests as well as in the humid peri-Andean forests (e.g., *Bufo poeppigii, Cochranella nola, Hyalinobatrachium bergeri, Eleutherodactylus cruralis, Leptodactylus rhodonotus*).

Although it is generally possible to associate amphibian species numbers with certain areas or ecoregions to obtain an impression of spatial patterns of species richness, the actual pattern of diversity is more complicated and less uniform. As a principal rule it can be said that the more diverse are the habitat types in an area the more diverse is the amphibian fauna to be expected. This general trend refers to recent climatic and ecological conditions. On the other hand, there might be more complicated patterns resulting from historical processes.

Another aspect of diversity is the degree of endemic species. Areas with high local endemism are now being ranked as sites with high conservation priorities, based on the substantial evidence that recent global patterns of extinction are dominated by regions rich in endemic species (e.g., Myers 1988, 1990, Myers et al. 2000, Pimm et al. 1995). The cloud forests as well as the upper montane rainforests are extremely rich in endemic species and the species composition may vary within relative short distances. The special role displayed by the so-called "La Siberia" region at the limits of the Departamentos Cochabamba and Santa Cruz was already emphasized by Köhler et al. (1998b). The diversity as well as the degree of endemism in this area is undoubtedly high, but recent fieldwork during this study revealed that several "Siberia" endemics also occur in neighboring cloud

Fig.20: Schematic map of Bolivia and its ecoregions showing some of the areas mentioned in the text with exceptional high species diversity or high degree of endemic species. 1 – Alto Madidi region (including Parque Nacional Madidi and Pilon Lajas); 2 – "La Siberia" region; 3 – Samaipata region including the upper Río Pirai valley and uppermost parts of Parque Nacional Amboró; 4 – eastern parts of Parque Nacional Amboró and its vicinity. The areas of montane rainforests and cloud forests are generally rich in endemic species which are in need of protection. These zones are stippled.

forest areas or that species previously known only from other regions also occur at "La Siberia". This demonstrates that we have to act very cautiously when identifying diversity patterns or hot spots. Every time when conducting field research, it becomes obvious that collecting gaps are still larger than one might imagine.

Nevertheless, I feel comfortable enough to state that the most species-rich areas in Bolivia are probably within the Amazonian forests of the Andean foot as well as the lower montane rainforests. This area has a limited extension and is a contact zone where species communities of two species-rich ecoregions interdigitate. In addition, the upper montane rainforests together with the adjacent cloud forests harbor a rich amphibian faunas, with most of the species being unique for a certain area or at least for the region. Combining these two aspects, highest species richness and highest degree in endemic species, the area of humid Andean slopes as a whole might be regarded the most diverse region in Bolivia with respect to amphibians. Conservation efforts should focus on these zones, especially on the fast diminishing cloud forests which are only peripherally included in protected areas.

Diversity and distribution in montane forest regions

In the following chapters, I provide the results obtained from the investigations in montane forest regions at the eastern slopes of the Bolivian Andes (see Study area: investigated sites). As this region appeared to contain highest levels of endemism, it was chosen as the particular study area to obtain information about differences in diversity within limited distances.

Species accounts

The following account lists amphibian species which were found during investigations in the study area described above, namely montane forest regions above 500 m a.s.l. The account includes species primarily linked to montane areas as well as certain lowland species which enter higher elevations rather than just the lowermost slopes. By far, most of these species were discovered and observed during own field work (for voucher specimens see appendix). Only some few are included with respect to literature records only. The main purpose of this chapter is to summarize newly obtained biological data of the species like for example advertisement call or notes on reproduction, and to comment on the taxonomic status of several populations. Some turned out to represent new undescribed species, whereas in other cases taxonomic problems are discussed but eventually remain unsolved. Under the subheading D i s t r i b u t i o n, the general known distribution of each species is summarized. Additionally, there might be some comments on records made during own fieldwork, particularly referring to the studied area, or other already known records which are not yet reported in the literature. If the species is considered to represent a Bolivian endemic, it is stated. The point N a t u r a l   H i s t o r y refers to habitat use, activity, behavior, reproduction, and

others. Unless accompanied by literature citations, the data provided are based on own observations. Tadpole stages are those of Gosner (1960). Under V o c a l i - z a t i o n, the anuran calls from own recordings for each species where available are described. All provided audiospectrograms and oscillograms refer to own recordings obtained in montane forest regions. Own data are compared and discussed with previously provided literature data, if available. In the cases where it was not possible to provide own data, the vocalization is briefly described from other publications. If vocalization is unknown, it is stated. The R e m a r k s may include notes on the taxonomic status of the species or particular populations, notes on intraspecific variation and/or diagnostic features, notes on sympatry with other species, or any other miscellaneous information not mentioned before. In some cases, where populations were identified as undescribed species, a brief D i a g n o s i s is added. Families, genera, and species are listed in alphabetical order. Snout-vent length is abbreviated SVL; labial tooth row formula is abbreviated LTRF. Webbing formulae follow Myers & Duellman (1982).

ANURA

Bufonidae

Atelopus tricolor **Boulenger, 1902**   Plate Ia, p.64

D i s t r i b u t i o n: The species occurs on the north-eastern versants of the Andes from southern Peru (Departamentos Cuzco and Puno) southward to the Provincia Chapare, Departamento Cochabamba, Bolivia, with an elevational range from approximately 600 to 2040 m above sea level. A lowland record from 227 m a.s.l. (Rurrenabaque, type locality of the synonym *A. willimani*) was considered to be doubtful (Lötters & De la Riva 1998). During this study, *A. tricolor* was only found along the Chapare transect between 1250 and 1650 m a.s.l. No records are known east of Provincia Chapare, Departamento Cochabamba, suggesting this area to represent the eastern distribution limit.

N a t u r a l   h i s t o r y: As far known, all localities where *A. tricolor* was found are situated within humid montane forests. Most individuals collected in this study were found at night perching on leaves at approximately 0.3–1.2 m height. The vegetation was disturbed primary forest and secondary growth at the edge of the road. One female was taken from the edge of a small stream around midday. A

Plate II: **a)** *Bufo veraguensis* Schmidt, 1857, male, Provincia Chapare, 1300 m; **b)** *Cochranella bejaranoi* (Cannatella, 1980), male, Sehuencas, 2100 m; **c)** *Cochranella nola* Harvey, 1996, female, La Hoyada, 1750 m; **d)** *Hyalinobatrachium bergeri* (Cannatella, 1980), male, Provincia Chapare, 500 m; **e)** *Epipedobates pictus* (Bibron in Tschudi, 1838), male, Provincia Chapare, 550 m; **f)** *Gastrotheca* cf. *testudinea* (Jiménez de la Espada, 1871), male, Provincia Chapare, 1300 m; **g)** *Gastrotheca* sp. A, female, Sehuencas, 2150 m; **h)** *Hyla andina* Müller, 1924, female, Sehuencas, 2150 m.

Plate II
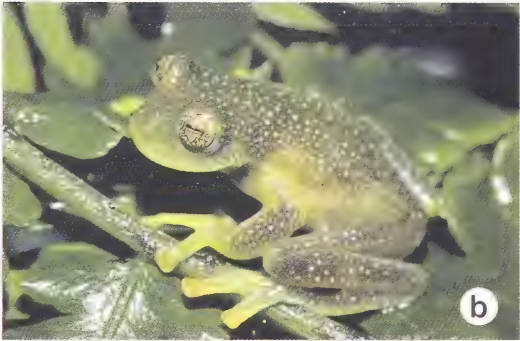
prolonged breeding period can be expected due to the per-humid conditions in the area. One captured specimen showed unken reflex behavior when handled. The tadpole is gastromyzophorous and was described by Lavilla et al. (1997).

Vocalization: Two different call types were noticed in *Atelopus tricolor*. One is a short unpulsed call which might have release function. Call duration in these short calls varied from 7 to 77 ms (mean 23.5 ± 21.2), with a frequency range of 2100–2900 Hz. These calls were emitted in irregular intervals while the male was handled. The other call is longer in duration and distinctly pulsed. This call type may have advertising function. Its duration varied between 92–108 ms (mean 103.1 ± 4.5). Call energy was recognizable between 2250–7000 Hz, with a dominant frequency range of 2970–3450 Hz. Each call consisted of 16–19 pulses (mean 17.8 ± 1.1). Calls were given in regular intervals at an approximate rate of 25 calls per minute. Fifteen pulsed calls of one individual analyzed; air temperature was 26.2°C during recording. These results were published by Lötters et al. (1999).

Remarks: The species was recently redescribed and diagnosed by Lötters & De la Riva (1998). The synonymy includes *Atelopus rugulosus* Noble, 1921 and *Atelopus willimani* Donoso-Barros, 1969. A studied specimen (ZFMK 69920) from the Provincia Chapare, 1200 m a.s.l., did not contain any tetrodotoxin (D. Mebs pers. comm.) like reported for other species in the genus (e.g., Yotsu-Yamashita et al. 1992, Mebs et al. 1995, Lötters 1996).
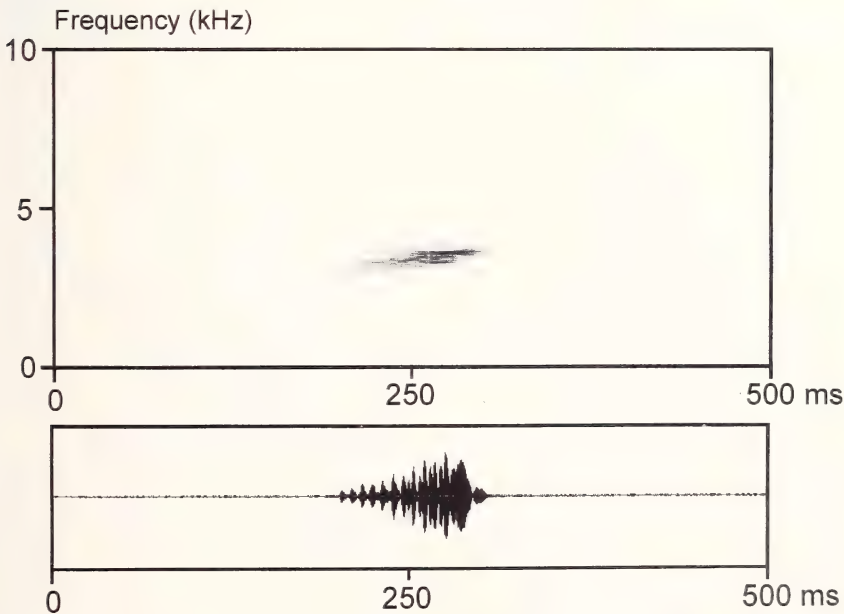
Fig.21: Audiospectrogram and oscillogram of the pulsed call of *Atelopus tricolor* from Provincia Chapare, 1200 m a.s.l. Recording obtained on 11 February 1998 in a terrarium. Air temperature 26.2°C.

Bufo amboroensis Harvey & Smith, 1993

Distribution: The species is known from the type locality 12.7 km north-west of Enpalme at 2150 m a.s.l., northward to southern Peru (Ergueta & Harvey 1996). Although the type locality was visited several times during this study, it was not possible to discover additional specimens.

Natural history: As far known, the species occurs in cloud forest along small streams. Specimens were found motionless on the bottom of a clear stream at daytime. Due to these findings and an extensive webbing on the feet, an aquatic habit was presumed (Harvey & Smith 1993).

Vocalization: Unknown.

Remarks: At the type locality the limits of the Departamentos Cochabamba and Santa Cruz seem not to be properly defined and information about the exact limits is contradictory. Therefore, it might be that the type locality actually is part of the Provincia Caballero, Departamento Santa Cruz, and not of the Departamento Cochabamba like stated by Harvey & Smith (1993). *Bufo amboroensis* was tentatively assigned to the *B. veraguensis* group (sensu Duellman & Schulte 1992) by Harvey & Smith (1993).

Bufo arenarum Hensel, 1867   Plate Ib, p.64

Distribution: The species occurs in central and northern Argentina, southern Brazil, Uruguay, and Andean regions of Bolivia (Cei 1980, Langone 1994). *Bufo arenarum* is known from elevations of approximately 300–2400 m a.s.l.

Natural history: In Bolivia, *Bufo arenarum* inhabits Chaco montane forests, Tucumanian-Bolivian montane forests, and inter-Andean dry valleys. Reproduction takes place during the rainy season, mainly in natural or artificial ponds and lagoons. In inter-Andean dry-valleys, specimens were commonly observed close to river beds. Subadults were obtained in November. The tadpole was described by Fernández (1926). Data on Argentinean populations were provided by Cei (1980).

Vocalization: The advertisement call of Argentinean *B. arenarum* was figured by Barrio (1964) as well as Straneck et al. (1993). It is a train of pulse groups, approximately four seconds in length, with the pulse groups repeated at an approximate rate of 16 per second. Frequency was distributed between 900 and 1300 Hz (estimated from the provided spectrograms).

Remarks: There is great sexual dimorphism in *B. arenarum* regarding dorsal coloration. Males exhibit a more or less uniform reddish brown dorsum, whereas females have distinct orange-red flecks on the cream colored dorsum.

Bufo fissipes Boulenger, 1903   Plate Ic, p.64

Distribution: The species is known from the Yungas de Cochabamba and La Paz, and from the Andean foot at Rurrenabaque, Departamento Beni, Bolivia, as

well as from Departamento Puno, Peru (Rodríguez et al. 1993). The elevational range is from 250–1700 m a.s.l.

Natural history: *Bufo fissipes* inhabits very humid montane rainforests as well as humid forests of the Andean foot. Specimens were found at night, moving on the floor at the forest edge near small streams. All females collected in December and January contain masses of black eggs (approximately 1 mm in diameter) in their ovaries. Males were not observed during this study.

Vocalización: Unknown

Remarks: *Bufo fissipes* was reported from the Departamento Cochabamba, Bolivia, by Frost (1985). However, it remained unclear on which specimens this record was based and until recently the species has not been recollected in Bolivia. Since the original description, *B. fissipes* was only rarely mentioned in the literature (e.g., Gallardo 1961a, Duellman & Schulte 1992) and information is sparse. The recent records from Bolivia provide some valuable new information on morphology and distribution. In the following, a diagnosis based on the recently collected Bolivian females and the holotype is provided:

(1) SVL of eight adult females 65.8–71.9 mm (mean 68.1 mm); (2) snout pointed in dorsal view, acute in lateral profile, protruding beyond margin of lip; (3) nostrils slightly protuberant at level of anterior margin of lower jaw; (4) canthal crest slightly elevated, supraorbital and prominent supratympanic crests, scapular crests present; (5) tympanum ovoid in females, distinct, its length one-third the eye

Fig.22: Dorsal and ventral view of preserved holotype of *Bufo fissipes* (BMNH 1947.2.20.64).

diameter (concealed in holotype); (6) bony protrusion at angle of jaws absent; (7) neural crests of vertebrae absent; (8) parotoid glands ovoid to triangular, only slightly elevated, not protruding laterally, continuing into lateral row of enlarged tubercles; (9) lateral row conical, spinous tubercles in females; (10) skin on dorsal and dorsolateral surfaces strongly tubercular, less intensive mid-dorsally; (11) skin of limbs tubercular or spinous; (12) first finger longer than second; (13) palmar tubercle large, ovoid, two or three times the size of ovoid thenar tubercle; (14) inner metatarsal tubercle ovoid, twice the size of outer more rounded metatarsal tubercle; (15) feet about one-half webbed; edges of webbing with distinct serration, toes with serrated fringes; (16) supernumerary tubercles present, numerous; (17) dorsum brown, with irregular dark markings and spots, pale middorsal line; venter cream with brown flecks and blotches, chest almost completely brown, throat densely mottled with brown.

The holotype of *B. fissipes* (BMNH 1947.2.20.64) has the following measurements (in mm): SVL 38.4; head width 12.0; head lenght 11.9; tibia length 11.5; eyelid width 3.6; interorbital distance 3.8; eye-nostril distance 3.0. There are no morphological differences between the Peruvian type and Bolivian specimens, except that the tympanum of the holotype is rather concealed, although the tympanic annulus is barely visible through the warty skin. Boulenger (1903) stated that the type specimen is a female. However, the type appears to be a subadult and it is rather difficult to determine its sex without dissecting the specimen. Therefore, it might also be a subadult male and the tympanum condition might refer to sexual dimorphism. Otherwise, it could be explained as intraspecific and geographical variation. According to the large similarities, there remains little doubt that Bolivian specimens are conspecific with *B. fissipes*.

Bufo justinanoi Harvey & Smith, 1994   Plate Id, p.64

Distribution: Formerly only known from the type locality El Chape, Provincia Florida, Departamento Santa Cruz and Campamento Fortaleza, Provincia Carrasco, Departamento Cochabamba, the species was now recorded from four more localities, one of them extending the western limits of the known distribution to the Provincia Nor Yungas, Departamento La Paz. Thus, *B. justinianoi* inhabits an area of at least 450 km east-west extension in the Yungas with an elevational range of 1400–2220 m a.s.l. It has to be considered an endemic species for the Yungas region of Bolivia.

Natural history: The species inhabits cloud and montane rainforest. Some sites are slightly disturbed by selective logging but presumably the species needs primary forest to survive. Tadpoles supposedly develop in streams (Harvey & Smith 1994). Freshly metamorphosed juveniles were found in the first days of January 1999. All specimens collected during this study and all but one of those collected by Harvey & Smith (1994) were found active during the day.

Vocalization: Unknown.

Remarks: A member of the *Bufo veraguensis* group according to the original description (Harvey & Smith 1994). Duellman & Schulte (1992) defined some phenetic groups of *Bufo*, among them the *B. veraguensis* group. Although, *B. justinanoi* shares morphological characters given for the group, some features (short limbs, short fingers and toes, ventrally directed anal tube, eyes directed nearly frontally, black iris with golden spotting) seem to be deviate from other members of the group, suggesting that *B. justinianoi* might represent a distinct phylogenetic lineage. It was found in sympatry with *Bufo fissipes, B. quechua, B. veraguensis, B. poeppigii*, and *B. stanlaii*.

Bufo paracnemis Lutz, 1925   Plate Ie, p.64

Distribution: The species is known from northern Argentina, Uruguay, Paraguay, Bolivia, and southeastern to northeastern Brazil (Frost 1985, Langone 1994). It occurs at elevations from sea level up to 1340 m a.s.l.

Natural history: *Bufo paracnemis* inhabits dry Chaco forests, Cerrado formations, savannas, as well as semi-humid montane forests. It is an explosive breeding species with reproduction at the beginning of the rainy season. Eggs are deposited in ephemeral ponds and lagoons. Other information on the biology of *B. paracnemis* was provided by several authors (e.g., Cochran 1955, Cei 1980, Guix 1993, Langone 1994).

Vocalization: The advertisement call of a Bolivian population from northern Departamento Santa Cruz was described by Köhler et al. (1997). The call consisted of a train of pulsed notes. Mean call duration was 2379 ms, mean note duration was 34.7 ms, mean number of notes per call was 33.2, and the dominant frequency was 700 Hz.

Bufo poeppigii Tschudi, 1845   Plate If, p.64

Distribution: The species occurs at least from the eastern versants of the Andes from Departamento San Martin, central Peru, southward to the Provincia Ichilo, Departamento Santa Cruz, Bolivia. It is known from the Andean foot at 260 m up to 1900 m a.s.l.

Natural history: *Bufo poeppigii* inhabits humid montane rainforests and lowland rainforests at the Andean foot. At Mataracú, specimens were found at night partly submerged in the water of a stream. At other localities, *B. poeppigii* usually was observed active during rain on roads within forest. In November 1998, an amplectant pair was observed at Karahuasi, 1800 m a.s.l., depositing egg strings in the water at the edge of a large stream. De la Riva et al. (1996a) reported males of the species calling from ephemeral puddles near human settlements.

Vocalization: The advertisement call of a Bolivian lowland population (Bulo Bulo, 260 m a.s.l.) was described by De la Riva et al. (1996a). It was a train of

10–45 pulse groups, with each pulse group consisting of 3–5 pulses. Call duration varied between 631 and 2680 ms. A mean dominant frequency peak was recognizable at 1033 Hz.

R e m a r k s : The specific status of *Bufo poeppigii* has been the subject of controversial opinions for a long time. Some authors considered it a synonym of *Bufo marinus* (e.g., Mertens 1952, Vellard 1959, Cei 1968, Gorham 1974), whereas others mentioned it as a valid species (e.g., Nieden 1923, Blair 1972, Bogart 1972, Guttman 1972, Duellman & Toft 1979, Frost 1985). Henle (1985) failed to elucidate the taxonomic status of *B. poeppigii* and treated it as a sympatric (!) subspecies of *B. marinus*. Recent collections in Bolivia and Peru provide evidence for the specific status of *B. poeppigii* (De la Riva pers. comm.). Most records of *B. marinus* from higher elevation montane forests might actually correspond to *B. poeppigii*. However, both species do occur sympatrically at some localities at the foot of the Bolivian Andes (De la Riva et al. 1996a, own observations).

There is a distinct sexual dimorphism in skin texture of adult *B. poeppigii*. Observed and examined males always had rugose skin with many tubercles bearing keratinized spicules. Females had much smoother skin and lack spicules. In contrast, there is no pronounced sexual dimorphism in body size.

Bufo quechua Gallardo, 1961   Plate Ig, p.64

D i s t r i b u t i o n : The species is known from the eastern versants of the Bolivian Andes at least from Provincia Chapare, Departamento Cochabamba, to Provincia Caballero, Departamento Santa Cruz, with an elevational range of 1900–2500 m a.s.l. Endemic to Bolivia.

N a t u r a l   h i s t o r y : *Bufo quechua* inhabits humid upper montane forests as well as cloud forests. It is a terrestrial species active at both, night and day. Individuals were found in leaf litter at the forest edge or within the forest. Amplectant pairs were observed in February at Incachaca. At Sehuencas, juveniles as well as subadults were observed in December, arguing for a prolonged breeding period. Presumably, eggs are deposited in lotic water. *Bufo quechua* frequently suffered from parasite infestation, visible as reddish pustules through the skin (Köhler et al. 1995a). According to De la Riva (1998), these pustules are caused by larvae of trombidioid mites.

V o c a l i z a t i o n : Unknown.

R e m a r k s : *Bufo quechua* occurs in sympatry with *B. amboroensis*, *B. justinanoi*, *B. veraguensis*, as well as *B. poeppigii*.

Bufo stanlaii Lötters & Köhler, 2000   Plate Ih, p.64

D i s t r i b u t i o n : The species is known from the eastern Andean slopes in the Departamentos Cochabamba and Santa Cruz (Provincias Chapare, Carrasco, and

Florida). The known elevation ranges from 1500–1900 m a.s.l. (Lötters & Köhler 2000a). Endemic to Bolivia.

Natural history: *Bufo stanlaii* inhabits lower and upper humid montane rainforests. Specimens were observed active during the day and at night in leaf litter. Two females, collected in February 1998 and December 1994, each contain masses of tan eggs in their ovaries (Lötters & Köhler 2000a).

Vocalization: Unknown.

Bufo veraguensis Schmidt, 1857 — Plate IIa, p.80

Distribution: The species is known from the eastern Andean slopes from southern Peru southward to Departamento Chuquisaca, Bolivia, as well as in inter-Andean valleys of Bolivia. The known elevational range is approximately 900–2100 m a.s.l.

Natural history: *Bufo veraguensis* inhabits humid montane rainforests and cloud forests, as well as semi-humid forests of the Andean slopes and inter-Andean dry-valleys. It is primarily a nocturnal species. Specimens were found in rocky river beds, climbing on boulders near streams, in the leaf litter at the edge of forests, as well as climbing on trunks of large trees in 2.0 m height. Many juveniles were found in December in semi-humid montane habitats south of Santa Cruz de la Sierra. The tadpole was described by Cadle & Altig (1991). It is specialized to its lotic habitat by a well-developed belly sucker.

Vocalization: Unknown.

Remarks: Bolivian populations exhibit remarkable intra- and interpopulational variation concerning the dorsal and ventral color pattern.

Centrolenidae

Cochranella bejaranoi (Cannatella, 1980) — Plate IIb, p.80

Distribution: The species is known from humid montane forests of the eastern slopes of the Bolivian Andes in the Departamentos La Paz, Cochabamba, and Santa Cruz from 1600–2400 m a.s.l. As far known, the species was not recorded from Peru and thus has to be considered a Bolivian endemic.

Natural history: Males and females were found to be abundant along small streams within cloud forest. Most individuals were found close to small cascades. Males called most intensively at night during light rain, perching on leaves above the water. South of Karahuasi, several males were observed calling from inside narrow rock clefts along a stream. These clefts were continuously moistured by water flowing from above. Minimal distance between calling males was only a few centimeters. Egg clutches were observed in December and early January. They were deposited on leaves above small streams or inside the mentioned rock

Frequency (kHz)

10 ⎤

5 ⎤

0 ⎤

0   500   1000 ms

0   500   1000 ms
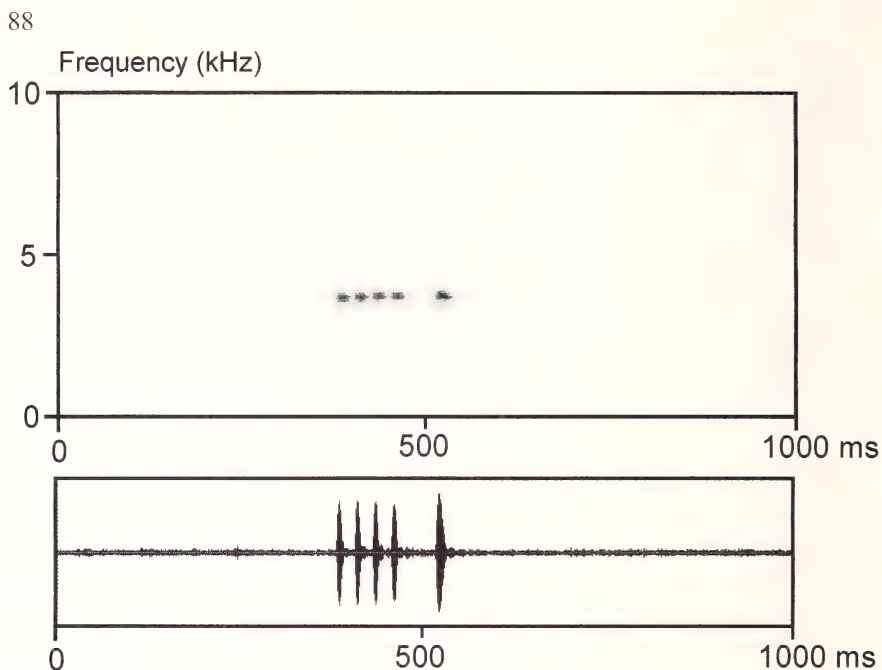
Fig.23: Audiospectrogram and oscillogram of the advertisement call of *Cochranella bejaranoi* from a point north of Remates, P.N. Amboró, 2300 m a.s.l. Recording obtained on 2 January 1998. Air temperature 14.1°C.

clefts and were approximately 40 mm in diameter and 10 mm in thickness. One clutch contained 21 developing larvae.

Vocalization: Advertisement calls were recorded on 2 January 1998 north of Remates, Parque Nacional Amboró, Provincia Florida, Departamento Santa Cruz, 2300 m a.s.l. Calls consisted of 4–8 notes, the first notes repeated in regular intervals of 14–16 ms, and the last one being separated by an interval of 59–61 ms. Call duration varied from 152–245 ms (mean 185.3 ± 40.2). Mean dominant frequency was 3560 Hz. The calls were emitted in regular intervals with a repetition rate of approximately seven calls per minute. Sixteen calls of two individuals analyzed; air temperature was 14.1°C during recording.

The calls described by Márquez et al. (1996) from Río Chua Kocha (recorded at approximately same temperature) differ somewhat with respect to a higher dominant frequency (4039 Hz), shorter intervals between notes (9 and 42 ms), and number of notes per call (6–7). These differences might correspond to individual variation, because individual call variation was also recognizable in recordings from north of Remates.

Remarks: *Cochranella flavidigitata* Reynolds & Foster, 1992 is a junior synonym of *C. bejaranoi* (Harvey 1996).

Cochranella nola **Harvey, 1996** Plate IIc, p.80

Distribution: The species was formerly known only from the type locality Quebrada El Fuerte, Provincia Florida, Departamento Santa Cruz, 1600 m a.s.l. (Harvey 1996). During this study, *C. nola* was discovered at La Hoyada in humid montane forest (1750 m a.s.l.) as well as in rainforest of the Andean foothills at Mataracú, Provincia Ichilo, Departamento Santa Cruz, 500 m a.s.l. It is predicted that *C. nola* occurs in the whole area of the Parque Nacional Amboró. Endemic to Bolivia.

Natural history: At the type locality, the natural habitat consisted of low semi-deciduous montane forest, whereas the zonal vegetation at La Hoyada is humid montane forest and that of Mataracú humid peri-Andean forest with Amazonian influence. At La Hoyada, a single female was found perching on a bush within the forest far away from any water bodies. However, the principal microhabitat, including persistently humid sites along streams, was comparable at Mataracú and Quebrada El Fuerte (Lötters & Köhler 2000b). Obviously, the occurrence of *C. nola* mainly depends on microclimatic conditions rather than on the absolute amount of precipitation. On 27 January 1998 (at about 1:00–2:00 h), during a very light rain, *C. nola* was abundant at the type locality. Within 30 minutes of searching, from the Santa Cruz-Samaipata road up-stream about 100 m, more than 15 specimens were seen and several additional males were heard calling. Males called isolated or in small groups of up to six individuals, separated from each other by only few centimeters (3–20 cm). They were found at heights from 0.3 to 5 m above ground, perching on large boulders inside the stream course or on riparian vegetation. Directly below the calling males the water was fast flowing, which is different from Harvey's (1996) observations. The water was always less than 1 m deep, occasionally only a few centimeters (5–25 cm). Some of the boulders from which *C. nola* called were cave-like and because of the swiftly flowing water below they rehydrated continuously; others were more dry. One obtained female was gravid.

Vocalization: Advertisement calls were recorded on 27 January 1998 at the type locality. Recordings of about 15 minutes containing calls of at least four different males were obtained. In total, 19 calls emitted by two different males were analyzed for call parameters (11 + 8). The call mostly consisted of a single high pitched note, but series of three notes were common. Note duration varied between 75–115 ms (mean 94 ms ± 11.97). Mean note repetition rate was 6.7 notes/min, whereas it was 618.2 notes/min within the calls consisting of three fast repeated notes. Call energy was distributed between 4400 and 6500 Hz, with a dominant frequency range of 4970–5590 Hz (mean 5460 ± 221). There were no structural differences between single and fast repeated notes. The calls were emitted at irregular intervals. No other anuran species were heard concomitantly. Air temperature was 23.0°C during recording.

Frequency (kHz)
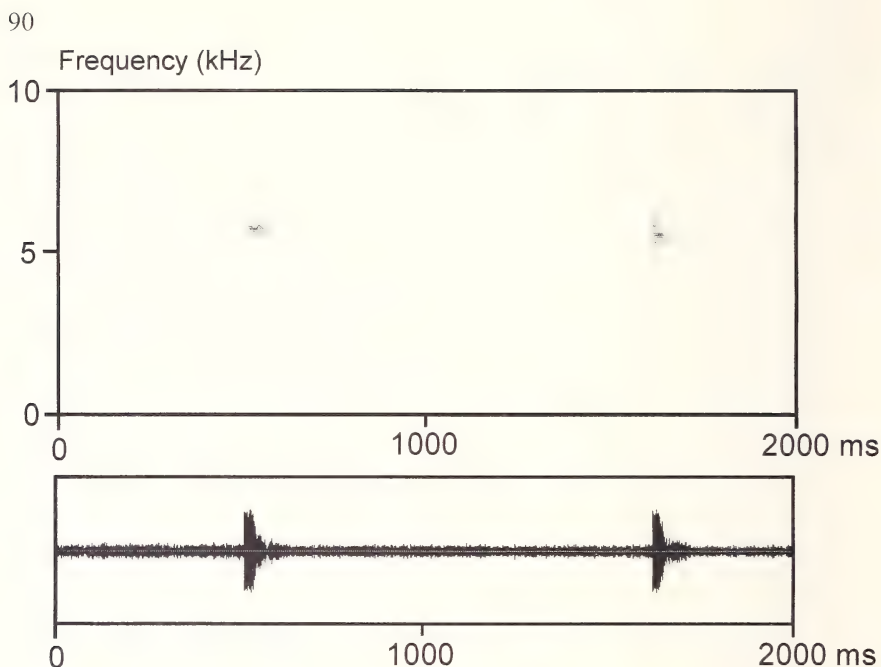
Fig.24: Audiospectrogram and oscillogram of the advertisement call of *Cochranella nola* from Quebrada El Fuerte (type locality), 1650 m a.s.l. Recording obtained on 27 January 1998. Air temperature 23.0°C.

R e m a r k s : Two obtained females, previously undescribed for this species, have SVL of 24.4 and 25.7 mm (NKA 3465, ZFMK 66378). Despite of the larger size they do not differ from males found in this study or described by Harvey (1996). The two males collected at Mataracú are slightly larger than those from the type locality. *Cochranella nola* occurs sympatrically with *Hyalinobatrachium bergeri* and at upper elevations also together with *Cochranella bejaranoi* (Lötters & Köhler 2000b).

Hyalinobatrachium bergeri (Cannatella, 1980)   Plate IId, p.80

D i s t r i b u t i o n : The species is distributed along the eastern slopes of the Andes from the Departamento Cuzco, Peru, southwards to the Departamento Santa Cruz, Bolivia. Formerly only reported from cloud forests from 1700–1980 m a.s.l. (Cannatella 1980, Cannatella & Duellman 1982), *H. bergeri* was recently record-ed from forests of the Andean foot at elevations as low as 300 m a.s.l. (Emmons 1991, Márquez et al. 1996), suggesting that the species principally occurs at all sites with suitable conditions between 300 and 1980 m a.s.l.

N a t u r a l   h i s t o r y : *Hyalinobatrachium bergeri* inhabits humid Amazonian forests along the Andean foot as well as humid montane and cloud forests up to

1980 m a.s.l. Males were reported calling at night from the underside of leaves of riparian trees at about 2.5 meters above the ground (Márquez et al. 1996). Cannatella (1980) figured an egg clutch of approximately 25 mm in diameter deposited at the underside of a leaf and containing 29 eggs. During this study, a single clutch was found in same position on 3 February 1998 at 500 m a.s.l. on the Chapare transect. This clutch contained only one undeveloped egg and a single larva.

Vocalization: Márquez et al. (1996) described the advertisement call from Río Cheyo, Provincia Ichilo, Departamento Santa Cruz, 700 m a.s.l. It consisted of a single short frequency modulated note with a mean duration of 151.4 ms and a mean dominant frequency peak at 4495 Hz.

Remarks: The species was found in sympatry with following other centrolenid species: *Cochranella bejaranoi*, *C. phenax*, *C. spiculata*, *C. truebae* (Cannatella & Duellman 1982), and *C. pluvialis* (Köhler & Reichle 1998).

Dendrobatidae

Colostethus mcdiarmidi Reynolds & Foster, 1992

Distribution: The species was formerly known only from the type locality in the Provincia Chapare, Departamento Cochabamba, 1693 m a.s.l. (Reynolds & Foster 1992). Recently, *C. mcdiarmidi* was recorded from the Parque Nacional Pilón Lajas in the Yungas de La Paz region (Gonzales et al. 1999). During this study, it was not possible to rediscover the species at the type locality. As far known, endemic to Bolivia.

Natural history: Specimens were found to be active during the day in undisturbed montane forest. The tadpole was described by Reynolds & Foster (1992).

Vocalization: Unknown

Epipedobates pictus Bibron *in* Tschudi, 1838   Plate IIe, p.80

Distribution: The species is widely distributed in the lowlands of the Bolivian Departamentos Santa Cruz, Cochabamba, Beni, and La Paz. At the Amazonian slopes of the Bolivian Andes, *E. pictus* was recorded up to 1300 m a.s.l. (De la Riva et al. 1996c). Haddad & Martins (1994) named some localities for the species in Mato Grosso do Sul, Brazil. Duellman & Thomas (1996) recorded *E. pictus* from Balta, Departamento Ucayali, Peru.

Natural history: *Epipedobates pictus* inhabits semi-deciduous forests and humid forests of the lowlands as well as lower montane rainforests at the Andean slopes. During this study, the species was observed active during the day in nearly all kinds of habitat (secondary growth, primary forest, stream beds, open habitat, etc.). A prolonged breeding period can be suspected, because males carrying tadpoles were found from November to February. Haddad & Martins (1994)

reported 14 tadpoles on the back of a male. Calling activity mainly depended on the weather conditions and also occurred around midday. Males mostly called from slightly elevated positions on the ground (e.g., dead tree branches, trunks). The tadpole of Santa Cruz specimens was described by Silverstone (1976) and Haddad & Martins (1994).

Vocalization: Advertisement calls were recorded on 16 November 1997 (9:20 h) at Mataracú, Provincia Ichilo, Departamento Santa Cruz, 500 m a.s.l. The call consisted of a single note with 41–49 ms duration (mean 43.6 ± 2.2). Notes were repeated in regular intervals with a mean rate of 170 notes per minute. The notes showed an upward modulation and a terminal drop in dominant frequency. It was 4120 Hz at the beginning of the note and 4270 Hz at its end. Call energy was also present in a harmonic frequency band at 6300 Hz. Notes lack pulsatile structures. Forty-five calls of one individual analyzed; air temperature was 23.3°C during recording.

The parameters in calls from Mataracú coincide relatively well with the calls described by Haddad & Martins (1994) for *E. pictus* from Santa Cruz de la Sierra. Calls described by De la Riva et al. (1996c) from Puerto Almacén, northern Departamento Santa Cruz, were somewhat shorter in duration (25.5–32.5 ms) and had a slightly lower dominant frequency (3843.2 Hz).

Remarks: Haddad & Martins (1994) suggested that *Epipedobates pictus* and *E. hahneli* might occur in sympatry in the northern Amazonian regions of Bolivia.
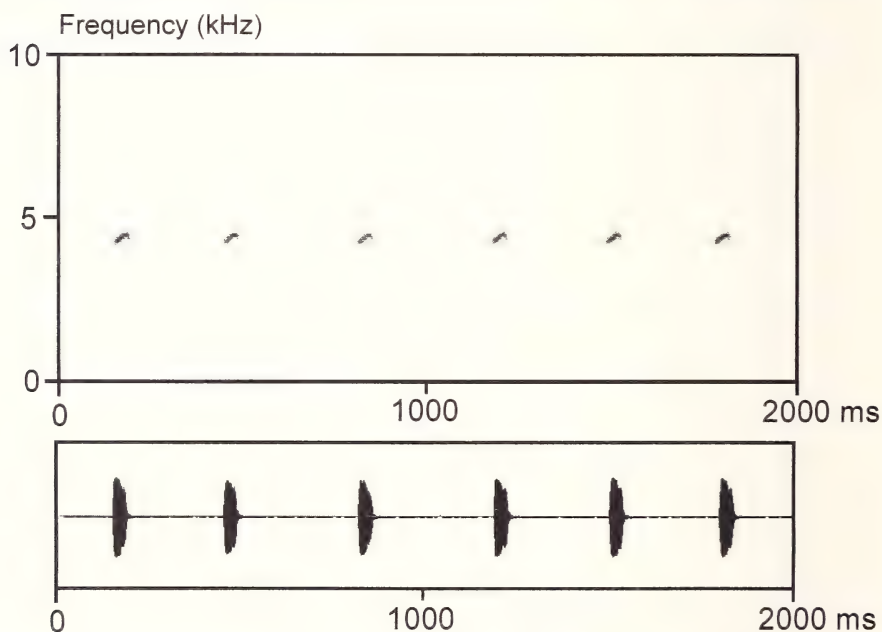
Fig.25: Audiospectrogram and oscillogram of the advertisement call of *Epipedobates pictus* from Mataracú, P.N. Amboró, 500 m a.s.l. Recording obtained on 16 November 1997. Air temperature 23.3°C.

This is supported by the record of *E. pictus* from Peru (Duellman & Thomas 1996). However, there are some difficulties concerning the bioacustic data of the population occurring at Panguana, Peru, reported by Schlüter (1980). These calls seem to have intermediate characters between *E. pictus* and *E. hahneli* (De la Riva et al. 1996c). Therefore, it has been suggested that possibly more than the two species are involved (Lötters et al. 1997, Köhler & Lötters 1999b). The specimens found during this study are clearly assignable to *E. pictus*.

Hylidae

Gastrotheca lauzuricae De la Riva, 1992

Distribution: The species is known only from a single female specimen from La Siberia, Provincia Carrasco, Departamento Cochabamba, 2800 m a.s.l. (De la Riva 1992a). Endemic to Bolivia.

Natural history: The specimen was found under a stone near to the Cochabamba–Santa Cruz road in an area of cloud forest (De la Riva 1992a). Nothing else is known.

Vocalization: Unknown.

Gastrotheca testudinea (Jiménez de la Espada, 1871)   Plate IIf, p.80

Distribution: The species is known from the eastern Andean slopes of southern Colombia, Ecuador, Peru, southward to the Departamento Cochabamba, Bolivia, between elevations of 1100–2275 m a.s.l. (Ruiz-Carranza et al. 1996, Duellman & Lynch 1988, W. E. Duellman pers. comm.).

Natural history: *Gastrotheca testudinea* inhabits montane rainforests. Like other species of the *G. ovifera* group, it is suggested to have direct development. In the Bolivian Provincia Chapare, the species seems to be quite arboreal. Few specimens were collected from the crown of a freshly fallen tree. Another male was found at night perching on a leaf in approximately 0.5 m height at the edge of a small stream.

Vocalization: Unknown.

Remarks: The distribution along the eastern Andean slopes from Colombia to Bolivia is rather unusual for a single species. A juvenile collected in February 1998 in the Chapare region is distinguished in morphological characters from Peruvian juveniles of *G. testudinea*. Further investigations are needed to clarify the taxonomic status of Bolivian populations.

Gastrotheca splendens (Schmidt, 1857)

Distribution: The species is known only from Abra de la Cruz, P.N. Amboró, north of San Juan del Potrero, Provincia Caballero, Departamento Santa Cruz,

Bolivia, 2286 m a.s.l. (Duellman & De la Riva 1999). This locality is close to what herein is described as Remates. Endemic to Bolivia.

Natural history: The general habitat of the known locality is cloud forest of medium height. Nothing else is known.

Vocalization: Unknown.

Remarks: *Gastrotheca splendens* was recently rediscovered and redescribed by Duellman & De la Riva (1999). The two known specimens have 44.7 mm (female) and 51.3 mm (male) SVL. A main morphological character to identify the species is the cranial coossification of the skin between the eyes.

Gastrotheca species A   Plate IIg, p.80

Distribution: The species is known between 1800 and 3000 m in the Departamentos Cochabamba and Santa Cruz, Bolivia. Findings of *Gastrotheca* specimens in Chuquisaca may also correspond to the same species or to *G. gracilis* (see remarks).

Natural history: *Gastrotheca* sp. A inhabits cloud forests and upper montane rainforests. In certain areas, it seems to be an abundant species. Males called while perching on low bushes and ferns. Females were frequently found moving on the ground. Single individuals were discovered at daytime in arboreal bromeliads. Reproduction supposedly takes place throughout the rainy season. Females carrying 30–50 eggs or tadpoles in their marsupium were observed in the months November to January. Tadpoles were released in stages 35–36 (sensu Gosner 1960) in puddles and roadside ditches. Some obtained females had only few larvae remaining in the marsupium, suggesting that tadpoles were released in several portions (see Köhler et al. 1995a [*G. marsupiata*]).

Vocalization: Advertisement calls were described by De la Riva et al. (1995) from the Yungas de Cochabamba region (as *G. marsupiata*). Calls consisted of two different note types, a first long pulsed note, followed by 1–3 shorter secondary notes; mean note duration was 1103 ms in the first and 316.4 in the secondary notes; pulse rate in the long notes was 31.1 pulses per second; secondary notes always had a slightly higher mean dominant frequency (2024.4 Hz) compared to the first pulsed notes (1913.6 Hz).

Remarks: De la Riva (1992a) distinguished high-Andean and forest populations of *G. marsupiata* in Bolivia and described their different morphology. The latter populations now turned out to represent a different species. There are remarkable differences in morphology, advertisement call, and egg numbers between *G. marsupiata* and the montane forest populations. However, a specific identification of these populations is not easy. Affinities to the Argentinian *G. gracilis* which probably occurs in southern Bolivia were suspected (W. E. Duellman pers. comm.). However, it appears more probable that Bolivian montane forest

populations represent an undescribed species or *G. lauzuricae*. Until no addition-al *G. lauzuricae*-like specimens become available, this problem remains unsolved.

Hyla andina Müller, 1924   Plate IIh, p.80

Distribution: The species is widely distributed in the eastern Andes and Andean pre-Cordilleras from northern Bolivia southward to Provincia Catamarca, Argentina. In the northern part of its range *H. andina* occurs at elevations from 1650–3400 m a.s.l., whereas in the southern part (Argentina) it occurs at 500–1640 m a.s.l. (Duellman et al. 1997).

Natural history: *Hyla andina* was always found near to water bodies, either lotic or lentic. At higher elevations, it inhabits grass lands along small streams, lagoons or ponds. At lower elevations, the species enters montane forest habitats. Usually, *H. andina* appeared to be more abundant in open habitats with lentic water, whereas it was seldom found within dense forest habitats and fast running streams. Males were observed calling from low bushes or from the ground at the edge of water bodies. Calling usually appeared at nighttime, but in some cases calls were also heard during the day. At day, individuals can be found under stones or they perch on branches of bushes, often exposed to direct sunlight (Duellman et al. 1997). When disturbed, individuals tried to escape by jumping into the water. In cloud forest habitats, juveniles were found from December to January. The tad-pole was described by Cei (1980), Lavilla (1984), Lavilla & Fabrezi (1987), as well as Duellman et al. (1997). In their tadpole description, the latter authors out-lined several inconsistencies to the description provided by Cei (1980).

Vocalization: Advertisement calls were recorded at Quebrada El Fuerte, near Samaipata, Provincia Florida, Departamento Santa Cruz, 1700 m a.s.l., show the following parameters: calls consisted of two fast repeated tonal notes; call dura-tion varied from 176–184 ms (mean 181.0 ± 3.5 ms); note duration varied from 48–65 ms (mean 57.0 ± 6.9 ms), the second note always being slightly shorter; calls were repeated in regular intervals, at a rate of approximately 35 calls per minute; a dominant frequency peak was recognizable at 2320 Hz, with harmonic frequency bands at 4640, 6960, and 9300 Hz; the second note of the call was fre-quency modulated, with the dominant frequency peak dropping down to 1880 Hz; notes lacked pulses; five calls of one individual analyzed; air temperature was 20.4°C at time of recording.

In general structure, these calls coincide relatively well with the two-note calls recorded by Reynolds & Foster (1992) or those reported by Márquez et al. (1993) for Bolivian populations, but there are significant differences concerning note duration, dominant frequency and presence of harmonics. Barrio (1965a) figured calls of *H. p. andina* from Argentina consisting of four notes and the same was described by Basso & Basso (1987). Finally, Duellman et al. (1997) described calls from Argentina consisting of three notes. The latter authors discussed the dif-ferences between all the call data published. Obviously, some of these differences

Frequency (kHz)
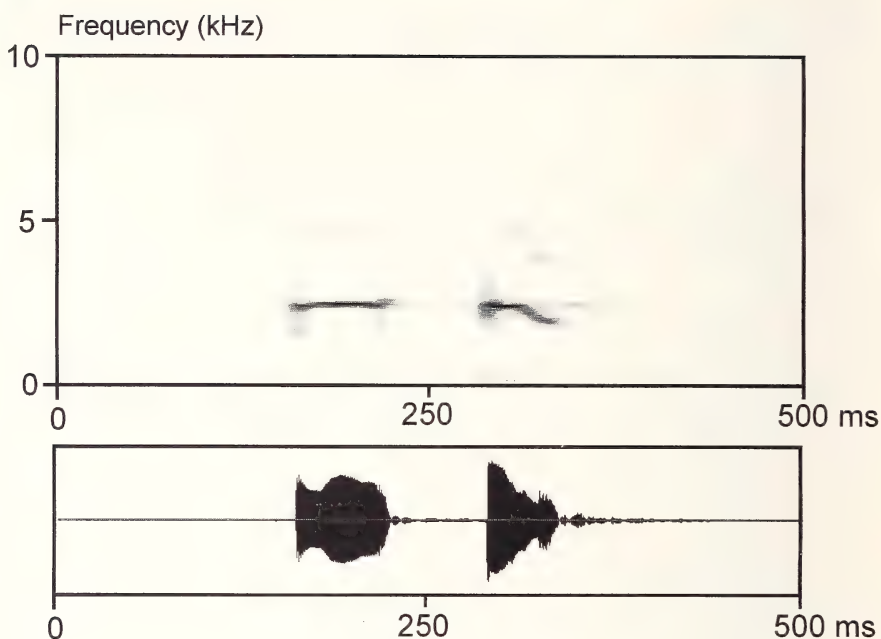
Fig.26: Audiospectrogram and oscillogram of the advertisement call of *Hyla andina* from Quebrada El Fuerte, 1700 m a.s.l. Recording obtained on 17 November 1994. Air temperature 20.4°C.

are partly due to different recording conditions and differences in calling motivation. Although, it was not possible to record others than the two-note calls described above, calls consisting of more than two notes were heard at La Siberia, Departamento Cochabamba (compare also Márquez et al. 1993). Like previously argued by Reynolds & Foster (1992), the presence of harmonic frequency bands may vary with the material and methods used for recording and analysis. However, differences noted in Bolivian populations to those from northern Argentina, may indicate that their taxonomic status has to be reconsidered.

R e m a r k s : During this study the species was found in sympatry with *Hyla marianitae* and *H.* cf. *callipleura*, two other species in the *H. pulchella* group. There is remarkable interpopulational variation concerning body size and coloration (see Duellman et al. 1999).

Plate III: **a)** *Hyla armata* Boulenger, 1902, male, Río Roncito, 1640 m; **b)** *Hyla* cf. *callipleura* Boulenger, 1902, male, Provincia Chapare, 1300 m; **c)** *Hyla marianitae* Carrizo, 1992, couple, Karahuasi, 1800 m; **d)** *Hyla minuta* Peters, 1872, male, La Hoyada, 1850 m; **e)** *Hyla* sp. A, female, Provincia Chapare, 950 m; **f)** *Phrynohyas venulosa* (Laurenti, 1768), female, W of Vaca Guzman, 1360 m; **g)** *Phyllomedusa boliviana* Boulenger, 1902, male, W of Vaca Guzman, 1360 m; **h)** *Scinax castroviejoi* De la Riva, 1993, male, Samaipata, 1700 m.

Plate III

Hyla armata **Boulenger, 1902**   Plate IIIa, p.96

Distribution: The species is distributed along the eastern slopes of the Andes from Departamento Ayacucho, Peru, southward to the Departamento Santa Cruz, Bolivia (Duellman et al. 1997), with an elevational range of 1400–2400 m a.s.l.

Natural history: *Hyla armata* always is associated with cascading streams, where adults perch on large boulders or on vegetation close to the water at night. Tadpoles develop in fast running water. They were described by Cadle & Altig (1991) and Duellman et al. (1997). A freshly metamorphosed juvenile was found end of November at the edge of a stream at Karahuasi.

Vocalization: The call was described as a high pitched "whirrr" (Cadle & Altig 1991) and consisted of a single monophasic slightly upward modulated note with a duration of 160–240 ms (Márquez et al. 1993, Duellman et al. 1997).

Remarks: When Duellman et al. (1997) defined the *Hyla armata* group they recognized only one member, *H. armata* itself. Recently, it turned out that *Hyla charazani* Vellard, 1970 has to be considered a second species of the group which is distinguished from *H. armata* by advertisement call and morphology (S. Reichle pers. comm.). Furthermore, recent studies revealed that populations of *H. armata* in the Yungas de La Paz region (the supposed type locality) are possibly not conspecific with populations in the Departamentos Cochabamba and Santa Cruz, a presumption mainly based on advertisement call differences (S. Reichle pers. comm.). Unfortunately, it was not possible to record calls during the present study and therefore populations included herein are regarded to represent *Hyla armata* until new data will be provided.

Hyla cf. *callipleura* **Boulenger, 1902**   Plate IIIb, p.96

Distribution: The species is at least known from the Yungas de Cochabamba region between 700 and 2300 m a.s.l., Bolivia (see remarks). Probably endemic to Bolivia.

Natural history: Between December and February in the Provincia Chapare, males were found at night calling during rain from vegetation above slow running water at 0.1–2.0 m height. Mostly, calling males formed small choruses at the forest edge. At Incachaca, males were found in an artificial pine forest.

Two tadpoles obtained on 17 December 1998 at 1650 m a.s.l., Provincia Chapare, were in stages 32 and 40 (sensu Gosner 1960) and had total lengths of 30.8 and 43.4 mm, respectively. In general morphology, they are very similar to the tadpoles described for *H. balzani* by Duellman et al. (1997). They differ only with respect to a more pointed tail tip. Their LTRF is 3(3)/4(1,4).

Vocalization: Advertisement calls were recorded on 18 December 1998 at 1250 m a.s.l. in the Provincia Chapare. Calls sounded like a moderately high pitched "trill" (single notes like a "tink") and consisted of 1–5 short notes (mean

Frequency (kHz)
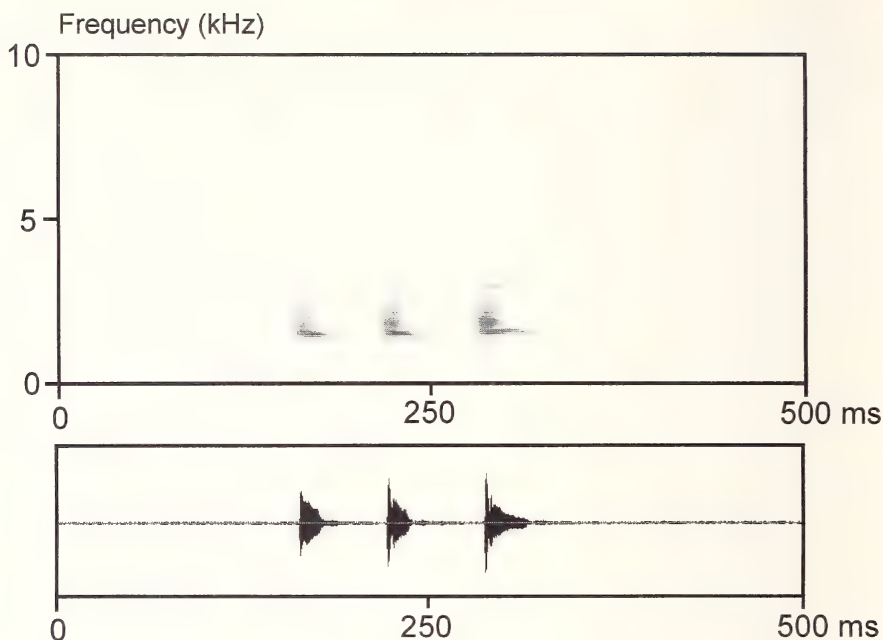
Fig.27: Audiospectrogram and oscillogram of the advertisement call of *Hyla* cf. *callipleura* from Provincia Chapare, 1250 m a.s.l. Recording obtained on 18 December 1998. Air temperature 16.1°C.

2.95 ± 0.94), repeated in regular intervals at a rate of 15–20 (mean 16.7 ± 1.2) notes per second; note duration varied from 17–35 ms (mean 24.6 ± 5.7); call duration varied from 29–244 ms (mean 135.5 ± 46.9), depending on the number of notes involved; calls were repeated in regular intervals with an approximate rate of 5–6 calls per minute; call energy was distributed between 1000 and 9000 Hz, with a dominant frequency peak between 1070 and 1380 Hz (mean 1240 ± 119); frequency bands were present at 2840, 4240, 7050, and 8450 Hz; notes exhibited a weak pulsatile structure, but pulses were not countable. Twenty-three calls of four individuals analyzed; air temperature was 16.1°C during recording. Calls sounded similar at all localities along the "old" Chapare road.

Reynolds & Foster (1992) described the calls of *H. callipleura* from the Provincia Chapare as a sharp moderately high-pitched "tink" which generally coincides with the observations described above. The call described by Márquez et al. (1993) as that of *Hyla callipleura* actually corresponds to *Hyla marianitae* (Duellman et al. 1997).

R e m a r k s : In their review of the Andean members of the *Hyla pulchella* group Duellman et al. (1997) treated *Hyla callipleura* Boulenger, 1902 as a junior synonym of *Hyla balzani* Boulenger, 1898 based on comparison of the type speci-

mens. The authors designated BMNH 1947.2.13.65 from Charuplaya, 1350 m, Bolivia, as the lectotype of *H. callipleura*. According to De la Riva (1990a), Charuplaya is located in the Provincia Ayopaya, Departamento Cochabamba, Bolivia. The type locality of *H. balzani* is in the Yungas de La Paz at approximately 1600 m a.s.l.

Duellman et al. (1997) described the advertisement call of *H. balzani* from near Santa Isabel, Departamento Cuzco, Peru, as a single low note with a duration of 170 ms. As is obvious from their provided oscillogram and description, the note is distinctly and homogeneously pulsed at a rate of approximately 80 pulses per second. Beside a somehow similar dominant frequency, the call figured and described by Duellman et al. (1997) does have nothing in common with the calls described above. Therefore, I conclude that the two different calls correspond to different species. The type locality of *Hyla balzani* is approximately 400 km airline apart from Santa Isabel, the locality from where Duellman et al. (1997) reported their calls.

Several possibilities now have to be discussed concerning the actual taxonomic status of the two involved taxa: (1) the two species with the two different calls broadly occur in sympatry from the Yungas de Cochabamba northward into southern Peru; none of the type specimens can be assigned to one of the calls with certainty; (2) Peruvian populations from which Duellman et al. (1997) described the call are distinguished from all Bolivian populations; the Bolivian populations represent *H. balzani*; *H. callipleura* remains a junior synonym of *H. balzani*; the Peruvian populations have to be considered an undescribed species; (3) three taxa are involved, one in southern Peru, one in the Yungas de La Paz, and one in the Chapare region; the Peruvian populations represent an undescribed species, the La Paz populations are *H. balzani*, and the populations from Chapare are *H. callipleura* or an undescribed taxon; (4) the call described by Duellman et al. (1997) corresponds to *H. balzani* which is distributed in the Yungas de la Paz region, Bolivia, northward into southern Peru; populations in Provincia Chapare, Departamento Cochabamba are not conspecific with *H. balzani* according to advertisement call differences; the name *Hyla callipleura* is assignable to the Chapare populations, because the type locality (Charuplaya, 1350 m, by lectotype designation) is close to the Provincia Chapare; *H. balzani* and *H. callipleura* may be distributed allopatric, parapatric or even sympatric in an area around the limits of the Departamentos Cochabamba and La Paz.

As is obvious, due to the lack of data it is currently not possible to clarify the taxonomic status of the populations from Provincia Chapare. Therefore, before assigning a new name to any of the populations, it is herein preferred to reestablish the available name *Hyla* cf. *callipleura* tentatively for the Chapare populations (as already done in the present work), just to express that more than one taxon is involved.

Hyla chlorostea **Reynolds & Foster 1992**

Distribution: The species is known only from a single specimen from Parjacti, Provincia Chapare, Departamento Cochabamba, Bolivia, 2044 m a.s.l. (Reynolds & Foster 1992). Endemic to Bolivia.

Natural history: The single known specimen was taken from a door knob at night in an area of humid montane forest (Reynolds & Foster 1992). Nothing else is known.

Vocalization: Unknown.

Remarks: According to Duellman et al. (1997), *Hyla chlorostea* is not assignable to any of the known groups of Andean *Hyla*. Therefore, the authors defined a *Hyla chlorostea* group.

Hyla marianitae **Carrizo, 1992**   Plate IIIc, p.96

Distribution: The species is known to occur at elevations from 700–2650 m a.s.l. in the Andes and Andean precordilleras of central Bolivia southward to northern Argentina (Duellman et al. 1997).

Natural history: *Hyla marianitae* occurs in semi-deciduous forests, adhanced to dry valleys, as well as in cloud and humid montane forests. Specimens were usually found near streams or ponds. At night, males called from low vegetation near water or from rocks at the edge or inside the water. Amplectant pairs were observed end of November (own observation) as well as on 9 March 1990 (Duellman et al. 1997) at Karahuasi. Obviously, the species has a prolonged breeding period, at least in the per-humid montane forests. Eggs are pigmented and are laid in clutches deposited below the water surface (Lötters et al. 1999). Almost all observed males had scars and scratches on their dorsum, presumably caused by prepollical spines of other males. The tadpole was described by Lötters et al. (1999).

Vocalization: Advertisement calls were recorded on 21 December 1997 at Quebrada El Fuerte, Provincia Florida, Departamento Santa Cruz, 1700 m a.s.l. Notes consisted of 13–33 (mean 21.1 ± 6.9) pulses, repeated in regular intervals at a rate of 26.4–38.5 (mean 33.1 ± 5.2) pulses per second; call duration varied from 398–924 ms (mean 589.6 ± 174.9) depending on the number of pulses involved; pulse duration varied from 8–15 ms (mean 11.4 ± 2.1); call energy was distributed between 500 and 4000 Hz, with a dominant frequency peak from 790–1100 Hz (mean 921.8 ± 111.0); most calls exhibited a moderate amplitude modulation; calls were emitted in irregular intervals. Eighteen calls of three individuals analyzed; air temperature was 21.8°C at time of recording.

The general characteristics coincide relatively well with the data provided for *H. callipleura* by Márquez et al. (1993) (actually the call of *H. marianitae*; see Duellman et al. 1997), as well as to those published by Duellman et al. (1997), except that the latter authors reported a call duration of only 25–59 ms
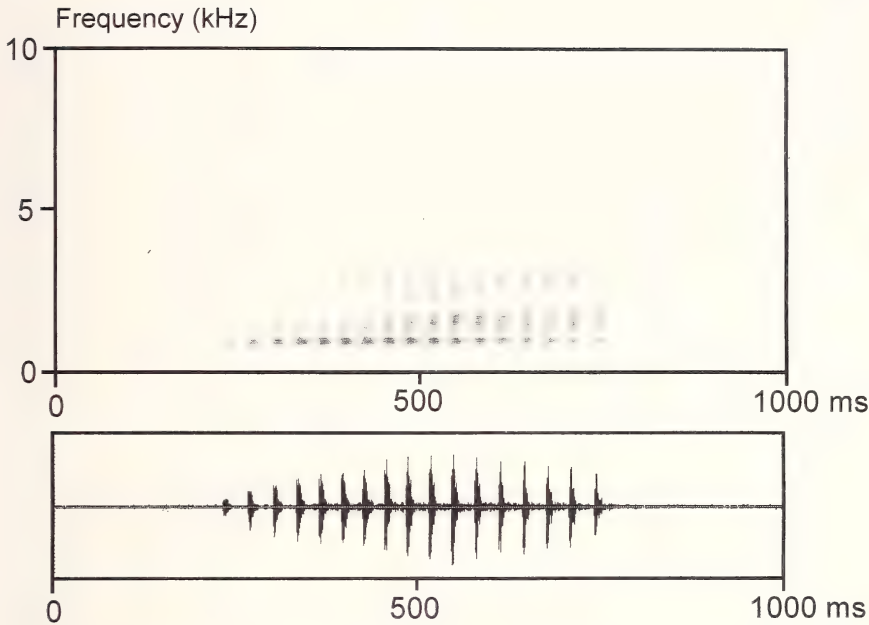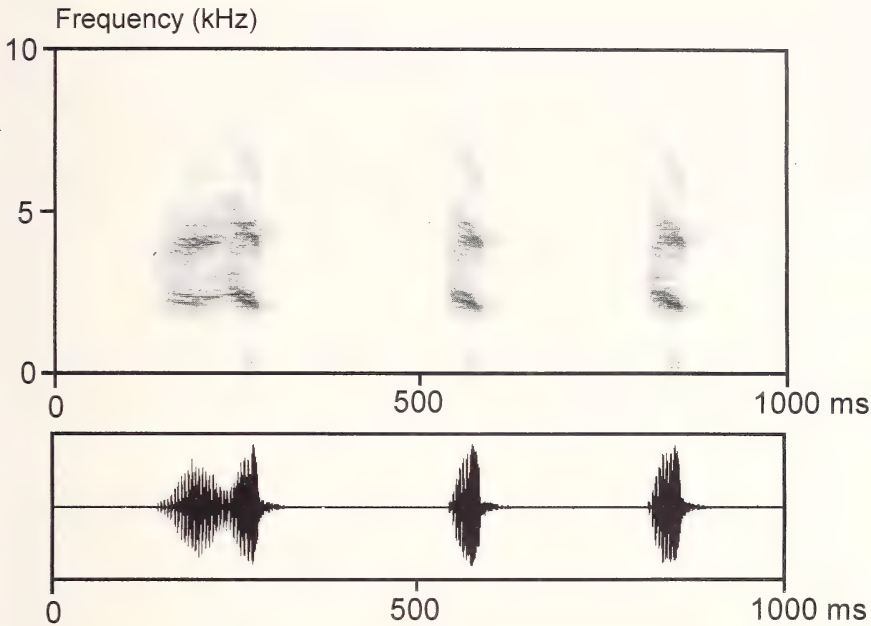
Fig.28: Audiospectrogram and oscillogram of the advertisement call of *Hyla marianitae* from Quebrada El Fuerte, 1700 m a.s.l. Recording obtained on 21 December 1997. Air temperature 21.8°C.

(0.025–0.059 sec.). However, the call figured in their spectrogram and oscillogram shows a quite longer duration. Therefore, I conclude that the call duration reported by Duellman et al. (1997) is due to a setting error of the decimal point and actually has to be read as 250–590 ms, a value overlapping with the results presented herein.

R e m a r k s : The specimens figured as *Hyla pulchella* by Köhler et al. (1995b; Figs. 5 and 6) actually correspond to *H. marianitae*. The legend of the figured advertisement call of *H. marianitae* (Fig.15) in Duellman et al. (1997) is in error. The call was recorded near Karahuasi (I. De la Riva pers. comm.). Within the study area, *H. marianitae* was found in sympatry with *H. andina*, *H. armata*, and *H. minuta*.

Hyla minuta Peters, 1872   Plate IIId, p.96

D i s t r i b u t i o n : *Hyla minuta* is distributed throughout the lowlands east of the Andes from Colombia, Venezuela, and Trinidad southward to Argentina, southeastern Brazil, and Uruguay (e.g., Frost 1985, Langone 1994, Murphy 1997). In Bolivia, it occurs up to 2000 m a.s.l. along the Andean slopes and precordilleras (Köhler et al. 1995b). See remarks.

Natural history: The Bolivian distribution includes temperate valleys of the eastern Andean slopes, semi-deciduous montane forests, secondary growth as well as open areas. Males of *Hyla minuta* called at night from bushes or grassy vegetation around ponds or slow running water or from emergent plants within the water. Usually, many males called synchronously within close distances. Several times, a satellite behavior in males like described by Haddad (1991) was observed. Egg clutches were deposited attached to water plants approximately 5 cm below the water surface (see Köhler et al. 1995b).

Vocalization: Advertisement calls were recorded on 9 December 1997 west of Río Seco, Provincia Cordillera, Departamento Santa Cruz, 900 m a.s.l. Calls consisted of a moderately long primary note usually followed by 2–3 shorter secondary notes; calls were repeated at a rate of about 10.5 calls per minute; call duration varied from 163–1011 ms (mean 602.3 ± 344.7), depending on the number of notes involved; duration of the first longer note varied from 163–186 ms (mean 176.4 ± 7.4), the duration of the secondary shorter notes varied from 67–81 ms (mean 73.7 ± 4.2); within the calls notes were repeated in regular intervals with an approximate rate of 3.5 notes per second; notes are distinctly pulsed, usually having a longer terminal pulse; long notes contained around 30 pulses and the shorter secondary notes contained 7–9 pulses; within notes pulses were repeated with a regular rate of 210 pulses per second; the first notes showed a moderate amplitude modulation; call energy was distributed within a broad band between 150 and 9500 Hz; the dominant frequency peak varied from 2040–2270 Hz (mean 2148 ± 84); a second frequency band with nearly equal intensity was present at 3980–4180 Hz, and a third one with lower intensity around 6200 Hz. These bands obviously reflect the pulstile character of the calls. Nine calls of one individual analyzed; air temperature was 22.3°C during recording.

These findings show similarity with the data from the calls obtained at Puerto Almacén, Departamento Santa Cruz, Bolivia, by Márquez et al. (1993). Differences concern the higher dominant frequency reported by these authors which is similar to our second harmonic. As stated above, the first and second harmonic may be nearly identical in their intensity. A principal difference regards the tonal character of the longer notes reported by Márquez et al. (1993). All notes (except a single one) within calls recorded near Río Seco had a distinct pulsatile character. As was argued by several authors (e.g., Cardoso & Haddad 1984, Martins & Cardoso 1987, Donelly & Myers 1991), some note types of frogs referred to *H. minuta* may have aggressive or territorial function and will only be emitted in appropriate situations. This is possibly the case in the tonal notes (see remarks for *Hyla* sp. A).

Haddad et al. (1988) published numerical data of calls of *H. minuta* from Minas Gerais, Brazil, which have a similar dominant frequency to the calls described above. The calls described by Donelly & Myers (1991) from Cerro Guaiquinima, Venezuela, show a duration intermediate to the long and short notes and a domi-

Fig.29: Audiospectrogram and oscillogram of the advertisement call of *Hyla minuta* from a point west of Río Seco, 900 m a.s.l. Recording obtained on 9 December 1997. Air temperature 22.3°C.

nant frequency similar to the second harmonic found in the Río Seco population. Calls described from the Venezuelan Escalera region by Duellman (1997) are nearly identical to those recorded in Bolivia, except that the author found the second harmonic to be dominant. Also calls from Boracéia, Brazil, (Heyer et al. 1990) are very similar in general structure, note duration, and pulse rate, but differ with respect to a higher dominant frequency (6000 Hz). Analysis of a tape recording of C. F. B. Haddad of *H. minuta* calls from Ribeirão Branco, São Paulo, Brazil, revealed a pulse rate of 175 pulses/s (air temperature 17.0°C). Their whole character is almost identical to the calls from the Río Seco population, Bolivia.

R e m a r k s : It has recently been argued that the frogs named *Hyla minuta* are most probably a complex of different species (e.g., Donelly & Myers 1991, Kaplan 1994). Probably, some available names recently regarded as junior synonyms have to be reestablished, other populations will have to be described as new species. The whole group is badly in need of a revision, but this is beyond the scope of the present work. What can be said is that the Bolivian populations of *Hyla minuta* considered herein seem to be different from populations found in the northernmost part of Bolivia (Cobija, Departamento Pando). The Bolivian montane populations might be more identical with populations occurring in the drier and semi-deciduous forests of the Chaco and Cerrado regions, because several

other species known from this area share sympatry with *H. minuta* in the montane forest regions of Bolivia (e.g., *Leptodactylus gracilis, Phrynohyas venulosa, Chiasmocleis albopunctata, Elachistocleis* cf. *ovalis*). They are probably also identical with topotypic *H. minuta* according to the nearly identical calls of populations from the Brazilian state of São Paulo, relatively close to the type locality of *H. minuta* (see above). Other species of *Hyla* found in sympatry with *H. minuta* in the humid and semi-humid montane forests include *H. andina, H. armata,* and *H. marianitae*.

Hyla species A   Plate IIIe, p.96

Distribution: The species is known only from the Provincia Chapare, Departamento Cochabamba, on the "old" road from Paractito to Cochabamba vía El Palmar, comprising an altitudinal range of 500–1500 m a.s.l. (Köhler & Lötters 2000). Endemic to Bolivia.

Diagnosis: A small species of *Hyla* characterized by sexual dimorphism in size, maximum snout-vent length 19.4 mm in males, 26.6 mm in females; large protruding eyes; small tympanum lacking an annulus; extensive axillary membrane; bifid distal subarticular tubercle under fourth finger; long anal sheath, extending to midlevel of thigh; outer edges of venter transparent in life; white supra-anal stripe; and white transversal line on heel.

Natural history: The distribution area comprises evergreen tropical Andean forests. The steep slopes are covered with many small creeks and rivers. On the nights of 6 February and 13 December 1998, males of *Hyla* sp. A called from bushes and grasses above slow running water at the edge of the road during rain. A prolonged breeding period can be expected for *Hyla* sp. A, because almost all females observed in February and December were gravid. Eggs are approximately 1.4 mm in diameter and have one hemisphere darkly pigmented. Tadpoles supposedly develop in slow running water, because ponds were not observed in the distribution area. There were considerable differences between dorsal day and night coloration in some specimens. Usually, males were colored bright yellow at night, whereas at daytime the same specimens were brownish.

Vocalization: Calls were recorded near Paracti, Provincia Chapare, Departamento Cochabamba, 500 m a.s.l. Generally, the vocalization of *Hyla* sp. A consisted of three different types of notes which were combined to two different call types. The three note types were long pulsed notes, short pulsed notes and unpulsed frequency modulated whistles. One call type (here named call type A) consisted of a long pulsed note followed by a short pulsed note, whereas the other type (call type B) was combined of a whistle followed by one or two short pulsed notes. These call types may have different functions and we refrain here referring one or both of the types as advertisement call. Calls were emitted at irregular intervals. Temporal and spectral characteristics of notes and calls were as follows: (1)
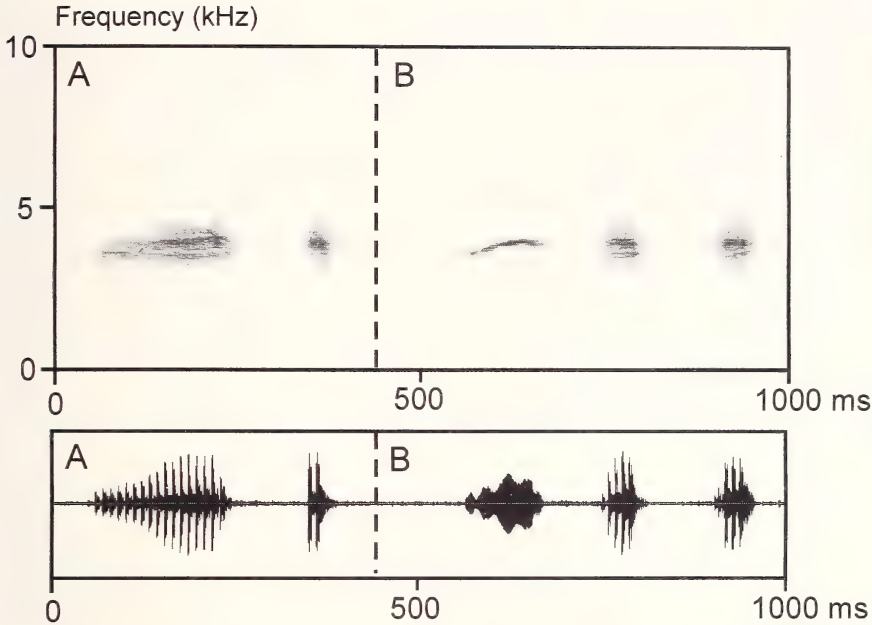
Fig.30: Audiospectrogram and oscillogram of the two call types of *Hyla* sp. A (type A, left; type B, right) from Provincia Chapare, 500 m a.s.l. Recording obtained on 13 December 1998. Air temperature 24.3°C.

long pulsed notes: 11–19 pulses per note (16.1 ± 2.5), duration 99–195 ms (165.1 ± 26.1), 88.4–108.1 pulses per second (95.7 ± 5.9), dominant frequency range 3360–4060 Hz (3699.2 ± 111.8); (2) short pulsed notes: pulses per note 2–5 (2.8 ± 0.9), duration 27–75 ms (36.6 ± 16.0), pulse rate is the same as in long pulsed notes, dominant frequency range 3340–3920 Hz (3582.7 ± 109.9); (3) whistles: duration 97–164 ms (128.2 ± 21.3), without pulses, upward frequency modulation from 3390 Hz at beginning to 3910 Hz at the end of note, dominant frequency range 3710–3820 Hz (3782.5 ± 49.2); (4) call type A: duration 310–327 ms (317.2 ± 6.4), inter note interval 82–134 ms (107.2 ± 12.9); (5) call type B: duration 309–452 ms (395.4 ± 51.9), inter note interval 79–103 ms (89.4 ± 8.2). Twenty-one calls of three individuals analyzed; air temperature was 24.3°C at time of recording.

Due to some morphological similarities of *Hyla* sp. A and *H. minuta*, it appears adequate to compare the call characteristics described above with published data of calls of *H. minuta*. The pulsed calls of *Hyla* sp. A differ mainly to known calls of *H. minuta* in a significant lower pulse repetition rate within the calls. In the following, pulse rates of calls of different populations of *H. minuta* provided in the literature are listed: 156–193 pulses per second, Puerto Almacén, Bolivia

(Márquez et al. 1993); 284–300 pulses per second, Belém, Brazil (Duellman & Pyles 1983); 160–180 pulses per second, Boracéia, Brazil (Heyer et al. 1990); about 144 pulses per second, Cerro Guaiquinima, Venezuela (Donelly & Myers 1991); 170–200 pulses per second, La Escalera region, Venezuela (Duellman 1997). In own recordings of calls of *H. minuta* from west of Río Seco, Departamento Santa Cruz, Bolivia, a pulse rate of approximately 210 pulses per second was measured (see above). In addition to these differences in pulse repetition rate, call energy in *Hyla* sp. A is distributed in a narrower frequency band compared with frequency ranges provided for *H. minuta*. Moreover, the terminal pulse in calls of *H. minuta* is usually of longer duration, whereas in *Hyla* sp. A all pulses within calls are equal in duration. To the human ear, *H. minuta* calls sound harsh or somehow distorted, whereas calls of *Hyla* sp. A sound clean. Martins & Cardoso (1987) figured the call of *H. xapuriensis* and in their spectrogram a pulse rate of approximately 60 pulses per second is measurable, a lower value compared to *Hyla* sp. A.

R e m a r k s : Among Andean *Hyla*, only two groups have been defined containing small species: the *Hyla columbiana* group (Duellman & Trueb 1983) and the *Hyla garagoensis* group (Kaplan & Ruíz 1997). These groups include species distributed in northern South America, namely Colombia and Ecuador (see also Duellman et al. 1997). Members of these groups have a diploid number of 30 chromosomes which is also assumed for *Hyla* sp. A. Some morphological characters of *Hyla* sp. A are shared with the *H. columbiana* group. However, data on larval morphology of *Hyla* sp. A are not available, but due to the geographical distance a relation of *Hyla* sp. A to one of these groups is more or less improbable. *Hyla* sp. A seems to be more likely related to *H. minuta*. Kaplan (1994) discussed the taxonomy of what presently is called *H. minuta* and stated that it most probably is a complex of different species. Furthermore, in describing *H. stingi* (a phenetically very similar species to *H. minuta*), Kaplan (1994) suggested it to represent a different phylogenetic lineage. With the data available, it is not possible to decide about the phylogenetic relationships of *Hyla* sp. A, whether it is more closely related to *H. minuta* or any other lineage represented by *H. minuta*-like frogs (Köhler & Lötters 2000).

Phyllomedusa boliviana Boulenger 1902   Plate IIIf, p.96

D i s t r i b u t i o n : Eastern Andean slopes from Departamento La Paz, Bolivia, southward to northern Argentina. The species also occurs in inter-Andean dry-valleys as well as in drier lowland forests of the Departamento Santa Cruz, Bolivia, and Mato Grosso, Brazil. The known elevational distribution ranges from 350–2000 m a.s.l. (Cannatella 1983).

N a t u r a l   h i s t o r y : *Phyllomedusa boliviana* inhabits semi-deciduous forests, humid montane forests, as well as dry forests of the inter-Andean valleys. As far

known, reproduction takes place during the rainy season from November to February. Males call at night from trees or bushes, or from grassy vegetation near the ground at the edge of ponds. Calling activity was observed to be most intensive during light rain. In the breeding season, abundance of individuals around water bodies was remarkably high. In dry-valley habitats, amplectant pairs were observed in late December. Larvae in stages 37–44 (sensu Gosner 1960) were found mid of November 1998 in an artificial pond at La Hoyada. Eggs are white and approximately 2–4 mm in diameter. Specimens are able to change their dorsal color from bright green to brown. In contrast to own observations, Cannatella (1983) found the species close to running water. Laurent (1967) and Cei (1980) described biological observations of Argentinean populations.

Vocalization: Advertisement calls were recorded on 16 December 1997 west of Vaca Guzman, Provincia Luis Calvo, Departamento Chuquisaca, 1340 m a.s.l. The call consisted of a sonorous, distinctly pulsed note with a duration of 69–97 ms (mean 83.6 ± 11.1); number of pulses per note varied from 9–13 (mean 11.0 ± 1.6), repeated at a rate of approximately 120 pulses per second; call energy was distributed between 500 and 5000 Hz, with a dominant frequency peak at 1320 Hz; notes showed a distinct amplitude modulation; calls usually were emitted in groups consisting of 3–5 calls. Seven calls of two individuals analyzed; air tem-
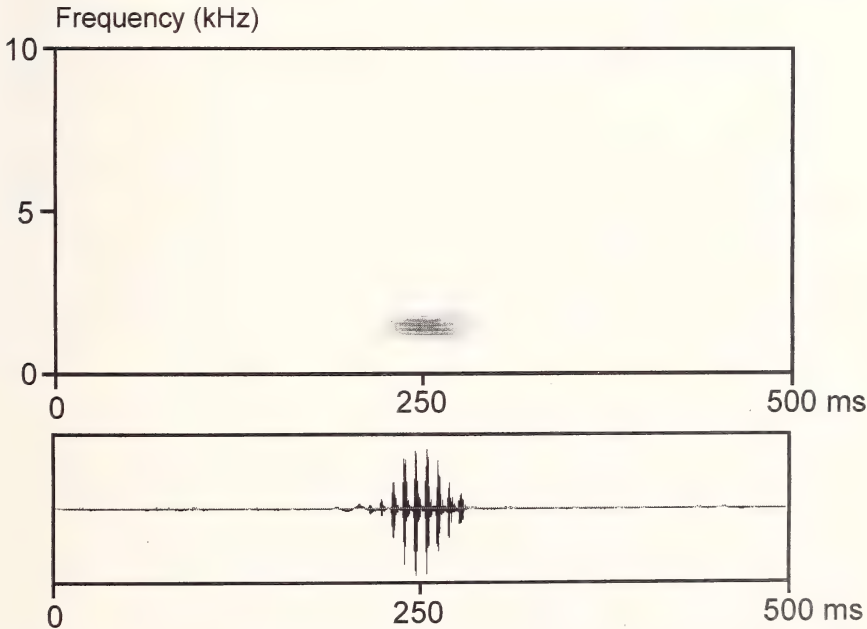
Fig.31: Audiospectrogram and oscillogram of the advertisement call of *Phyllomedusa boliviana* from west of Vaca Guzman, 1340 m a.s.l. Recording obtained on 16 December 1997. Air temperature 19.7°C.

perature was 19.7°C during recording. These data coincide well with those provided by Barrio (1976) of a population from Río Pescado, Provincia Salta, Argentina.

R e m a r k s : Most lowland records of *P. boliviana* from humid Amazonian forests (e.g., Aparicio 1992) actually correspond to *P. camba* (see De la Riva 2000).

Phrynohyas venulosa **(Laurenti, 1768)**   Plate IIIg, p.96

D i s t r i b u t i o n : The species occurs in a wide range, from southern Mexico and Central America throughout the whole Amazon basin, southward to northern Argentina, Paraguay and southern Brazil. It is distributed from sea level up to elevations of 2500 m a.s.l. (Frost 1985). In Bolivia, *P. venulosa* was recorded throughout the lowland tropics, as well as in semi-deciduous montane forests adjacent to dry-valleys up to 1800 m a.s.l. (Köhler et al. 1995a).

N a t u r a l   h i s t o r y : *Phrynohyas venulosa* inhabits various kinds of different habitat types within its distribution area, including dry Chaco forests, humid Amazonian forests, transition forests, savannas, and semi-humid montane forests. Reproduction starts at the beginning of the rainy season. Males call while floating on the water surface as well as from bushes at the edge of water (De la Riva et al. 1995). Eggs are deposited as a film on the water surface (e.g., Cei 1980, Hödl 1990). During handling, individuals release sticky, toxic skin secretions. Notes on the biology of different populations throughout the distribution range were provided by various authors (e.g., Duellman 1970, Lutz 1973, Cei 1980, Lavilla et al. 1995).

V o c a l i z a t i o n : Description of calls of *P. venulosa* were provided several times in the literature (e.g., Porter 1962, Zweifel 1964, Duellman 1970, Zimmerman & Hödl 1983). Here, I only refer to calls from a Bolivian population described by De la Riva et al. (1995). Calls consisted of a single, long note with a high number of pulses (45–60 pulses/note). Note duration varied from 291–384 ms; notes were repeated at a rate of 54.8 notes per minute. Call energy was dominant between 1878-2564 Hz.

Scinax castroviejoi **De la Riva, 1993**   Plate IIIh, p.96

D i s t r i b u t i o n : The species occurs in temperate valleys of the eastern slopes of the Andes from Bolivia to northern Argentina between 1100 and 1800 m a.s.l. (De la Riva 1993a, Köhler et al. 1995b). See remarks.

N a t u r a l   h i s t o r y : Habitats include disturbed montane forests as well as open areas. Males called from grassy vegetation or from the ground at the edge of ponds or from emergent plants within the water. Reproduction takes place in ponds. Eggs are about 1 mm in diameter with one hemisphere black and the other white. A prolonged breeding period was presumed (De la Riva 1993a, Köhler et al. 1995b).

Vocalization: The advertisement call was described as always consisting of two similar notes emitted together in a rapid succession. Dominant call energy is distributed between 2400 and 2850 Hz (De la Riva 1993a, De la Riva et al. 1994). See remarks.

Remarks: De la Riva (1993a) described the species mainly based on advertisement call characteristics which distinguish it from the related species *S. fuscovarius* and *S. nasicus*.

During this study, a population of *Scinax* was discovered at a pond situated within humid montane forest at approximately 1900 m a.s.l. Although, the area around the pond was cleared from trees, the habitat appeared rather inappropriate for a species of *Scinax*. On the night of 9 February 1998, calls were recorded at the pond. Two different call types alternately emitted by two individuals were recognizable. The recorded calls are figured below. Surprisingly, the analysis of the two different calls revealed that one corresponds exactly to what is described for *S. castroviejoi* (De la Riva 1993a, De la Riva et al. 1994), whereas the other is similar to calls of *S. ruber* (e.g., De la Riva et al. 1994). The collected specimens did not show any differences in external morphology. The per-humid and high altitude conditions of the locality seem not to fit well with the known distribution of *S. ruber*, a species inhabiting open areas within humid and semi-humid Amazonian
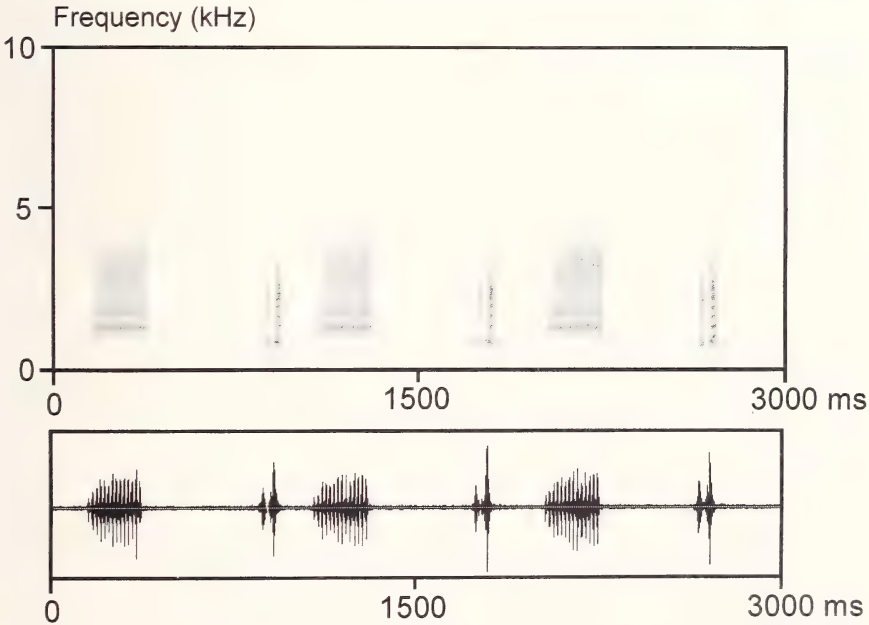
Fig.32: Audiospectrogram and oscillogram of the calls of two individuals of *Scinax* recorded at a pond in Provincia Chapare, 1900 m a.s.l. Recording obtained on 9 February 1998. Air temperature 18.8°C.

lowland forests. An occurrence of *S. castroviejoi* in such montane conditions appears more probable, since some other anuran species inhabit a similar range along the Andean slopes from northern Argentina to central Bolivia (e.g., *Hyla marianitae, Phyllomedusa boliviana, Eleutherodactylus discoidalis*). However, a syntopical occurrence of both species at the described pond seems improbable. One possibility to explain these observations could be that *S. castroviejoi* is able to emit two different types of calls, one of them similar to that of *S. ruber*. Typical *S. castroviejoi* calls were heard only at La Hoyada, Provincia Florida, Departamento Santa Cruz. At all other localities, even in regions and habitats suitable for *S. castroviejoi* (e.g., near Vaca Guzman, Departamento Chuquisaca, 1340 m a.s.l.), typical calls of *S. fuscovarius* were heard (and recorded). These observations are quite confusing and in the distribution analysis, it is referred to *S. castroviejoi* only when typical calls were heard at the respective locality.

Scinax fuscovarius (Lutz, 1925)   Plate IVa, p.112

Distribution: The species is known from southeastern Brazil, northern Argentina, Paraguay, and Bolivia (Frost 1985). *Scinax fuscovarius* is distributed at elevations from 150–1800 m a.s.l.

Natural history: *Scinax fuscovarius* inhabits dry Chaco forests, semi-deciduous lowland forests, Cerrado formations, Tucumanian-Bolivian montane forests, and inter-Andean dry-valleys. It is an explosive breeder, reproducing at the beginning of the rainy season in ephemeral ponds and lagoons. Males called from the ground at the edge of water bodies or from low grasses. On 15 December 1997 at approximately 13 km west of Vaca Guzman, 1340 m a.s.l., several thousand individuals appeared around a large artificial lagoon (together with large numbers of *Physalaemus biligonigerus, Pleurodema cinereum, Phyllomedusa boliviana*, and *Phrynohyas venulosa*). After three hours of calling and mating activity, some females were found dead within the water.

Vocalization: Advertisement calls were recorded on 7 January 1998 approximately 29 km southeast by road from Guadalupe, Provincia Vallegrande, Departamento Santa Cruz, 1650 m a.s.l. Calls consisted of low, pulsed notes; note duration varied from 208–261 ms (mean 230.6 ± 21.7); notes were composed of 9–11 pulses (mean 9.8 ± 0.9), repeated at a rate of approximately 42 pulses per second; calls were repeated at regular intervals, at a rate of 58 calls per minute; call energy was distributed between 500 and 3500 Hz, with a dominant frequency peak at 780 Hz. Eleven calls of two individuals analyzed; air temperature was 18.0°C at time of recording. During male-male encounters, a different soft and tonal aggressive call was recognized.

Compared to calls described from Puerto Almacén, northern Departamento Santa Cruz (De la Riva et al. 1994), the calls described above differ slightly with respect to a longer note duration, lower dominant frequency, lower pulse rate, and lower

Frequency (kHz)
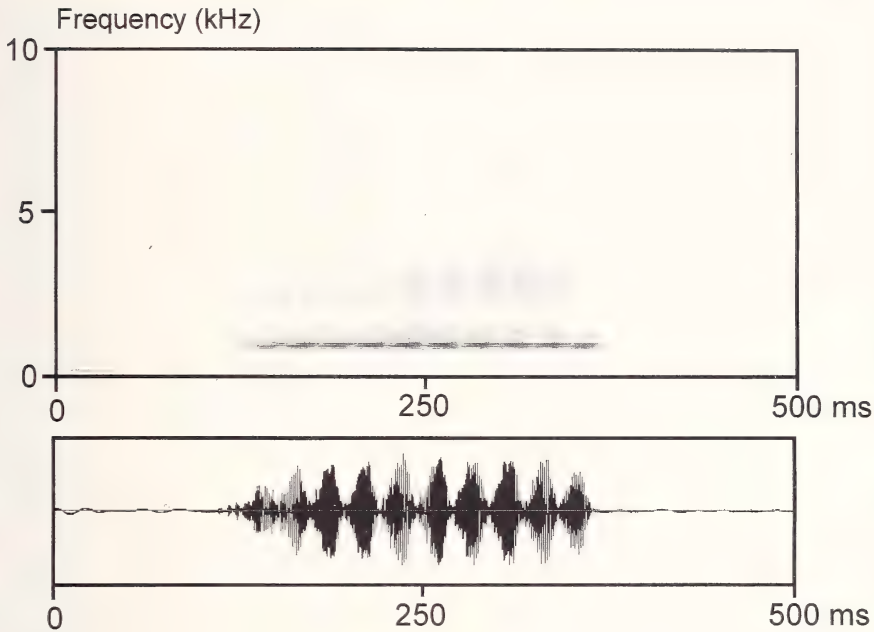
Fig.33: Audiospectrogram and oscillogram of the advertisement call of *Scinax fuscovarius* from SE of Guadalupe, 1650 m a.s.l. Recording obtained on 7 January 1998. Air temperature 18.0°C.

call repetition rate. However, in general characters the calls are identical and mentioned differences can easily be explained by temperature differences (no temperatures provided by De la Riva et al. 1994).

Leptodactylidae

Adenomera hylaedactyla (Cope, 1868)   Plate IVb, p.112

Distribution: The species is known to occur from southeast Colombia, Venezuela, the Guianas, southward to central Brazil, Peru, and Bolivia (Frost 1985). The elevational range is from a few meters above sea level up to approximately 1000 m a.s.l.

Natural history: *Adenomera hylaedactyla* inhabits humid and semi-humid forests of the Amazon basin, as well as humid submontane forests at the Andean foot. The species supposedly has a prolonged breeding season. Males were observed calling at day and night from the ground, mostly hidden in grassy vegetation. Development of the tadpoles takes place in terrestrial foam nests.

Information on reproduction and activity patterns was provided by Aichinger (1987, 1992). De la Riva (1995b) gave an overview about the reproductive modes within the genus.

Vocalization: Advertisement calls of Bolivian populations were described by Márquez et al. (1995). Calls consisted of single notes, repeated at regular intervals at a rate of 132.2 notes per minute. Mean note duration was 56.8 ms and the dominant frequency was 4448.2 Hz (Márquez et al. 1995).

Eleutherodactylus ashkapara Köhler, 2000   Plate IVc, p.112

Distribution: The species was found only at 2100 m a.s.l. on the "old" Chapare road, Provincia Chapare, Bolivia, but the specific calls were recognized along this road at all localities between 1800 and 2200 m a.s.l. (Köhler 2000a). Endemic to Bolivia.

Natural history: *Eleutherodactylus ashkapara* is an arboreal species. Calls were heard from the canopy at approximately 5–10 m height. One individual called from a branch in approximately 2.5 m height. The specimen was completely covered by moss while calling. Calling activity in December and January was most intensive at night, but also occurred in the late evening during rain or heavy fog. Mostly, calls were emitted within choruses of several individuals.

Vocalization: Advertisement calls were recorded on 30 January 1999 at 2100 m a.s.l., Provincia Chapare, Departamento Cochabamba. Calls consisted of a short, single note and sounded like a sonorous "clack", reminiscent of two hard wooden sticks beaten together. The notes had a duration of 24–43 ms (mean 36.0 ± 5.9), and were repeated at a rate of 0.93–1.23 notes per second (mean 1.12 ± 0.11). Principal calls sometimes were followed by a series of fast repeated notes (5–7) of same character, with a repetition rate of approximately 3.5 notes/second. Call energy was distributed between 1150 and 1830 Hz, with a dominant frequency peak at 1470 Hz. Notes lacked pulses and harmonics. Air temperature was 15.9°C during time of recording; 43 calls of two individuals analyzed.

Remarks: As is obvious from the figures, *Eleutherodactylus ashkapara* is phenetically similar to the species *E. fraudator* and *E. pluvicanorus*. I consider all three species to be closely related. When Lynch & McDiarmid (1987) described *E. fraudator*, they tentatively assigned the species to the *E. conspicillatus* group.

Plate IV: **a)** *Scinax fuscovarius* (Lutz, 1925), male, W of Vaca Guzman, 1360 m; **b)** *Adenomera hylaedactyla* Müller, 1923, male, Cobija, 250 m; **c)** *Eleutherodactylus ashkapara* Köhler, 2000, male, Provincia Chapare, 2100 m; **d)** *Eleutherodactylus cruralis* (Boulenger, 1902), male, Provincia Chapare, 1400 m; **e)** *Eleutherodactylus danae* Duellman, 1978, male, Provincia Chapare, 700 m; **f)** *Eleutherodactylus fenestratus* (Steindachner, 1864), male, Provincia Chapare, 600 m; **g)** *Eleutherodactylus fraudator* Lynch & McDiarmid, 1987, male, La Siberia, 2850 m; **h)** *Eleutherodactylus llojsintuta* Köhler & Lötters, 1999, male, Sehuencas, 2150 m.
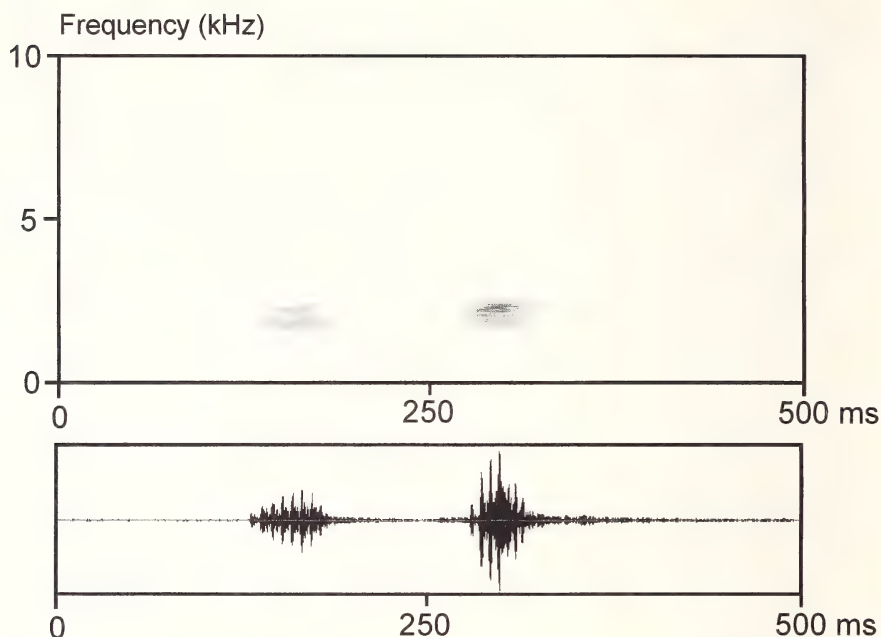
Plate IV

Frequency (kHz)
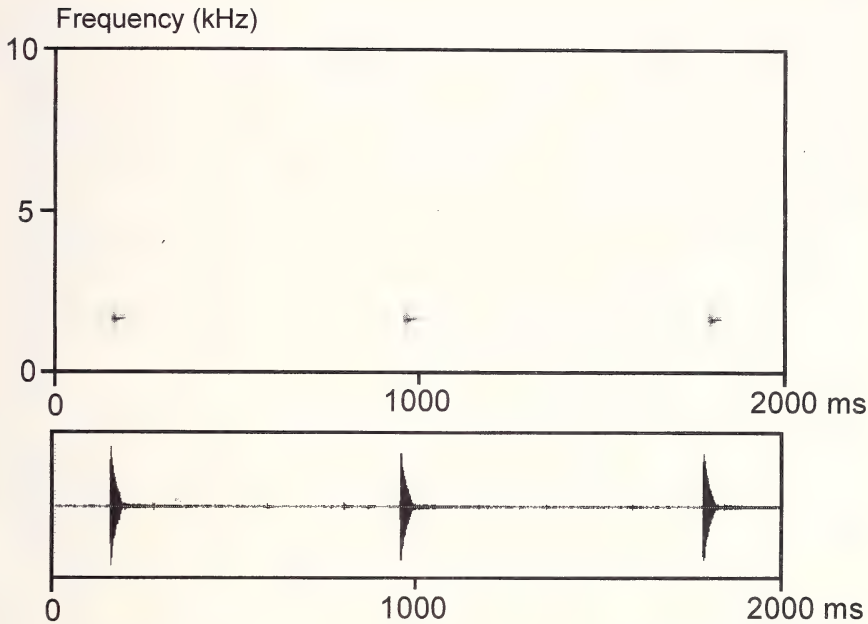
Fig.34: Audiospectrogram and oscillogram of the advertisement call of *Eleutherodactylus ashkapara* from Provincia Chapare, 2100 m a.s.l. Recording obtained on 30 January 1999. Air temperature 15.9°C.

Subsequently, De la Riva & Lynch (1997) provided additional data on *E. fraudator* and described the closely related *E. pluvicanorus*. Both species were then tentatively assigned to the subgenus *Craugastor* which usually exhibits a Middle American distribution (Lynch 1986b). This tentative assignment was based on the presence of the "E" condition of the trigeminal nerve (mandibular ramus medial to the most superficial adductor muscle; Lynch 1986b). Dissection of a specimen of *E. ashkapara* also revealed the "E" condition of the trigeminal nerve. In addition, *E. ashkapara* seems to exhibit a frontoparietal fontanelle which is imaginable from a radiograph taken of the type specimens. This character also is present in *E. fraudator* and *E. pluvicanorus*, as well as in another Bolivian species, *E. mercedesae* (Lynch & McDiarmid 1987, De la Riva & Lynch 1997).

Because of the consistent morphological characters present in the three species *E. ashkapara*, *E. fraudator*, and *E. pluvicanorus*, I consider them to be a lineage distinct from other groups of South American *Eleutherodactylus* (and probably also distinct from the Middle American subgenus *Craugastor*). I propose to regard the three species mentioned above as the *Eleutherodactylus fraudator* species group, defined by the following combination of characters: moderate to medium-sized frogs (SVL in males 23–50 mm) with narrow heads and short snouts; sexually

dimorphic in size; cranial crests absent; body robust; limbs moderately long; skin of venter smooth; dorsolateral folds present; vomerine odontophores oval; males with vocal slits and large vocal sac; "E" condition of the trigeminal nerve (sensu Lynch 1986b); tympanic membrane present; canthus rostralis sharp; discs on fingers and toes broad; finger I slightly longer than finger II; toe V slightly shorter or equal the length of toe III, not reaching distal subarticular tubercle of toe IV; no webbing on toes; no tubercles or folds on heel or tarsus.

A fourth species of the group, more similar to *E. fraudator*, was already discovered in the Yungas de La Paz region (M. Harvey in litt.). Also *E. mercedesae* shares some characters with the *E. fraudator* group and is possibly related to it. However, further investigations are needed to throw light on the relationships of this rare Bolivian species (see Köhler 2000a).

***Eleutherodactylus cruralis* (Boulenger, 1902)**   Plate IVd, p.112

D i s t r i b u t i o n : The species is known to occur at the eastern Andean slopes and Andean foothills from central Peru (Rodríguez et al. 1993) to the Departamento Santa Cruz, Bolivia, from 200–2000 m a.s.l. The type locality "La Paz, 4000 m" most probably is in error (Lynch 1989, De la Riva 1990a, 1993b).
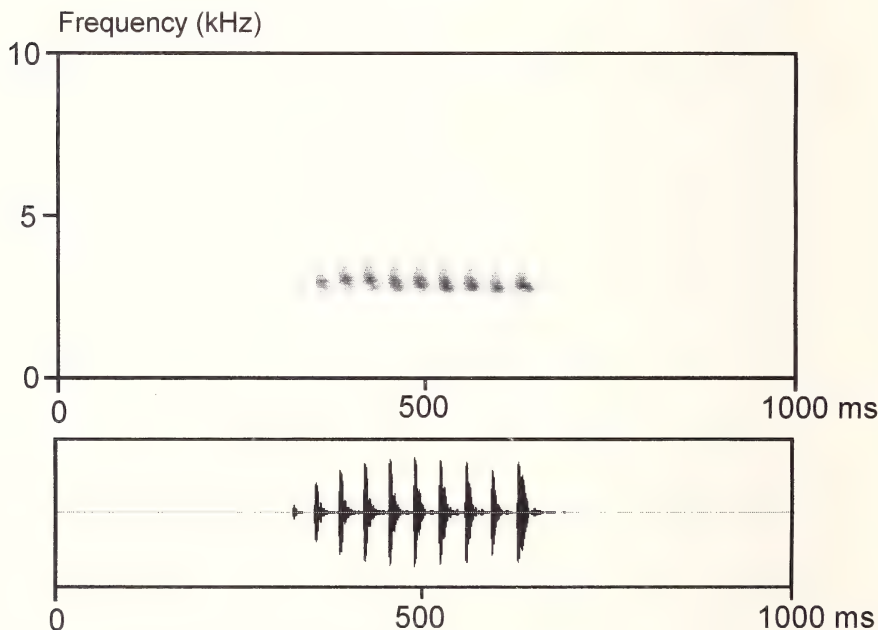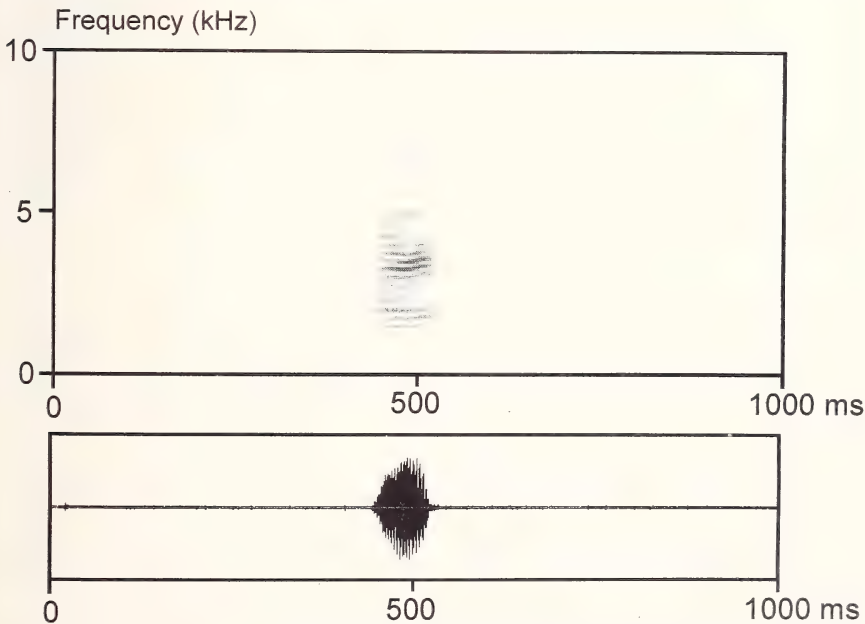

Fig.35: Audiospectrogram and oscillogram of the advertisement call of *Eleutherodactylus* cf. *cruralis* from La Hoyada, 1700 m a.s.l. Recording obtained on 16 November 1998. Air temperature 20.3°C.

Natural history: *Eleutherodactylus cruralis* occurs from humid rainforests at the Andean foot to humid upper montane forests. It primarily is a terrestrial species commonly found in disturbed areas, e.g. at the forest edge along roads. Males called at day and night from the ground or from branches of low vegetation. Individuals were never observed calling from exposed positions, they always were hidden in dense vegetation and therefore relatively difficult to discover. Calling activity was most intensive during light rain at dusk. Gravid females were obtained in January and February.

Vocalization: Advertisement calls were recorded on 16 November 1998 at La Hoyada, Provincia Florida, Departamento Santa Cruz, 1700 m a.s.l. Calls were composed of 9–10 notes (mean 9.3 ± 0.5), repeated in regular intervals at a rate of approximately 30 notes per second; call duration varied from 314–362 ms (mean 331.6 ± 15.2); an amplitude modulation was recognizable within the calls, with the first note always being relatively weak; in some calls the terminal note was of slightly longer duration and separated from the other notes by a slightly longer interval; calls were repeated at a rate of about 7.2 calls per minute; call energy was distributed between 1000 and 4500 Hz, with a dominant frequency peak of 2760 Hz. Eight calls of one individual analyzed; air temperature was 20.3°C during recording.

Márquez et al. (1995) provided information on calls of *E. cruralis* from Masicurí, Departamento Santa Cruz, Bolivia, but their calls differ from those described above by a lower number of notes per call (6 versus 9–10), higher note repetition rate (40.2 versus 30 notes per second), and a fundamental frequency of 1599.2 Hz (lacking in calls from La Hoyada). The Masicurí population most probably corresponds to another, undescribed species of *Eleutherodactylus* (see remarks below).

Remarks: Certain Bolivian populations referred to as *Eleutherodactylus cruralis* by De la Riva (1993), Köhler et al. (1995b), Márquez et al. (1995), and Reichle & Köhler (1997) actually represent an undescribed species in the *E. discoidalis* group. I herein refer to this new species as *Eleutherodactylus* sp. A (see below). However, specimens from the lower Chapare province and other localities at the foot of the Bolivian Andes agree morphologically well with the holotype of *E. cruralis* (BMNH 1947.2.15.70) which probably is from the Yungas de La Paz region. Specimens from La Hoyada, 1700 m a.s.l., differ slightly in external morphology and possibly represent another undescribed species. However, up to date, data are too sparse to differentiate the populations as two separate species and I here treat the La Hoyada population as *E.* cf. *cruralis*.

Eleutherodactylus danae Duellman, 1978   Plate IVe, p.112

Distribution: The species is known from the eastern slopes of the Andes from the Cosñipata valley, southeastern Peru, and from the Provincia Chapare, Departamento Cochabamba, Bolivia. Known elevations range from 500–1700 m
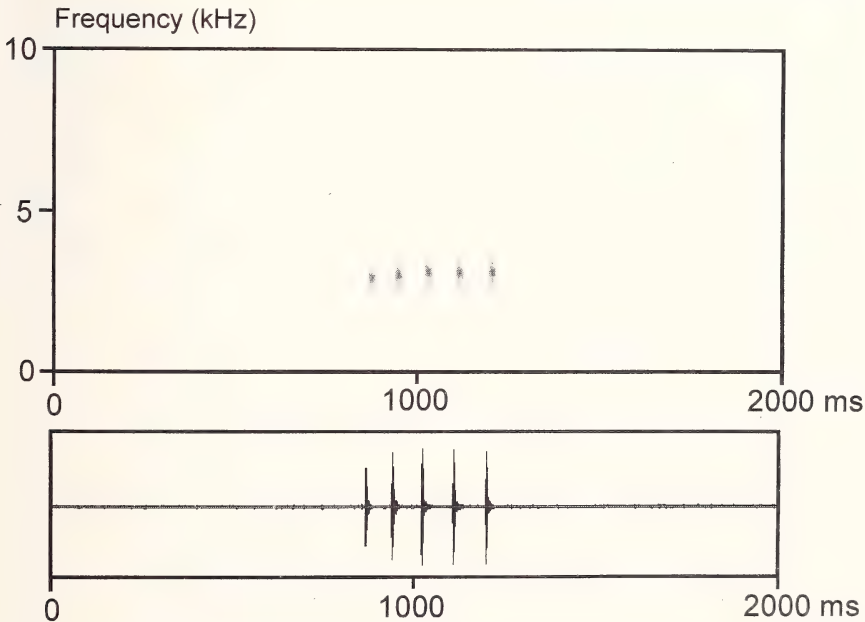
Fig.36: Audiospectrogram and oscillogram of the advertisement call of *Eleutherodactylus danae* from Provincia Chapare, 1250 m a.s.l. Recording obtained on 18 December 1998. Air temperature 16.7°C.

a.s.l. (Duellman 1978b, Köhler & Jungfer 1995). The species can be expected to occur also in the Yungas de La Paz region.

Natural history: All specimens were found at night perching on leaves of bushes or ferns at 0.5–2.0 m height at the edge of humid montane primary forest. Calling activity was highest at dusk during light rain. Juveniles were found from December to February.

Vocalization: Advertisement calls were recorded on 18 December 1998 at 1250 m a.s.l., Provincia Chapare, Departamento Cochabamba. Calls always consisted of two pulsed notes repeated in a rapid succession; call duration varied from 194–214 ms (mean 203.3 ± 10.0); note duration varied from 49–68 ms (mean 55.8 ± 8.5), with the second note being slightly longer; within notes pulses were repeated in regular intervals at a rate of 155–194 pulses per second (mean 176.5 ± 16.3); call energy was distributed between 1400 and 2800 Hz; an upward frequency modulation was recognizable within the calls, with the first note having a dominant frequency peak at approximately 1700 Hz and the second note having the peak at approximately 2200 Hz; the second note showed a higher amplitude; calls were emitted in irregular intervals. Three calls of two individuals analyzed; air temperature was 16.7°C during recording.

Remarks: The species was originally placed in the *E. unistrigatus* group by Duellman (1978b). More recently, a relationship of *E. danae* to the *conspicillatus* lineage was suggested by Lynch & Duellman (1997).

Eleutherodactylus discoidalis (Peracca, 1895)

Distribution: The species is known to occur along the eastern Andean slopes of northern Argentina (Provincias Tucumán and Jujuy) northward to the Provincia Florida, Departamento Santa Cruz, Bolivia. Recent collecting confirmed the species presence in the Departamento Tarija, Bolivia. *Eleutherodactylus discoidalis* is known from elevations of 960–2000 m a.s.l. (Lynch 1989, De la Riva 1993).

Natural history: *Eleutherodactylus discoidalis* inhabits the semi-humid Tucumanian-Bolivian montane forests as well as humid cloud forests in its northern distribution area.

Vocalization: Unknown.

Eleutherodactylus fenestratus (Steindachner, 1864)   Plate IVf, p.112

Distribution: The species occurs throughout a wide range in the Amazon basin. It is known from Bolivia, Brazil, Guyana, and Peru. *Eleutherodactylus fen-*
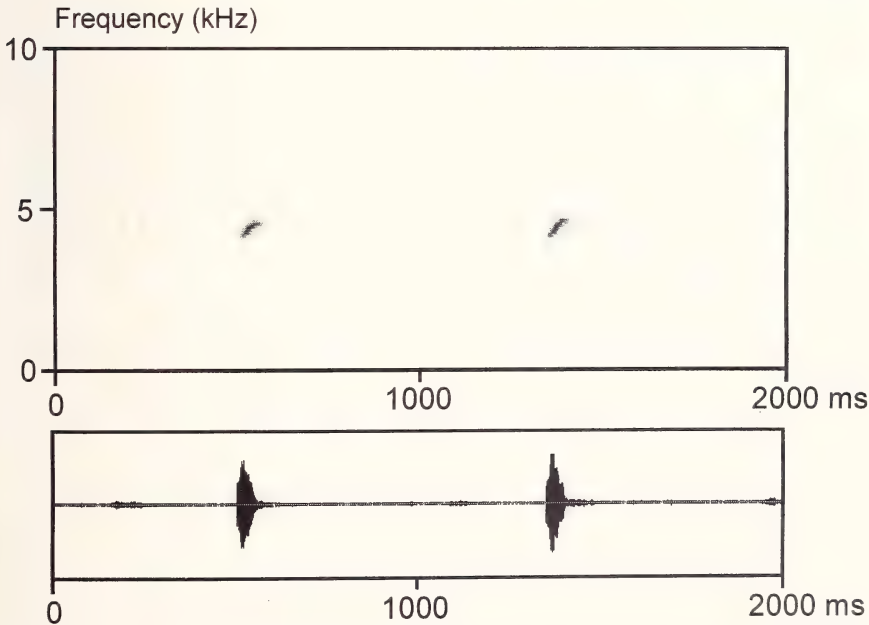

Fig.37: Audiospectrogram and oscillogram of the advertisement call of *Eleutherodactylus fenestratus* from Provincia Chapare, 500 m a.s.l. Recording obtained on 13 December 1998. Air temperature 24.7°C.

estratus is distributed at elevations from 100–1800 m a.s.l. at the Andean slopes (Lynch 1980).

Natural history: *Eleutherodactylus fenestratus* inhabits seasonal Amazonian forests as well as humid montane forests of the Andean foot. It was reported to occur in disturbed and open habitats (Rodríguez 1994). In the lower Chapare region, males called at night during rain from the ground or from low vegetation at the forest edge.

Vocalization: Advertisement calls were recorded on 13 December 1998 in Provincia Chapare, Departamento Cochabamba, 500 m a.s.l. Calls consisted of single pulsatile notes, with a mean duration of 75 ms; approximately 15 pulses are barely countable within notes; calls were repeated at irregular intervals; main call energy was distributed between 1300 and 5000 Hz, with a dominant frequency peak of 3270 Hz. Two calls of one individual analyzed; air temperature was 24.7°C at time of recording.

Calls described from Tambopata, Peru, by Heyer & Muñoz (1999) consisted of 2–3 notes (mean 2.75) and had a mean duration of 180–310 ms; note duration was approximately 70 ms; no numerical frequency data provided. Rodríguez (1994) described calls from Cocha Cashu, Peru, consisting of 1–3 notes (mean 3) and showing a similar dominant frequency (3100 Hz). However, note duration is considerably shorter (45 ms) and notes contain a lower number of pulses (7–9) compared to calls from Bolivia. The single notes of the Bolivian population described above may be the result of low calling motivation of the frog individual recorded. In other characteristics the Bolivian calls coincide well with those reported by Heyer & Muñoz (1999). Calls from the Beni, Bolivia (Reichle 1999), generally coincide in their parameters with those from the Chapare. Calls described by Márquez et al. (1995) from Masicurí, Departamento Santa Cruz, Bolivia, actually correspond to *E. samaipatae*.

Remarks: See remarks for *Eleutherodactylus samaipatae*.

Eleutherodactylus fraudator Lynch & McDiarmid, 1987   Plate IVg, p.112

Distribution: The species is known to occur in Andean cloud forests from the upper Provincia Chapare, Departamento Cochabamba, to the La Siberia area at the limits of the Departamentos Cochabamba and Santa Cruz, between 2050 and 2900 m a.s.l. (De la Riva & Lynch 1997). Endemic to Bolivia.

Natural history: *Eleutherodactylus fraudator* inhabits the upper humid montane forests and cloud forests where relatively low temperatures occur. It seems to be mostly a nocturnal and terrestrial species, although individuals were also found perching on leaves of bushes and ferns as well as active on the forest floor during the day (see Köhler et al. 1995a). De la Riva & Lynch (1997) reported a female found under a stone together with a clutch of 30 developing eggs having a diameter of 4.8–8.9 mm.

Vocalization: Unknown.

Remarks: The species was tentatively assigned to the *E. conspicillatus* group by Lynch & McDiarmid (1987). Subsequently, De la Riva & Lynch (1997) discussed a relationship to the Middle American subgenus *Craugastor*. Herein, *E. fraudator* is suggested to represent a distinct phylogenetic lineage forming an own species group together with two other Bolivian species of *Eleutherodactylus* (see remarks for *E. ashkapara*).

Eleutherodactylus llojsintuta Köhler & Lötters, 1999   Plate IVh, p.112

Distribution: Beside the type locality Sehuencas, Departamento Cochabamba, Bolivia, the species was now discovered on the "old" Chapare road at 2000–2200 m a.s.l. and near Karahuasi, Departamento Santa Cruz, Bolivia, 2150 m a.s.l., thus inhabiting an area of upper montane rainforests with at least 130 km east-west extension along the north-eastern versants of the Bolivian Andes. Endemic to Bolivia.

Natural history: On 19 December 1997, *E. llojsintuta* was abundant at Sehuencas. Males were observed at night during light rain calling from bushes and ferns at 0.3–2.0 m height. All males of *E. llojsintuta* were discovered by their call. Males of *E. platydactylus* called syntopically, but in contrast to *E. llojsintuta* started calling in the late afternoon, indicating that *E. llojsintuta* is probably more noc-
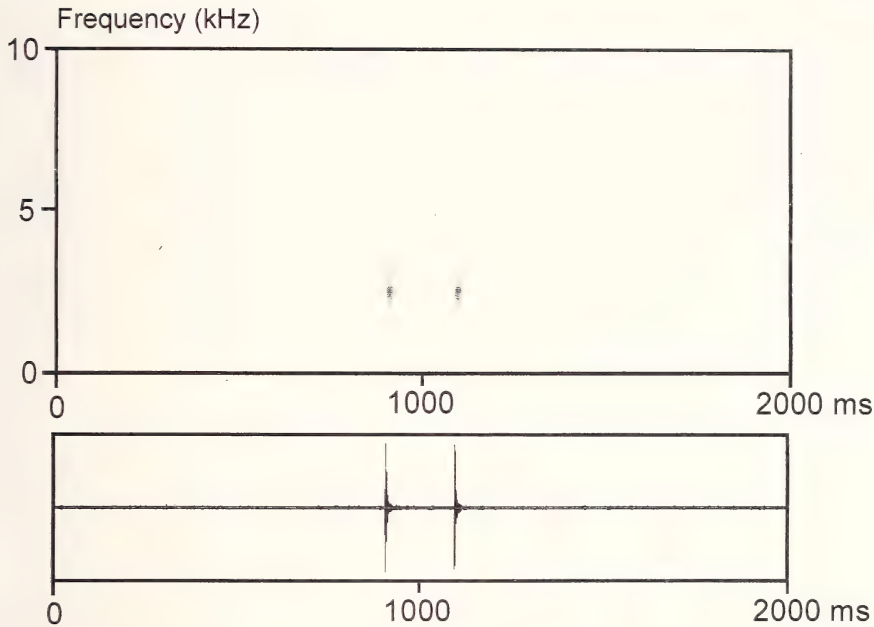

Fig.38: Audiospectrogram and oscillogram of the advertisement call of *Eleutherodactylus llojsintuta* from Sehuencas, 2150 m a.s.l. Recording obtained on 19 December 1997. Air temperature 15.6°C.

turnal. Specimens with red pustules under the skin were common. These pustules are caused by larvae of trombidioid mites.

Vocalization: Advertisement calls were recorded on 19 December 1997 at Sehuencas, Provincia Carrasco, Departamento Cochabamba, 2150 m a.s.l. Calls always consisted of a series of 5–6 notes; mean call duration was 367.5 ms, with a mean dominant frequency of 2850 Hz, and a mean note repetition rate within the call of 12 notes per second; each note consisted of a single pulse; there was noticeable frequency modulation within the call; the first note of the call had most power at 2750 Hz, whereas the last had at 2900 Hz; call energy was also recognizable in two emphasized frequency bands at 5830 and 8630 Hz. Calls were emitted at regular intervals. Seventeen calls of one individual analyzed; air temperature was 15.6°C at time of recording (see Köhler & Lötters 1999a).

Remarks: *Eleutherodactylus llojsintuta* is a member of the *E. unistrigatus* group (sensu Lynch & Duellman 1997). Morphologically, it is most similar to *E. platydactylus* but is mainly distinguished by its advertisement call (Köhler & Lötters 1999a). Females are unknown.

Eleutherodactylus mercedesae Lynch & McDiarmid, 1987   Plate Va, p.128

Distribution: According to the original description (Lynch & McDiarmid 1987), the species was known from two localities, both situated in the Provincia Chapare, Departamento Cochabamba, Bolivia, at 1690 and 1950 m a.s.l. During this study the species was found on the "old" Chapare road between 1400 and 1700 m a.s.l. A single adult specimen (deposited in the CBF) was recently discovered in the Yungas de La Paz region, near Caranavi (S. Reichle pers. comm.). Endemic to Bolivia.

Natural history: The species is distributed in humid montane forests. Lynch & McDiarmid (1987) reported the holotype of *E. mercedesae* being found active during the day on the forest floor. During this study juveniles were found in December and January active on the ground during the day or perching on leaves of bushes at the edge of the forest at night.

Vocalization: Unknown.

Remarks: The obtained juveniles of *E. mercedesae* have SVL of 11.8–15.7 mm (mean 13.9 ± 1.5; n = 6). In life, their ventral color was white with black spotting; the throat is nearly completely black laterally with a white ◇-shaped mark in its center; dorsal ground color was bright green with irregular brown markings; hind limbs green with four brown transversal bars; upper and lower lips white with black bars. The dorsal skin has prominent scattered tubercles, giving the specimens a moss appearance. It seems to be a rare species. *Eleutherodactylus mercedesae* is possibly related to the *E. fraudator* group (see remarks for *E. ashkapara*) according to the presence of a frontoparietal fontanelle (De la Riva & Lynch 1997).

Eleutherodactylus olivaceus **Köhler, Morales, Lötters, Reichle & Aparicio, 1998**   Plate Vb, p.128

Distribution: The species is known from Estación Pakitza, P.N. Manu, Departamento Madre de Dios, Peru, 350 m a.s.l. and from the Bolivian Provincia Chapare between 500 and 1650 m a.s.l. The nearest known Bolivian and Peruvian localities are separated by a distance of approximately 700 km (Köhler et al. 1998c). Additionally, calls of *E. olivaceus* were heard at Mataracú, Departamento Santa Cruz, Bolivia, 500 m a.s.l.

Natural history: The distribution comprises tropical lowland rainforest as well as humid montane rainforest with an elevational range of 350–1650 m a.s.l. Along the "old" Chapare road, *E. olivaceus* was found to be an abundant species. Between December and February, males were commonly observed calling from bushes and trees in up to 10–15 m height. Calling activity was most intensive during rain and heavy down-pours and in the early evening. Later in the night calling motivation usually decreased.

Vocalization: Advertisement calls were recorded on 13 December 1998 in Provincia Chapare, Departamento Cochabamba, 500 m a.s.l. Calls consisted of single frequency modulated whistle with a note duration of 51–68 ms (mean 59.6

Fig.39: Audiospectrogram and oscillogram of the advertisement call of *Eleutherodactylus olivaceus* from Provincia Chapare, 500 m a.s.l. Recording obtained on 13 December 1998. Air temperature 27.7°C.

± 4.4); notes were repeated with a mean rate of 1.01 notes per second; call energy was distributed between 4080 and 4800 Hz, with a dominant frequency peak at 4470 Hz; notes lack harmonics and pulses. Sixteen calls of one individual analyzed; air temperature was 27.7°C at time of recording.

These data coincide well with the calls described by Köhler et al. (1998c) for *E. olivaceus* from the same general area. Calls from Estación Pakitza, P.N. Manú, Peru, are very similar to the calls reported from Bolivian populations (V.R. Morales pers. comm.).

R e m a r k s : A member of the *Eleutherodactylus unistrigatus* group (sensu Lynch & Duellman 1997). The olive green dorsal coloration in life and the papilla on the tip of snout distinguish *E. olivaceus* from all other Bolivian members of the *E. unistrigatus* group. A single obtained female has 24.2 mm SVL. Records of *Eleutherodactylus mendax* from Bolivia (Harding 1983, Lynch 1986a, De la Riva 1990a) were most probably based on specimens referable to *E. olivaceus* (see Köhler et al. 1998c).

Eleutherodactylus platydactylus (Boulenger, 1903)   Plate Vc, p.128

D i s t r i b u t i o n : The species is known from the eastern slopes of the Andes from Departamento Ayacucho, Peru, to Departamento Santa Cruz, Bolivia, from 950–3470 m a.s.l. A record from Rurrenabaque, 227 m a.s.l. (type locality of the synonym *E. bockermanni*), was considered doubtful (De la Riva 1998).

N a t u r a l   h i s t o r y : *Eleutherodactylus platydactylus* inhabits humid montane rainforests, cloud forests, as well as sub-paramo formations. At some sites it appears to be extremely abundant. It is a mostly nocturnal species, although calls were also heard during the day especially in upper cloud forest areas (e.g., La Siberia) when heavy fog appeared. Within forests males called perching on leaves at 0.5–2.0 m height, whereas in sub-paramo the species called from grassy vegetation on the ground. Sometimes many males called simultaneously, other times only few isolated males called. At day, specimens were found under fallen logs and stones as well as in arboreal bromeliads. Females collected from November to July were reproductively active, having ovarian and oviductal eggs. Two amplectant pairs were observed in February. Females seem to be more common than males (De la Riva 1998). *Eleutherodactylus platydactylus* frequently suffered from parasite infestation, visible as reddish pustules through the skin (Köhler et al. 1995a). According to De la Riva (1998), these pustules are caused by larvae of trombidioid mites.

V o c a l i z a t i o n : Advertisement calls were recorded on 19 December 1997 at Sehuencas, Provincia Carrasco, Departamento Cochabamba, 2150 m a.s.l. Calls consisted of 1–7 short notes repeated in regular intervals at a rate of approximately 5.2 notes per second; note duration varied from 13–22 ms (mean 19.7 ± 2.7); calls consisting of two notes were the most common ones; calls were emitted in

Frequency (kHz)

10

5

0

0   1000   2000 ms
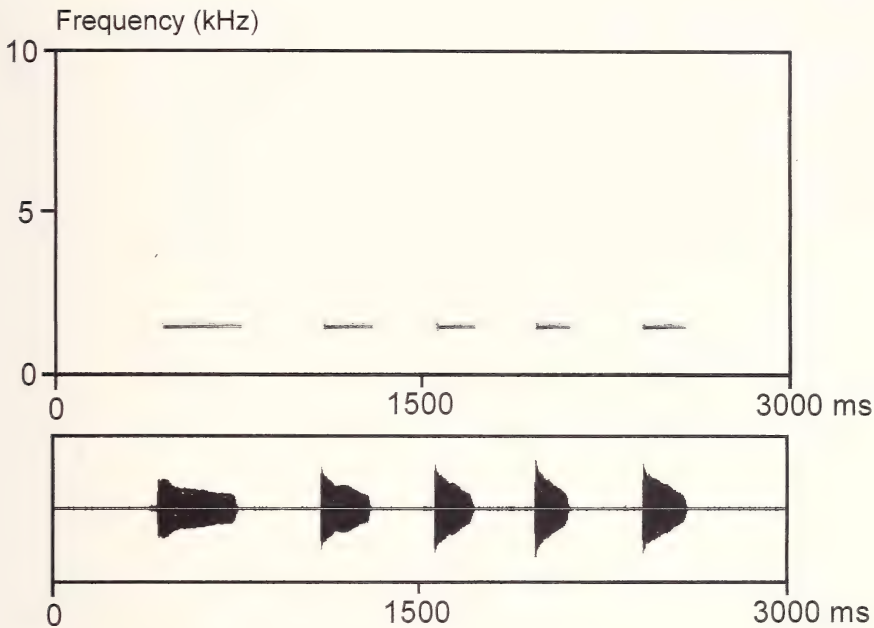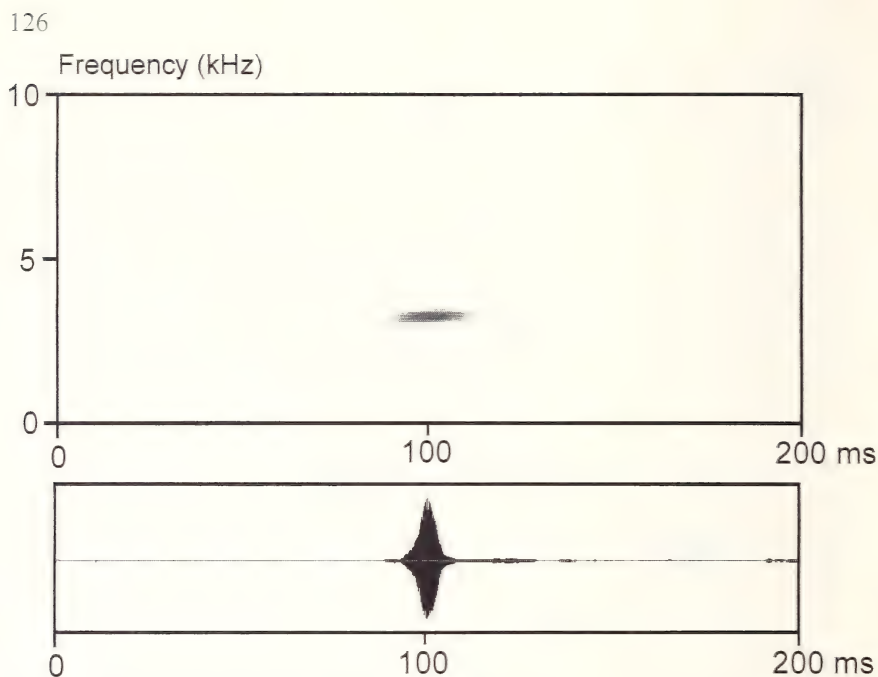
0   1000   2000 ms

Fig.40: Audiospectrogram and oscillogram of the advertisement call of *Eleutherodactylus platydactylus* from Sehuencas, 2150 m a.s.l. Recording obtained on 19 December 1997. Air temperature 15.6°C.

regular intervals at a rate of 5.6 calls per minute; call energy was distributed between 1500 and 7200 Hz, with a dominant frequency peak at 2390 Hz; harmonic frequency bands were recognizable at 4600 and 6979 Hz. Nine calls of one individual analyzed; Air temperature was 15.6°C during recording.

At La Hoyada, Provincia Florida, Departamento Santa Cruz, 1700 m a.s.l., as well as at a point south of Karahuasi, Provincia Carrasco, Departamento Cochabamba, 2170 m a.s.l., beside single notes three series of notes were recorded in total, each consisting of 14 notes (!) repeated with an approximate rate of 4.0 notes per second. Air temperature during both recordings was around 16.0°C.

Data of the calls from Sehuencas coincide relatively well with the data of calls from La Siberia provided by Márquez et al. (1995), except that the authors reported a shorter note duration. The longer calls recorded at La Hoyada and near Karahuasi consisted of a remarkably large number of notes, not reported before. Differences in vocalization among Bolivian populations of *E. platydactylus* may indicate that additional species are involved.

R e m a r k s : *Eleutherodactylus platydactylus* is an extremely polymorphic species (De la Riva 1993b, 1998, Köhler et al. 1995a). There is large intra- and interpopulational variation in coloration, body size, as well as in skin texture. It

was argued by De la Riva (1998) that additional species are still contained in *E. platydactylus* sensu lato. This view was recently supported by bioacustic investigations which lead to the description of a new sibling species, *E. llojsintuta* (Köhler & Lötters 1999a).

Populations observed along the "old" Chapare road, Provincia Chapare, Departamento Cochabamba, between 950 and 1700 m a.s.l. show remarkably little variation in size and coloration. All collected specimens exhibit a prominent papilla on the tip of the snout. Males of these populations exclusively emitted very soft low calls consisting of several repeated notes (no recordings available). Single notes were not heard. Possibly, these populations correspond to another undescribed species related to *E. platydactylus*.

Eleutherodactylus pluvicanorus **De la Riva & Lynch, 1997**   Plate Vd, p.128

Distribution: The species is known to occur along the eastern Andean slopes from the Provincia Chapare, Departamento Cochabamba, southward to Provincia Florida, Departamento Santa Cruz, Bolivia. *Eleutherodactylus pluvicanorus* occurs between 2000 and 2550 m a.s.l. Endemic to Bolivia.

Natural history: *Eleutherodactylus pluvicanorus* inhabits upper montane rainforests and cloud forests. It is a terrestrial species, active during the day and night in the forest litter, but specimens were also found perching on leaves up to 1.5 m height (Köhler et al. 1995a). At more dry weather conditions, adults were found under fallen logs or stones at daytime. Calls were heard at daytime during rain or heavy fog as well as in the evening. De la Riva & Lynch (1997) reported on amplectant pairs found in March and April.

Vocalization: Calls were recorded on 20 December 1997 at Sehuencas, Provincia Carrasco, Departamento Cochabamba, 2150 m a.s.l. The call is a tonal, moderately long note sounding like a soft whistle; note duration varied from 210–440 ms (mean 310.5 ± 72.2); notes were repeated at a rate of approximately 35 notes per minute; these primary notes sometimes were followed by a succession of shorter whistles; note duration in these shorter notes varied from 99–184 ms (mean 136.2 ± 33.9); they were repeated with a maximum rate of 190 notes per minute; call energy was distributed within a narrow band between 1100 and 1600 Hz; a dominant frequency peak was recognizable at 1360 Hz. Twenty-five calls of one individual analyzed; air temperature was 16.4°C at time of recording. In all general characteristics these data are very similar to those provided for *E. pluvicanorus* by De la Riva & Lynch (1997).

Remarks: De la Riva & Lynch (1997) discussed a relationship to the Middle American subgenus *Craugastor*. Herein, *E. pluvicanorus* is suggested to represent a distinct phylogenetic lineage forming an own species group together with two other Bolivian species of *Eleutherodactylus* (see remarks for *E. ashkapara*).

Fig.41: Audiospectrogram and oscillogram of the call of *Eleutherodactylus pluvicanorus* from Sehuencas, 2150 m a.s.l. Recording obtained on 20 December 1997. Air temperature 16.4°C.

Eleutherodactylus rhabdolaemus Duellman, 1978   Plate Ve, p.128

Distribution: The species is known to occur along the eastern slopes of the Andes from the Peruvian Departamentos Ayacucho, Cuzco, and Huánuco, southward to the Provincia Florida, Departamento Santa Cruz, Bolivia. The known elevations approximately range from 1000–2700 m a.s.l. Records from lower elevations (Duellman 1978a, De la Riva 1993b) are in error and partly correspond to *E. toftae* (I. De la Riva pers. comm.).

Natural history: Specimens were found in humid montane forests as well as cloud forest habitats. Usually, males called at night from leaves of ferns and bushes at approximately 0.5–1.5 m height. Calling activity was highest at dusk during light rain. Along the "old" Chapare road few males also called during the day from the forest floor. At daytime, adults were discovered active on the forest floor or in more open habitats under rocks or fallen logs. Juveniles were observed from November to February, mostly perching on leaves at night.

Vocalization: Advertisement calls were recorded on 25 November 1998 south of Karahuasi, Provincia Carrasco, Departamento Cochabamba, 2170 m a.s.l. Calls consisted of short tonal notes; note duration varied from 13–22 ms (mean 19.0 ± 2.5); notes were repeated in regular intervals at a rate of approximately 43 notes per minute; call energy was distributed in a narrow band of about 500 Hz between

126

Frequency (kHz)

10

5

0

0   100   200 ms

0   100   200 ms

Fig.42: Audiospectrogram and oscillogram of the advertisement call of *Eleutherodactylus rhabdolaemus* from south of Karahuasi, 2170 m a.s.l. Recording obtained on 25 November 1998. Air temperature 15.8°C.

2400 and 3900 Hz, obviously depending on the body size of the calling male; the dominant frequency peak varied from 2870–3650 Hz (mean 3117 ± 296); notes lack pulses and harmonic structures. Twenty-two calls of four individuals analyzed; air temperature was 15.8°C during recording.

Eleutherodactylus rhabdolaemus often calls concomitantly with *E. platydactylus*. The call of the latter always sounds like a 'click', whereas the call of *E. rhabdolaemus* is a short whistle with call energy distributed in a much narrower frequency band.

Remarks: Coloration can change considerably in living specimens (see also Lynch & McDiarmid 1987). Some are nearly black dorsally, whereas others are light brown. Generally, the coloration exhibited at daytime is much darker. Dorsal dark chevrons may be more or less distinct. In many specimens a turquoise colored iris periphery was recognizable.

Eleutherodactylus samaipatae Köhler & Jungfer, 1995   Plate Vf, p.128

Distribution: The species is at least known from the eastern Andean slopes in the Provincias Florida, Vallegrande, and Cordillera, Departamento Santa Cruz, Bolivia. The known elevational range is 800–2000 m a.s.l. Endemic to Bolivia.
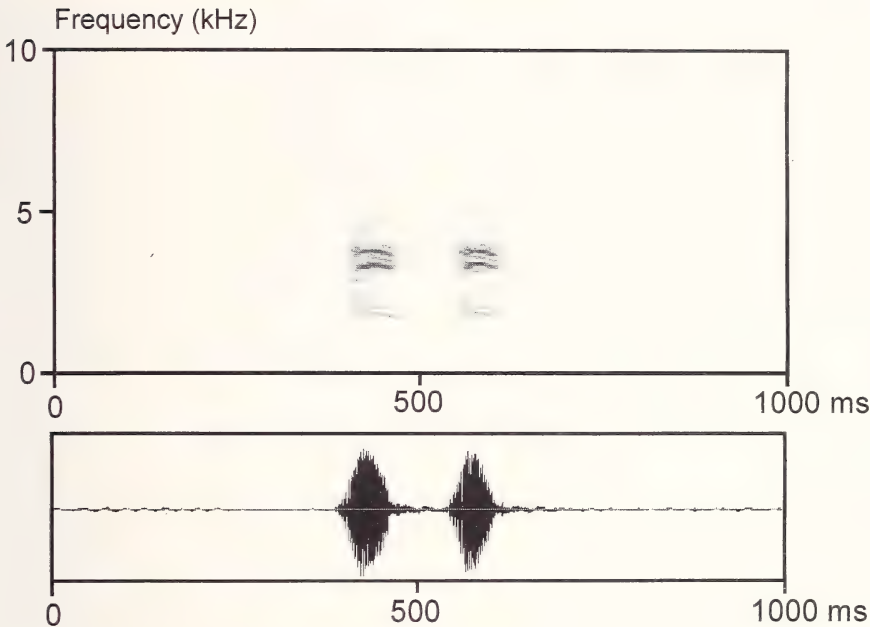
Fig.43: Audiospectrogram and oscillogram of the advertisement call of *Eleutherodactylus samaipatae* from west of Río Seco, 1000 m a.s.l. Recording obtained on 8 December 1997. Air temperature 24.3°C.

Natural history: The species occurs in semi-humid forests as well as in disturbed areas. At some sites, including the type locality, it appears to be an abundant species. Males called at dusk and night from bushes 0.6–2.0 m above the ground, often near to small rivers. Gravid females were obtained in November. Reichle (1999) provided some notes on the calling behavior.

Vocalization: Advertisement calls were recorded on 8 December 1997 west of Río Seco, Provincia Cordillera, Departamento Santa Cruz, 1000 m a.s.l. Calls were composed of two pulsatile notes in a rapid succession; call duration varied from 225–231 ms (mean 228.0 ± 3.0); note duration varied from 73–90 ms (mean 82.5 ± 6.6), the second note always being slightly shorter; calls were emitted at irregular intervals, with an approximate rate of 3–4 calls per minute; call energy was distributed in a broad band from 1200–6800 Hz, with a dominant frequency peak at 3180 Hz. Three calls of one individual analyzed; air temperature 24.3°C. These call characteristics are almost identical to those reported by Márquez et al. (1995) for a population from Masicurí, Provincia Vallegrande, Departamento Santa Cruz, 900 m a.s.l., a site relatively close to the locality of own recordings. There remains little doubt that the recordings of Márquez et al. (1995) actually correspond to *E. samaipatae* instead to the Amazonian species *E. fenestratus* like stated by the authors. Recently, Reichle (1999) described calls of *E. samaipatae* from its type

locality, generally coinciding with the results presented herein. The only difference refers to a slightly longer call duration reported by Reichle (1999), which is probably due to temperature differences (temperatures not provided by Reichle 1999).

R e m a r k s : When describing *Eleutherodactylus samaipatae*, Köhler & Jungfer (1995) overlooked the available name *Hylodes gollmeri* var. *bisignata* Werner, 1899, considered a synonym of *E. fenestratus* by Lynch (1980) and Lynch & Duellman (1997). Examination of the female *bisignatus* holotype (NMW 16502) revealed differences in coloration, length of hindlimbs, length of fingers, and head shape compared to *E. samaipatae* and *E. fenestratus*. Thus, *E. bisignatus* is herein suggested a valid species (see annotations to the checklist).

Köhler & Jungfer (1995) stated that *E. fenestratus* differs from *E. samaipatae* by the lack of a tarsal fold. Examination of the syntypes of *E. fenestratus* (NMW 19940 [1,2]; NMW 19940.1 was recently designated as lectotype by Reichle 1999) as well as *E. fenestratus* specimens from Amazonian Bolivia revealed that Köhler & Jungfer's (1995) statement was wrong and a tarsal fold is also present in *E. fenestratus*, although barely visible in the type specimens. However, direct comparison of the *E. fenestratus* specimens with *E. samaipatae* from different localities revealed that *E. samaipatae* is always paler colored and has considerably longer hindlimbs (tibio-tarsal articulation reaching beyond tip of snout when hindlimb flexed parallel to body versus reaching nostril in *E. fenestratus*). In addition, the dorsum of *E. samaipatae* is almost uniformly shagreen and lacks the scattered enlarged tubercles present in *E. fenestratus*.

A somewhat confusing point are the calls. Advertisement calls of *E. fenestratus* have been described from Manaus, Brazil (Zimmerman & Bogart 1984), Cocha Cashu, Peru (Rodríguez 1994), and Tambopata, Peru (Heyer & Muñoz 1999). In general characteristics, the calls described are similar to those of *E. samaipatae*, but Rodríguez (1994) as well as Heyer & Muñoz (1999) figured calls composed of three notes. Although *E. fenestratus* may also emit single or two note calls like *E. samaipatae*, calls consisting of three notes were never recognized in the latter.

Eleutherodactylus species A   Plate Vg, p.128

D i s t r i b u t i o n : The species is known from at least four localities on the eastern versants of the Andes in the Provincias Cordillera, Florida, and Vallegrande, Departamento Santa Cruz, Bolivia (Masicurí, "El Fuerte" Samaipata, near

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Plate V: **a)** *Eleutherodactylus mercedesae* Lynch & McDiarmid, 1987, juvenile, Provincia Chapare, 1650 m; **b)** *Eleutherodactylus olivaceus* Köhler et al., 1998, male, Provincia Chapare, 700 m; **c)** *Eleutherodactylus platydactylus* (Boulenger, 1903), male, Sehuencas, 2150 m; **d)** *Eleutherodactylus pluvicanorus* De la Riva & Lynch, 1997, male, La Yunga, 2300 m; **e)** *Eleutherodactylus rhabdolaemus* Duellman, 1978, female, La Yunga, 2300 m; **f)** *Eleutherodactylus samaipatae* Köhler & Jungfer, 1995, female, El Fuerte, 1850 m; **g)** *Eleutherodactylus* sp. A, female, El Fuerte, 1900 m; **h)** *Ischnocnema sanctaecrucis* Harvey & Keck, 1995, male, N of Karahuasi, 2200 m.

Plate V
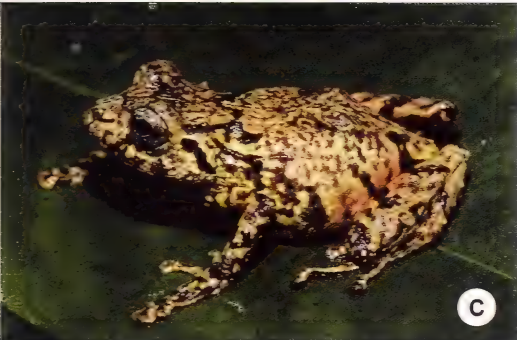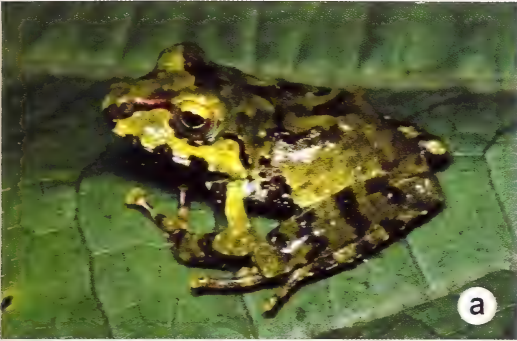
Bermejo, and west of Río Seco), comprising an elevational range of 700–1900 m a.s.l. (see remarks). Endemic to Bolivia.

D i a g n o s i s : A species in the *Eleutherodactylus discoidalis* group (sensu Lynch 1989), distinguished from other species of *Eleutherodactylus* by the following combination of characters: (1) skin on dorsum tuberculate, dorsolateral folds absent; skin of venter smooth, discoidal folds well anteriad to groin; (2) tympanic membrane distinct, round; tympanic annulus distinct, its diameter larger than half the eye length; (3) snout subacuminate in dorsal view, rounded lateral profile; canthus rostralis rounded; (4) upper eyelid bearing low tubercles, slightly narrower than IOD; (5) vomerine odontophores oval, prominent, narrowly separated, median behind choanae; (6) males with vocal slits and vocal sac; males without nuptial pads; (7) first finger about equal in length than second; tips of outer two fingers truncate, with large pads, tips of inner two fingers rounded, only slightly expanded; (8) fingers with weakly defined lateral fringes; (9) no ulnar tubercles; (10) no tubercles or folds on heel and tarsus; (11) inner metatarsal tubercle oval and elevated, outer smaller, rounded; supernumerary plantar tubercles absent; (12) toes with weak lateral fringes; webbing absent; third toe longer than fifth, not reaching penultimate subarticular tubercle of fourth toe; toe tips truncate, expanded, smaller than those of outer fingers; (13) dorsum brownish with diffuse darker markings; upper lip with irregular mottling; venter cream, throat finely mottled with brown; (14) adults moderate-sized, SVL of male 31.0 mm, female 38.1 mm.

N a t u r a l   h i s t o r y : The species inhabits semi-humid montane forests. Specimens were discovered fallen in burrows and calling at night from the edge of roads during light rain (S. Reichle pers. comm.).

V o c a l i z a t i o n : Advertisement calls referable to *Eleutherodactylus* sp. A were published by Márquez et al. (1995) (as *E. cruralis*): The call consisted of six notes, repeated with a mean rate of 40.2 notes per second; call duration varied from 144.5–155.8 ms; calls were repeated at a rate of 10.5–23.1 calls per minute; mean dominant frequency was 2588.7 Hz, with a fundamental frequency of 1599.2 Hz.

R e m a r k s : Morphological differences of populations from above mentioned localities in comparison to *E. cruralis* from Bolivian Yunga regions was already recognized by De la Riva (1993b) and Köhler et al. (1995b). The authors interpreted the differences as intraspecific variation. As a result, *Eleutherodactylus* sp. A was already figured in publications (De la Riva 1993b:fig. 3A, Köhler et al. 1995b:fig. 13, Reichle & Köhler 1997:fig. 2). However, recent discoveries of additional specimens as well as the analysis of advertisement calls revealed that more species are involved. The calls described by Márquez et al. (1995) from Masicurí most probably correspond to this undescribed taxon. The species is being described by S. Reichle, S. Lötters, and I. De la Riva.

Ischnocnema sanctaecrucis Harvey & Keck, 1995   Plate Vh, p.128

D i s t r i b u t i o n : Formerly known only from the type locality El Chape, Provincia Florida, Departamento Santa Cruz, 2060 m a.s.l. (Harvey & Keck

Frequency (kHz)
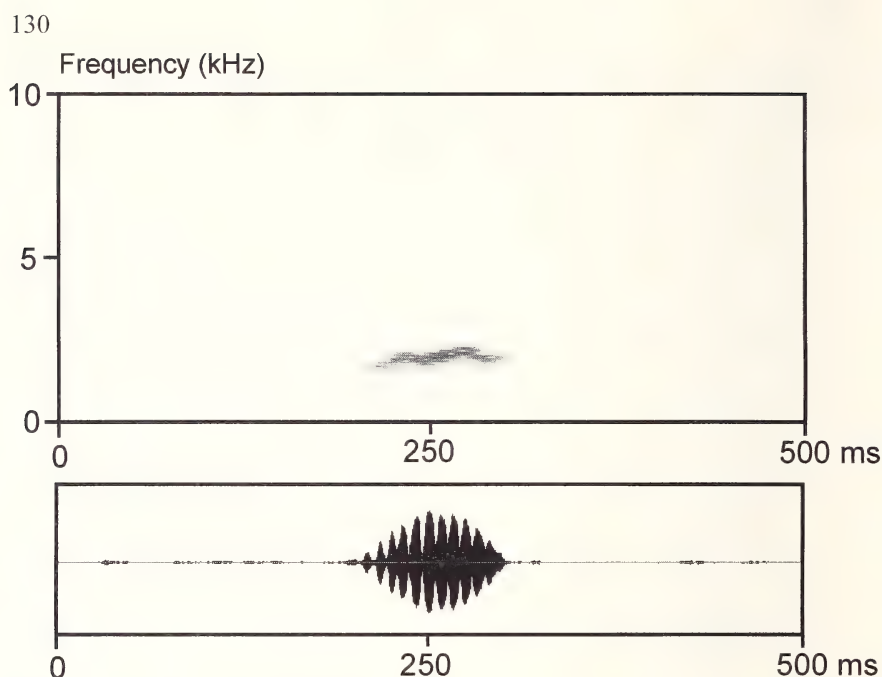
Fig.44: Audiospectrogram and oscillogram of the advertisement call of *Ischnocnema sanctaecrucis* from south of Karahuasi, 2150 m a.s.l. Recording obtained on 25 November 1998. Air temperature 15.8°C.

1995), *I. sanctaecrucis* was now discovered at the nearby site La Hoyada, south of Karahuasi (2150 m a.s.l.), as well as on the "old" Chapare road, Departamento Cochabamba, 1500 m a.s.l. Therefore, the species at least inhabits the Yungas of the Departamentos Cochabamba and Santa Cruz with an east-west extension of approximately 200 km and an elevational range of 1500–2150 m a.s.l. Endemic to Bolivia.

Natural history: The habitat in the distribution area comprises humid montane rainforest and cloud forest. Calling males were observed at night perching on low vegetation in secondary growth as well as in disturbed primary forest apart from any water bodies. During dry conditions, calls were emitted only sporadically, whereas during rain calling activity increased to regular repeated calls like described below. Harvey & Keck (1995) found their specimens during the day under rocks and reported a defensive posture in the obtained female.

Vocalization: Advertisement calls were recorded on 25 November 1998 at a point south of Karahuasi, Provincia Carrasco, Departamento Cochabamba, 2150 m a.s.l. Calls consisted of a single pulsed notes with a duration of 91–97 ms (mean 92.8 ± 2.5) and were repeated in regular intervals at a rate of approximately 22 calls per minute; each note was composed of 11 pulses, repeated at a rate of 120 pulses per second; call energy was distributed from 1400–2200 Hz, with a modu-

lated dominant frequency peak of 1620 Hz at beginning of the note and 1920 at its end; all notes show a moderate amplitude modulation. Five calls of one individual analyzed; air temperature was 15.8°C during recording.

Leptodactylus chaquensis Cei, 1950   Plate VIa, p.144

Distribution: The species is known from northern Argentina, Bolivia, Paraguay, Uruguay, and Mato Grosso do Sul, Brazil (Frost 1985, Langone 1994), at elevations of approximately 150–1340 m a.s.l. (see remarks).

Natural history: *Leptodactylus chaquensis* inhabits open areas within dry and semi-deciduous forests, Cerrado formations, and moist savannas. Reproduction takes place in ephemeral ponds. Individuals of both sexes formed large aggregations resulting in a large shared foam nest of approximately 2.0 m in diameter. Males were observed during heavy competitions within the foam nests, clasping each other with their hypertrophied forearms (Reichle 1997b). The tadpole has been described by Cei (1980).

Vocalization: The advertisement call was described by Barrio (1966) and Reichle (1996). In the Bolivian population from the Departamento Beni, two types of notes were recognized. The first note of the call consisted of 14–17 pulses and had a mean duration of 639 ms. The secondary notes are much shorter in duration (mean 119 ms) and comprise 7–11 pulses. As a consequence, the pulse rate in the secondary notes is much higher (80 pulses per second versus 23.5 pulses per second in the first long notes). The dominant call energy was distributed between 700 and 1200 Hz (Reichle 1996).

Remarks: Statements about the validity of *Leptodactylus macrosternum* Miranda-Ribeiro, 1926 are somewhat chaotic (W. R. Heyer pers. comm.). Populations from the northern Amazon have been considered different from *L. chaquensis* and/or *L. ocellatus* (e.g., Péfaur 1992, Murphy 1997), but hitherto the taxonomic status of populations from northern Amazonia was not clarified (see also De la Riva & Maldonado 1999).

Leptodactylus gracilis Duméril & Bibron, 1841   Plate VIb, p.144

Distribution: *Leptodactylus gracilis* is known to occur from Uruguay, Paraguay, and southeastern Brazil to northern Argentina and the inter-Andean dry-valleys of Bolivia at elevations of approximately 200–2000 m a.s.l. (Heyer 1978, Langone 1994, Köhler & Lötters 1999c).

Natural history: The species inhabits dry and semi-deciduous forests as well as Cerrado formations. In Bolivia, *L. gracilis* occurs in semi-humid montane forests as well as in open areas. An observed male called at night during light rain from the ground, hidden under a fallen log at the edge of a roadside ditch. Calls were also heard at dusk in the valley of Vallegrande. Juveniles were found in February 1998 under rocks at El Fuerte. Foam nests are deposited in digged cavities at the edge of ephemeral puddles where the tadpoles develop (Langone 1994).
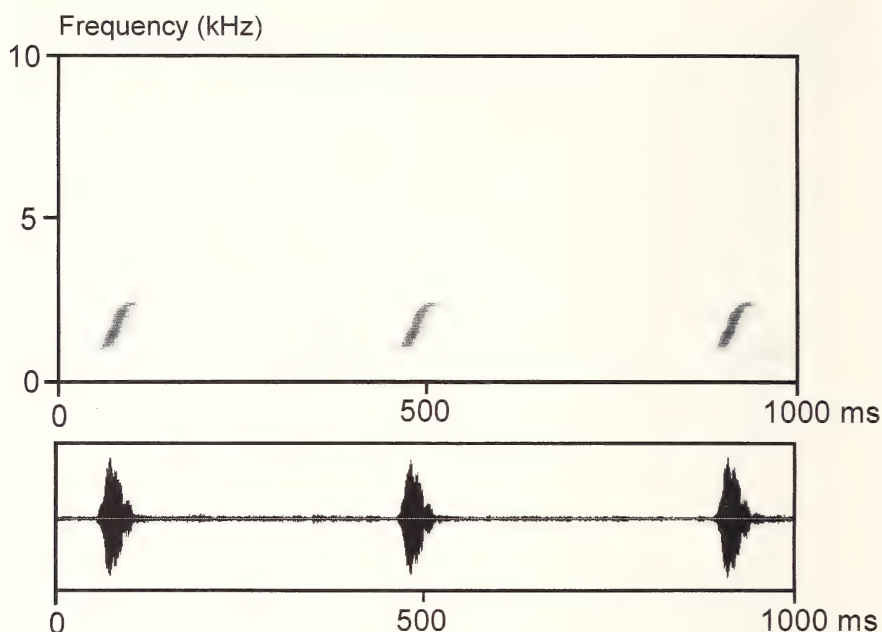
Fig.45: Audiospectrogram and oscillogram of the advertisement call of *Leptodactylus gracilis* from southeast of Guadalupe, 1650 m a.s.l. Recording obtained on 7 January 1998. Air temperature 18.0°C.

Vocalization: Advertisement calls were recorded on 17 January 1998 approximately 29 km southeast of Guadalupe, Provincia Vallegrande, Departamento Santa Cruz, 1650 m a.s.l. The call consisted of a single frequency modulated note with a duration of 67–87 ms (mean 74.9 ± 6.7); notes were repeated at regular intervals at a rate of 89–182 notes per minute (mean 127.8 ± 19.2); call energy was distributed between 830 and 2320 Hz, with a dominant frequency peak at 1970 Hz; calls were indistinctly pulsed and lacked harmonic structures. Twenty-three calls of one individual analyzed; air temperature was 18.0°C during recording. These data differ only slightly from calls of *L. gracilis* from Buenos Aires, Argentina (Barrio 1965b, 1973, Heyer 1978), with respect to a slightly longer note duration and little bit lower note repetition rate (Köhler & Lötters 1999c).

Leptodactylus griseigularis (Henle, 1981)   Plate VIc, p.144

Distribution: The species was previously known from the eastern slopes of the Andes from central Peru southward to the Yungas de La Paz region, Bolivia, inhabiting elevations of 100–1800 m a.s.l. (Heyer 1994). During this study, *L. griseigularis* was collected in Provincia Chapare, Departamento Cochabamba, Bolivia, which represents the southern and easternmost record for the species.

Natural history: A single specimen was found during the day at the edge of a puddle on a road within humid montane forest at approximately 1300 m a.s.l. A foam nest (presumably belonging to the species) was found close to the specimen. It was about 10 cm in diameter and was floating on the water surface.

Vocalization: The advertisement call was described from Tingo Maria, Peru, and consisted of a very short frequency modulated note repeated at a rate of 1.8 notes per second. Frequency was distributed between 1380 and 3060 Hz, with a dominant frequency peak at 2770 Hz (Heyer & Morales 1995).

Leptodactylus labyrinthicus (Spix, 1824)

Distribution: The species is known from south and northeastern Brazil, Bolivia, Paraguay, northern Argentina, as well as in coastal Venezuela (Heyer 1979, Péfaur & Sierra 1995). *Leptodactylus labyrinthicus* was recorded from sea level up to 1000 m a.s.l.

Natural history: *Leptodactylus labyrinthicus* inhabits Cerrado and Caatinga formations, semi-deciduous forest regions, seasonal Amazonian forests, as well as Chaco montane forests of the eastern Andean slopes. Reproduction takes place during the rainy season. Males called from the edge of water bodies. Large foam nests were deposited in ephemeral pools and ponds (see Köhler & Böhme 1996). The tadpole was described by Heyer (1979).

Vocalization: Advertisement calls of a Bolivian population were described by Márquez et al. (1995). Calls consisted of single, frequency modulated notes, with a mean duration of 208.7 ms, and a low mean dominant frequency of 394.3 Hz; calls were repeated at a mean rate of 53.9 calls per minute. Calls described from Serra Canastra, Minas Gerais, Brazil (Haddad et al. 1988), had significant lower note duration (about 130 ms).

Leptodactylus leptodactyloides (Andersson, 1941)   Plate VId, p.144

Distribution: The species occurs throughout the greater Amazon basin and the Guianas (Heyer 1994). It is known from elevations of 15–1130 m a.s.l. (Köhler 1995b).

Natural history: *Leptodactylus leptodactyloides* inhabits various types of habitats within the Amazon basin. In Bolivia, specimens were found during the day under fallen logs close to a lagoon. The tadpole was described by Heyer (1994).

Vocalization: Calls were described by Heyer (1994) and consisted of single frequency modulated notes, with a duration of 10–40 ms; notes were repeated at rates of 0.3–3.3 calls per second; call energy between 650–600 Hz; dominant frequency peak at 1100–1300 Hz.

Leptodactylus rhodonotus **(Günther, 1869)**   Plate VIe, p.144

Distribution: The species is known to occur on the Andean slopes and the lowlands of the upper Amazon basin of Bolivia and Peru between 200 and 2050 m a.s.l. (Reynolds & Foster 1992, Rodríguez & Duellman 1994).

Natural history: The species inhabits lowland rainforests, humid montane rainforests as well as disturbed and open habitats within these forests. Males called from roadside ditches and smaller puddles at night. In contrast to the observations of Henle (1992), calling activity was highest during heavy rain. Foam nests were deposited under rotten logs or stones close to the water. During the day, also adult individuals were found under these logs and stones. Tadpoles develop in puddles, roadside ditches and slow running water. The tadpole was characterized by Heyer (1979) as well as Henle (1992). Juveniles were observed from November to February.

Vocalization: Advertisement calls were recorded on 8 February 1998 at the "old" Chapare road, Provincia Chapare, Departamento Cochabamba, 650 m a.s.l. Calls consisted of a single frequency modulated notes repeated in regular intervals at a rate of 106–214 notes per minute (mean 173.2 ± 31.7); note duration varied from 45–66 ms (mean 54.7 ± 4.9); main call energy was distributed between 1680
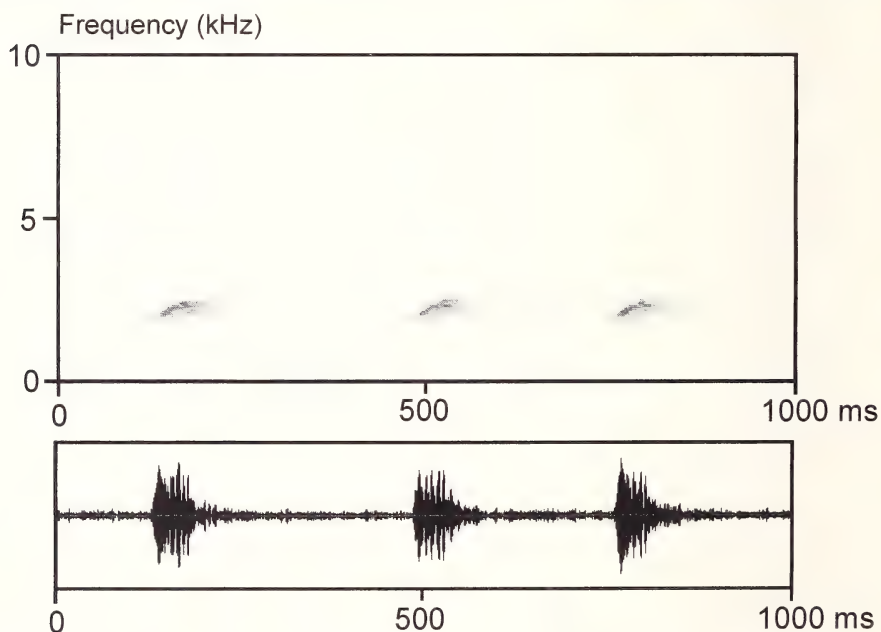
Fig.46: Audiospectrogram and oscillogram of the advertisement call of *Leptodactylus rhodonotus* from Provincia Chapare, 650 m a.s.l. Recording obtained on 8 February 1998. Air temperature 24.8°C.

and 2530 Hz, with a dominant frequency peak at 2160 Hz; notes are distinctly pulsed; in some notes six to eight pulses are countable, in others the pulse structure appears to be more complex; harmonic structures present. Twenty-five calls of one individual analyzed; air temperature was 24.8°C during recording (see Köhler & Lötters 1999c).

Phrynopus kempffi De la Riva, 1992

Distribution: The species is known only from the region known as "La Siberia" at the limits of the Departamentos Cochabamba and Santa Cruz, Bolivia. *Phrynopus kempffi* was found at elevations of 2500–2900 m a.s.l. (De la Riva 1992b). Endemic to Bolivia.

Natural history: The zonal vegetation of the known distribution area is cloud forest. Specimens were found under stones or in moss between tree roots from where males were calling (De la Riva 1992b). Nothing else is known.

Vocalization: The advertisement call was described by Márquez et al. (1995) as a short whistle with a mean duration of 101.4 ms and a mean dominant frequency of 3253.5 Hz. Calls were repeated at a mean rate of 11.2 calls per minute.

Phyllonastes carrascoicola De la Riva & Köhler, 1998   Plate VIg, p.144

Distribution: The species is distributed along the northeastern Andean slopes, at least from Provincia Chapare, Departamento Cochabamba, eastward to Provincia Caballero, Departamento Santa Cruz, Bolivia, from 1850–2700 m a.s.l. Endemic to Bolivia.

Natural history: As far known, *Phyllonastes carrascoicola* occurs in the very humid upper montane rainforests adjacent to cloud forest formations. Most individuals were found during the day in leaf litter of the forest, a single specimen was discovered in an epiphytic bromeliad 3–4 m above the ground (De la Riva & Köhler 1998). In December and February in the upper Provincia Chapare, several males called in the morning from the leaf litter, especially during fog, forming choruses like reported by Reynolds & Foster (1992). Females obtained at the end of the dry season had large, unpigmented oviductal eggs, or enlarged empty oviducts indicating that a clutch had recently been laid (De la Riva & Köhler 1998).

Vocalization: Advertisement calls were recorded on 29 January 1999 on the "old" Chapare road, Provincia Chapare, Departamento Cochabamba, 2100 m a.s.l. Calls consisted of a series of 5–8 soft notes (mean 6.0 ± 1.2); call duration varied from 254–436 ms (mean 332.3 ± 62.6); note duration varied from 12–20 ms; notes were repeated in regular intervals at a rate of approximately 16 notes per second; calls were repeated in regular intervals at a rate of approximately 10 calls per minute; call energy was distributed from 2500–5000 Hz; calls showed a upward frequency modulation with the first note having a dominant frequency of approx-

Frequency (kHz)
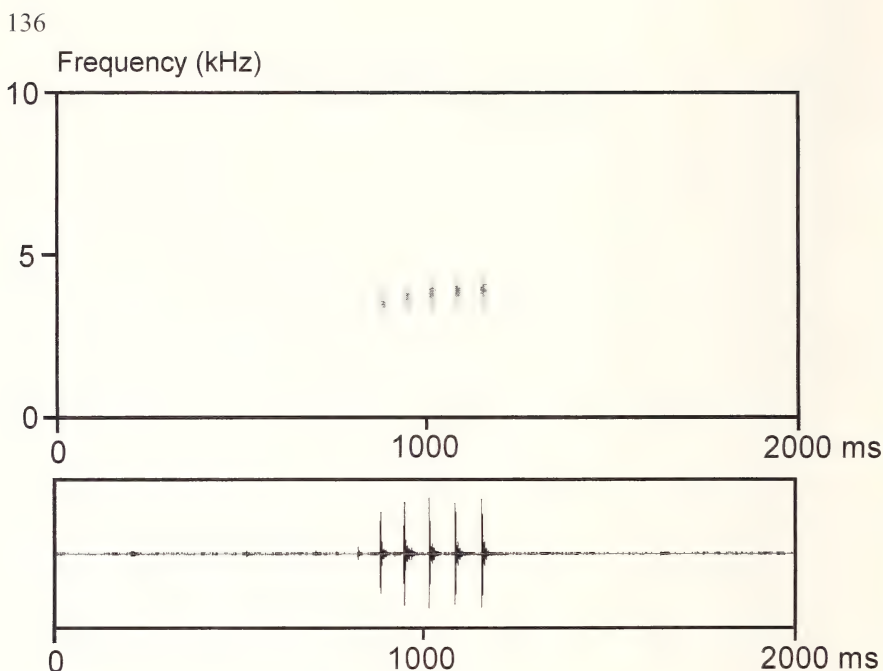
Fig.47: Audiospectrogram and oscillogram of the advertisement call of *Phyllonastes carrascoicola* from Provincia Chapare, 2100 m a.s.l. Recording obtained on 29 January 1999. Air temperature 16.4°C.

imately 3300 Hz and the last one having it at almost 4000 Hz. Sixteen calls of three individuals analyzed; air temperature was 16.4°C during recording.

The call of *Phyllonastes carrascoicola* can be confused with that of the sympatric *Eleutherodactylus llojsintuta*. However, the call of *P. carrascoicola* is softer, has a higher note repetition rate, a higher dominant frequency, a more distinct frequency modulation, and it was emitted only during the day from the ground. Reynolds & Foster (1992) reported low-pitched, clicky, two-note calls in a chorus made up by males from which the specimen USNM 257845 was taken. This description generally coincides with the data presented above, although the calls analyzed were composed of a larger number of notes.

R e m a r k s : When De la Riva & Köhler (1998) described *Phyllonastes carrascoicola*, only six specimens were referable to this species. The status of another specimen (USNM 257845) from the upper Chapare region of Bolivia (also reported by Reynolds & Foster 1992) was discussed but remained questionable. Recent collections at different sites added material in which the variation is as follows. The female type specimens of *Phyllonastes carrascoicola* are all relatively dark colored and exhibit pale white lines middorsally, along the posterior surface of hind limbs, as well as midventrally (the midventral line is missing only in ZFMK 59569). The venter is brown with fine white spotting and dark inguinal spots are

present except in one specimen (De la Riva & Köhler 1998). A more recently collected female from Sehuencas (ZFMK 66829; SVL 14.7 mm) is similar in having relatively dark dorsal color but it lacks a pale midventral line and a pale line on the posterior surface of hind limbs. Ventrally, a white line is present only on the throat. The ventral sides of hind limbs and the outer regions of the belly are distinctly spotted with white and therefore appear pale. A dark brown hourglass-shaped marking is hardly visible on the dorsum. The female ZFMK 71643 (SVL 15.7 mm), collected at 50.5 km on the "old" road from Paractito to Cochabamba, Provincia Chapare, 2100 m a.s.l., exhibits a nearly identical coloration and there remains no doubt that both specimens are conspecific. Two males (CBF [number unknown], ZFMK 66991; SVL 12.3 mm) from the same locality generally exhibit the same pattern when compared with the female, but are much paler. The dorsum is pale brown and ventral surfaces are cream with brown mottling. This color pattern coincides well with the male specimen USNM 257845, collected at a nearby locality (see De la Riva & Köhler, 1998). In contrast, a juvenile specimen (ZFMK 71644; SVL 9.2 mm) from the upper Provincia Chapare has a dark venter and a distinct pale line on the posterior surface of hind limbs like present in the *P. carrascoicola* type specimens from Sehuencas. Dark inguinal spots or flecks are present in all of the recently collected specimens.

Summarizing, there is considerable intrapopulational variation regarding color pattern. At both localities, Sehuencas and the upper Provincia Chapare, specimens occur showing pale lines on dorsum, venter, and/or posterior surface of thighs, as do specimens which lack these lines (or at least part of them) and have a somewhat paler venter. Furthermore, the specimens do not differ in other morphological characters (i.e. condition of digit tips, tympanum, and tubercles). Thus, the only resolved conclusion is that the specimens and populations mentioned above correspond to a single species with intraspecific color variation, *Phyllonastes carrascoicola*. There seems to be sexual dimorphism in *P. carrascoicola*, with the males being smaller and paler colored.

An additional species of minute leptodactylid frog, seemingly related to *Phyllonastes*, has been discovered in the Yungas de La Paz region. This new taxon will be described as a new genus (Harvey & McDiarmid in prep.). It may turn out that *P. carrascoicola* actually is more closely related to this new genus than to other species of *Phyllonastes*.

Phyllonastes ritarasquinae Köhler, 2000   Plate VIh, p.144

Distribution: The species is known only from Provincia Chapare, Departamento Cochabamba, Bolivia, 1250 m a.s.l. (Köhler 2000b). Endemic to Bolivia.

Natural history: A single female was discovered being active during the day in leaf litter at the edge of primary forest. It has enlarged, empty oviducts indicating that a clutch had recently been laid. Nothing else is known.

Vocalization: Unknown.

Physalaemus albonotatus **(Steindachner, 1863)** Plate VIId, p.160

Distribution: The species is known to occur in central and northern Argentina, Bolivia, Paraguay, and Brazil (Mato Grosso and Mato Grosso do Sul) (Frost 1985, Langone 1994). The distribution area comprises elevations of approximately 200–1400 m a.s.l.

Natural history: *Physalaemus albonotatus* inhabits open areas in dry and semi-deciduous forests, as well as Cerrado formations. Reproduction takes place at the beginning of the rainy season, mostly in ephemeral ponds. Males called from the water surface, often covered by grassy vegetation and therefore difficult to detect. Foam nests were deposited on the water surface attached to plants. De la Riva (1993d) described the biology of a population from Puerto Almacén, Departamento Santa Cruz.

Vocalization: Advertisement calls were recorded on 15 December 1997 west of Vaca Guzman, Provincia Luis Calvo, Departamento Chuquisaca, 1340 m a.s.l. Calls consisted of long pulsatile, amplitude modulated notes; call duration varied from 1590–1897 ms (mean 1704.4 ± 82.1); calls were repeated at regular intervals at a rate of approximately 13.7 calls per minute; frequency was distributed between 350 and 3300 Hz, with seven harmonic frequency bands recognizable; a
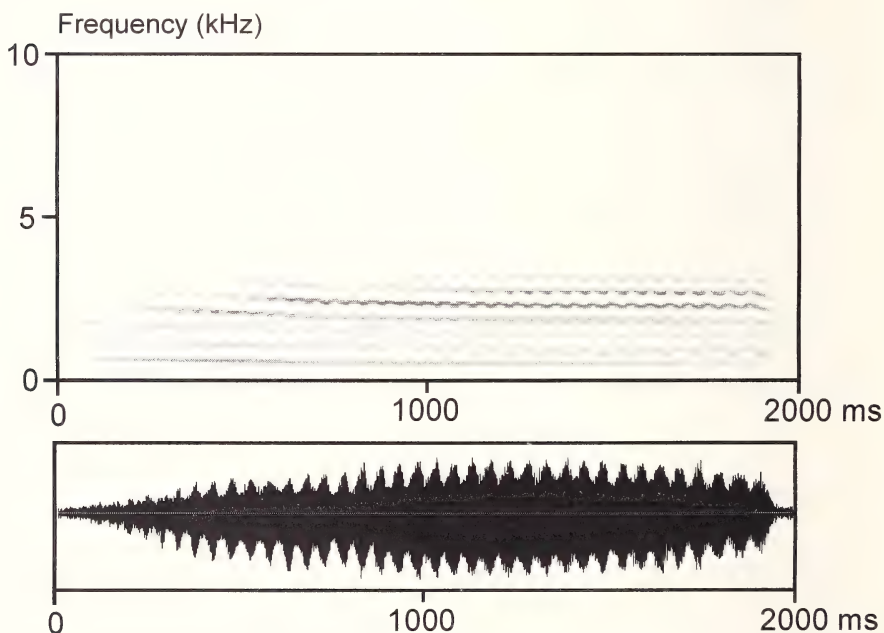
Fig.48: Audiospectrogram and oscillogram of the advertisement call of *Physalaemus albonotatus* from west of Vaca Guzman, 1340 m a.s.l. Recording obtained on 15 December 1997. Air temperature 20.0°C.

dominant frequency peak was present at 2230 Hz. Ten calls of one individual analyzed; air temperature 20.0°C at time of recording. Call duration might vary considerably between individuals. On 16 December 1997 an individual recorded at the same locality emitted calls with a mean duration of approximately 950 ms only. In other characteristics these calls did not differ to those described above.

The data coincide very well with those published by Márquez et al. (1995) for a population from northern Departamento Santa Cruz, Bolivia, as well as with those from Argentinean populations reported by Barrio (1965c).

Physalaemus biligonigerus (Cope, 1861)   Plate VIIe, p.160

Distribution: The species is known from Uruguay, northern and central Argentina, Paraguay, Bolivia, and southern Brazil (Frost 1985, Langone 1994). The elevational range is approximately 200–1400 m a.s.l.

Natural history: *Physalaemus biligonigerus* inhabits open areas within dry Chaco lowland and montane forests as well as Cerrado formations. Reproduction takes place at beginning of the rainy season in ephemeral puddles and ponds. In contrast to *P. albonotatus*, males called while floating on the water surface. Fresh foam nests also were floating on the surface. At some localities, the species was extremely abundant.

Vocalization: Calls were described by Barrio (1965c) and Márquez et al. (1995). In Bolivian populations, the call consisted of single notes with a mean duration of 1049.7 ms and a downward frequency sweep, with a mean dominant frequency peak at 950.6 Hz (Márquez et al. 1995).

Pleurodema cinereum Cope, 1877   Plate VIf, p.144

Distribution: The species is known from the Andes of southern Peru, Bolivia, and northern Argentina (Cei 1980), with an elevational range of at least 1000–4200 m a.s.l. (see remarks).

Natural history: *Pleurodema cinereum* occurs in a wide range of different habitats, including Puna, inter-Andean dry-valleys, semi-deciduous forests of the eastern Andean slopes, and partly enters humid montane forests. Males were observed calling at the edge of ephemeral puddles floating on the water surface at the beginning of the rainy season. Foam nests were deposited on the surface, mostly attached to vegetation at the edge. Populations in the Bolivian Altiplano were active during the day, whereas populations from lower elevations exclusively were observed active at night. This can be explained by low nightly temperatures occurring in the highlands, not allowing any activity (Köhler et al. 1995b). Christmann (1995) provided data on the reproduction of specimens from Samaipata, Departamento Santa Cruz, kept in captivity, and Hulse (1979) reported biological data of Argentinean populations.

Vocalization: Advertisement calls were recorded on 7 January 1998 southeast of Guadalupe, Provincia Vallegrande, Departamento Santa Cruz, 1650 m a.s.l. Calls consisted of single pulsatile notes, repeated at a rate of 79–180 calls per minute (mean 136.3 ± 45.7); note duration varied from 86–112 ms (mean 98.4 ± 9.7); notes were composed of 13–15 pulses, repeated at a rate of approximately 110 pulses per second; the inter-pulse intervals were shorter between the terminal pulses of some calls; call energy was distributed in a broad band from 50–8000 Hz; a dominant frequency peak was recognizable at 760 Hz. Fourteen calls of two individuals analyzed; water temperature was 21.4°C during recording.

These calls coincide relatively well with the data provided by Márquez et al. (1995) for a population from Tiraque, Departamento Cochabamba. Differences are recognizable only with respect to a slightly shorter note duration and a higher pulse rate in my recordings. These differences could be explained by a lower temperature during recording of the Tiraque population (no temperature provided). In addition, Márquez et al. (1995) found the second frequency band at 1530.2 Hz to be dominant. Their given fundamental frequency coincides with the dominant frequency in the recordings described above.

Remarks: Populations from lower elevations of the Andes were suggested to represent *Pleurodema borellii* (Gallardo 1968, Duellman & Veloso 1977, Crump
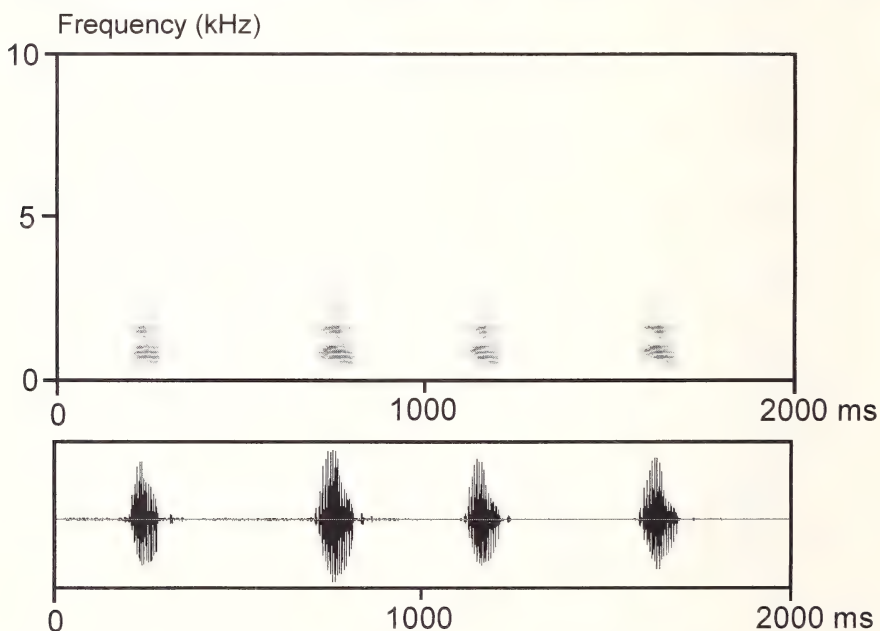
Fig.49: Audiospectrogram and oscillogram of the advertisement call of *Pleurodema cinereum* from southeast of Guadalupe, 1650 m a.s.l. Recording obtained on 7 January 1998. Water temperature 21.4°C (males called while floating on the water surface).

& Vaira 1991), whereas other authors considered *P. borellii* a junior synonym of *P. cinereum* (Parker 1927b, Barrio & Rinaldi de Chieri 1970). At least the populations considered in this study are referable to *P. cinereum* according to advertisement call characteristics. Although morphologically slightly different from highland populations, specimens from west of Vaca Guzman, Departamento Chuquisaca, 1100 m a.s.l., emitted calls equal to those described above or reported by Márquez et al. (1995). This corroborates the molecular results of McLister et al. (1991) who did not find any differences between highland and lowland populations. However, it is not excluded that *P. borellii* might be a valid species occurring at the lower Andean slopes of northern Argentina and possibly also in southern Bolivia.

Telmatobius edaphonastes De la Riva, 1995

Distribution: The species is known only from the La Siberia region at the limits of the Departamentos Cochabamba and Santa Cruz at approximately 2600 m a.s.l. (De la Riva 1995d). Endemic to Bolivia.

Natural history: As far known, only three specimens of *T. edaphonastes* became available from the very humid cloud forests of La Siberia. It seems to be a rare nocturnal and quite terrestrial species of *Telmatobius* having nearly no webbing between the toes. One male was observed calling from a branch of a bush in approximately 1.5 m height (S. Reichle pers. comm.).

Vocalization: De la Riva (1995d) reported a call consisting of 3–4 loud low notes in a rapid succession heard at the type locality which may correspond to the species. A similar call was observed by S. Reichle (pers. comm.).

Telmatobius cf. *simonsi* Parker, 1940   Plate VIIa, p.160

Distribution: The species is known from the inter-Andean valleys of the Bolivian Departamentos Chuquisaca and Cochabamba, as well as from adjacent cloud forests and montane rainforests at the northeastern flank of the Andes in the Departamentos Cochabamba and Santa Cruz. *Telmatobius simonsi* occurs at elevations from 1650–2800 m a.s.l. Endemic to Bolivia.

Natural history: *Telmatobius simonsi* inhabits areas of wet puna and Andean grass lands, as well as upper montane rainforests and cloud forests. Specimens were found at night in roadside ditches and puddles, as well as in small streams. During handling, individuals released an extremely sticky skin secretion.

Vocalization: Unknown.

Remarks: The montane forest populations of *T. simonsi* occur in completely different habitats than the inter-Andean valley populations. Current investigations may reveal that the forest populations correspond to an undescribed species (I. De la Riva pers. comm.) and they are therefore treated as *T.* cf. *simonsi* herein.

Telmatobius yuracare De la Riva, 1994   Plate VIIb, p.160

D i s t r i b u t i o n : The species is distributed at the eastern versants of the Bolivian Andes between Provincia Chapare, Departamento Cochabamba, and Provincia Caballero, Departamento Santa Cruz. It is known from elevations of 2000 to nearly 3000 m a.s.l. (De la Riva 1994a). Endemic to Bolivia.

N a t u r a l h i s t o r y : *Telmatobius yuracare* occurs in streams of the upper montane rainforests and cloud forests. It seems to be primarily aquatic moving on the ground of streams and adjacent pools (De la Riva 1994a), although individuals have been found apart from rivers moving on the ground during rain (Köhler et al. 1995a). During handling, individuals left a sticky secretion (De la Riva 1994a, Köhler et al. 1995a). The tadpole was described by De la Riva (1994a).

V o c a l i z a t i o n : Advertisement calls are unknown, but soft harmonic notes were emitted during handling of individuals (De la Riva 1994a, Köhler 1995a, Köhler et al. 1995a).

Telmatobius species A   Plate VIIc, p.160

D i s t r i b u t i o n : The species is known from the La Siberia region at the limits of the Departamentos Cochabamba and Santa Cruz (Provincias Carrasco and Caballero), as well as from north of San Juan del Potrero, Provincia Florida, Departamento Santa Cruz. The known distribution comprises elevations from approximately 2000–2550 m a.s.l. Endemic to Bolivia.

D i a g n o s i s : *Telmatobius* sp. A differs from other members in the genus by the following combination of characters: a well marked pattern on dorsum and head; horny spicules and pustules of different sizes on dorsum; sole of foot smooth. The species is most similar to *T. simonsi* from which it mainly differs by a smooth sole of foot and a well patterned dorsum.

N a t u r a l h i s t o r y : *Telmatobius* sp. A inhabits upper montane rainforests as well as cloud forests. It seems to be a quite terrestrial species. Specimens were found under rocks at day or near roadside ditches at night. Juveniles and subadults were found in early January 1998. A single male was discovered in a water-filled cattle footprint together with a mass of large, gray eggs (I. De la Riva unpubl.).

V o c a l i z a t i o n : Calls consisting of a series of low, fast repeated notes were recognized but not recorded (I. De la Riva unpubl.).

R e m a r k s : This species is being described by I. De la Riva and M. Harvey (pers. comm.).

Microhylidae

Elachistocleis bicolor (Valenciennes, 1838)   Plate VIIg, p.160

D i s t r i b u t i o n : The species occurs in central and northern Argentina, Paraguay, Amazonian Brazil, Bolivia, and southeastern Peru (e.g., Frost 1985, De la Riva

1990a, Henle 1992, Reichle & Köhler 1998, Köhler & Lötters 1999b). Specimens referable to *E. bicolor* are known from elevations of 100–1130 m a.s.l. (Köhler 1995b).

Natural history: *Elachistocleis bicolor* inhabits a wide range of habitats, including Cerrado formations, dry Chaco forests, seasonal Amazonian rainforests, savannas, semi-humid lower montane forests of the Andean slopes, as well as various transition zones in-between. It is an explosive breeder, reproducing in ephemeral ponds and puddles, or close to small lagoons. Eggs are deposited as a single layer on the water surface. At day, specimens were discovered under fallen logs.

Vocalization: Advertisement calls from Bolivian populations (Puerto Almacén, Departamento Santa Cruz) have been described by De la Riva et al. (1996b). Calls consisted of a sustained chirp, with a mean dominant frequency of 5741.3 Hz; call duration varied from 1546.2–1949.1 ms. Generally, the call is higher pitched than that of *E. ovalis* (see below).

Remarks: There is much taxonomic confusion concerning the two species names *bicolor* and *ovalis* within the genus *Elachistocleis* (see discussion in Frost 1985). Like Köhler (1995b), De la Riva et al. (1996b), Reichle & Köhler (1998), and Köhler & Lötters (1999b) formerly did for Bolivian populations, specimens with immaculate yellow venter are assigned to *E. bicolor*.

Elachistocleis ovalis (Schneider, 1799)   Plate VIIh, p.160

Distribution: The species is known to occur from Panama throughout the South American lowlands east of the Andes, southward to central Argentina and Uruguay (e.g., Frost 1985, Langone 1994). *Elachistocleis ovalis* is distributed in lowland regions as well as inter-Andean valleys. During this study, specimens referable to this species were discovered at 2150 m a.s.l. (P.N. Amboró, Provincia Florida, Departamento Santa Cruz).

Natural history: *Elachistocleis ovalis* inhabits a wide range of different habitats as is obvious from its wide distribution range. In contrast to *E. bicolor*, it was frequently observed in forest habitats. Males called at night from the water surface close to grassy vegetation. Amplectant pairs were observed at beginning of December, tadpoles were obtained in January in stages 25–34 (sensu Gosner 1960). Like *E. bicolor*, *E. ovalis* is an explosive breeder having a similar habit.

Vocalization: Advertisement calls were recorded on 9 December 1997 west of Río Seco, Provincia Cordillera, Departamento Santa Cruz, 900 m a.s.l. Calls consisted of a very long pulsatile note, with a duration of 2044–3037 ms (mean 2618 ± 438); pulse repetition rate within notes was approximately 245 pulses per second; call energy was distributed between 2800 and 4300 Hz, with a dominant frequency peak of 3630 Hz; a slight upward frequency modulation was present at beginning of the calls; due to the pulsatile nature, parallel harmonic frequency
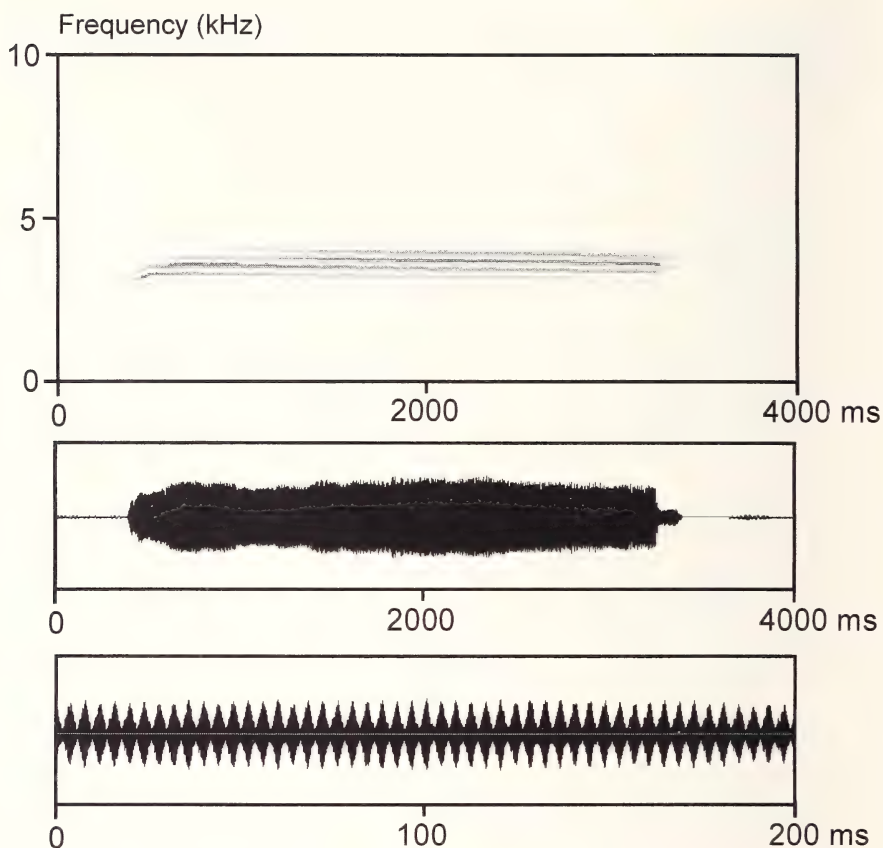
Fig.50: Audiospectrogram and oscillograms of the advertisement call of *Elachistocleis ovalis* from west of Río Seco, 900 m a.s.l. Recording obtained on 9 December 1997. Air temperature 22.3°C.

bands were recognizable; calls were emitted at an approximate rate of 3.7 calls per minute. Four calls of one individual analyzed; air temperature was 22.3°C at time of recording.

Plate VI: **a)** *Leptodactylus chaquensis* Cei, 1950, male, W of Vaca Guzman, 1360 m; **b)** *Leptodactylus gracilis* Duméril & Bibron, 1841, male, SE of Guadalupe, 1650 m; **c)** *Leptodactylus griseigularis* (Henle, 1981), male, Provincia Chapare, 1300 m; **d)** *Leptodactylus leptodactyloides* (Andersson, 1945), male, Macuñucu, 500 m; **e)** *Leptodactylus rhodonotus* (Günther, 1869), male, Provincia Chapare, 500 m; **f)** *Pleurodema cinereum* Cope, 1877, male, La Hoyada, 1700 m; **g)** *Phyllonastes carrascoicola* De la Riva & Köhler, 1998, female, Provincia Chapare, 2100 m; **h)** *Phyllonastes ritarasquinae* Köhler, 2000, female, Provincia Chapare, 1250 m.

Plate VI

Calls of *E. ovalis* from Puerto Almacén, Departamento Santa Cruz, described by De la Riva et al. (1996b) differ only with respect to a shorter call duration which was found to be quite variable in different individuals. The data above also coincide well with calls from Serra da Canastra, Minas Gerais, Brazil (Haddad et al. 1988). Nelson (1973) described several calls of *Elachistocleis* from various Latin American localities. His data show remarkable variation concerning call duration and frequency. However, the calls from west of Río Seco fall within the variation of the calls présented by Nelson (1973).

Remarks: The record of specimens in an area of cloud forest at 2150 m a.s.l. appears quite unusual for the species. Unfortunately, no males of this population were calling. Although morphologically very similar to other Bolivian populations, it seems at least possible that another cryptic species is involved. Both species, *E. bicolor* and *E. ovalis*, were found in sympatry at several Bolivian lowland sites (De la Riva et al. 1995b, Reichle 1997b). See also remarks for *Elachistocleis bicolor*.

Chiasmocleis albopunctata (Boettger, 1885)   Plate VIIf, p.160

Distribution: The species is known to occur in central Brazil (Goiás, Mato Grosso, São Paulo), Paraguay, and eastern Bolivia (Frost 1985) at elevations from 100–950 m a.s.l.

Natural history: The species inhabits semi-deciduous forests, open Cerrado formations, as well as semi-humid Amazonian transition forests. Reproduction takes place from November to March, throughout the rainy season (De la Riva 1993d). Specimens were found at night during light rain, partly submerged at the edge of puddles and ponds. They always were observed grasping grassy vegetation, never floating free on the water surface.

Vocalization: Advertisement calls were described from Puerto Almacén, Departamento Santa Cruz, Bolivia. They consisted of short, irregular pulsed notes combined to long call groups (more than 23 seconds nonstop). Calls had a mean duration of 51.9 ms, a pulse repetition rate of 110.9–212.8 pulses per second, and a mean dominant frequency of 4431.5 Hz. Calls were repeated at a rate of 584.8–907.7 calls per minute (De la Riva et al. 1996b).

URODELA

Plethodontidae

Bolitoglossa species A

Distribution: This species is known from Provincia Chapare, Departamento Cochabamba, at elevations between 460 and 1000 m a.s.l. (Wake et al. 1982 as *B. altamazonicus*). A recent record from Mataracú, Provincia Ichilo, Departamento

Santa Cruz, 500 m a.s.l. may also correspond to this species (see remarks). Most probably endemic to Bolivia.

Natural history: Individuals were found at night on a leave at approximately 0.5 m height and in a pitfall trap, respectively (Reichle et al. in press).

Remarks: Bolivian specimens of *Bolitoglossa* formerly referred to as *B. alta-mazonicus* by Wake et al. (1982) actually represent an undescribed species (D.B. Wake pers. comm.). There are some arguments supporting the view that the specimen from Mataracú represents another species distinct from the Chapare populations (Reichle et al. in press). However, until the taxonomic status of the mentioned populations is solved they are regarded as a single taxon herein.

A transect model

To obtain an imagination of distribution and diversity patterns of amphibians inhabiting montane forest regions, the sites studied in particular were chosen along three almost virtual transects within the eastern versant of the Andes. This three transects include elevational gradients as well as different longitude and latitude. The schematic figure 51 shows the principal locations of these transects (for more detailed descriptions of the single sites investigated see Study area, investigated sites; voucher specimens are listed in the appendix). Due to partly very difficult access of montane forest areas, these transects were not thoroughly sampled at all elevations, with the exception of the Chapare region (transect 1). However, I tried to compensate lacking data through the inclusion of literature information about species distributions. Obviously, this is only an insufficient method and surely many results remain undiscovered until further fieldwork will take place. Therefore, this transect study has to be regarded as a helping model which simplifies the description of actually existent patterns.

The Chapare transect (1) roughly equals the Río San Mateo valley which is located at the borders of Provincia Chapare and Provincia Tiraque in the Departamento Cochabamba. Access to this area is facilitated by the existence of an old road which connected Paractito at the Andean foot via the village El Palmar with the town of Cochabamba. Therefore, the data for this transect all resulted from own fieldwork. The Amboró transect (2) actually contained most of the sites investigated. However, due to very difficult access of the core zone of the Amboró National Park, fieldwork was limited to sites which are relatively close to the park boundaries. As a consequence, data from mid-elevations (1100–1700 m a.s.l.) are partly lacking. Beside other publications, Lavilla et al. (1996) provided some results from herpetofaunal studies in the same area in an unpublished report. However, parts of the records provided in the tables are seemingly in error. Thus, only the reliable records have been included. The Río Seco transect (3) has an east-west extension approximately along 18°30' S latitude and its lower end root-
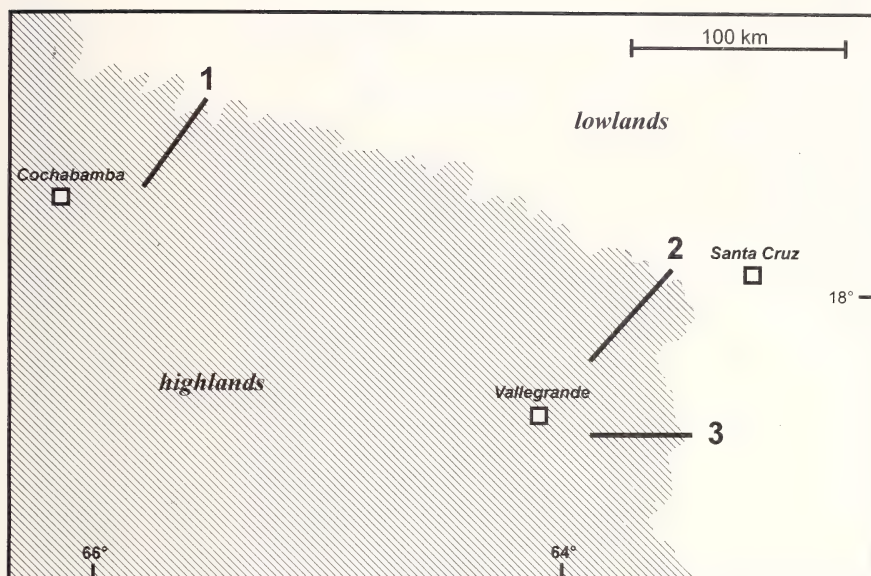
Fig.51: Schematic map of the study area showing part of the Bolivian Andes and principal locations of the transects considered in the analysis: 1 – Chapare transect; 2 – Amboró transect; 3 – Río Seco transect. Shaded area indicates elevations above 1000 m a.s.l.

ed in the village Río Seco. Sites within this transect were investigated at most elevations, with the exception of the lowermost part (500 m a.s.l.). Here, I mainly profited from recently published results by Gonzáles (1998).

Chapare transect

In total, 36 amphibian species were found above 500 m a.s.l. along the transect and additional three species which I was unable to rediscover were recorded previously from the same general area (e.g., Reynolds & Foster 1992, Wake et al. 1982). Not included are species found at 500 m a.s.l. but not distinctly exceeding this elevation (i.e., *Bufo "typhonius"*, *Hyla lanciformis*, *Osteocephalus buckleyi*, and *Rana palmipes*).

The amphibian fauna in the montane forests of the Chapare region is largely dominated by leptodactylids (19 species), especially of the genus *Eleutherodactylus* (11 species), followed by bufonids and hylids. For comparison, at Amazonian lowland sites hylid frogs make up the greatest species numbers (e.g., De la Riva 1993d, Rodríguez & Duellman 1994). The fauna is composed of species exclusively inhabiting humid montane forests (19 of them are endemic to Bolivia) and lowland species which enter the forests of the Andean foothills and the lower

148
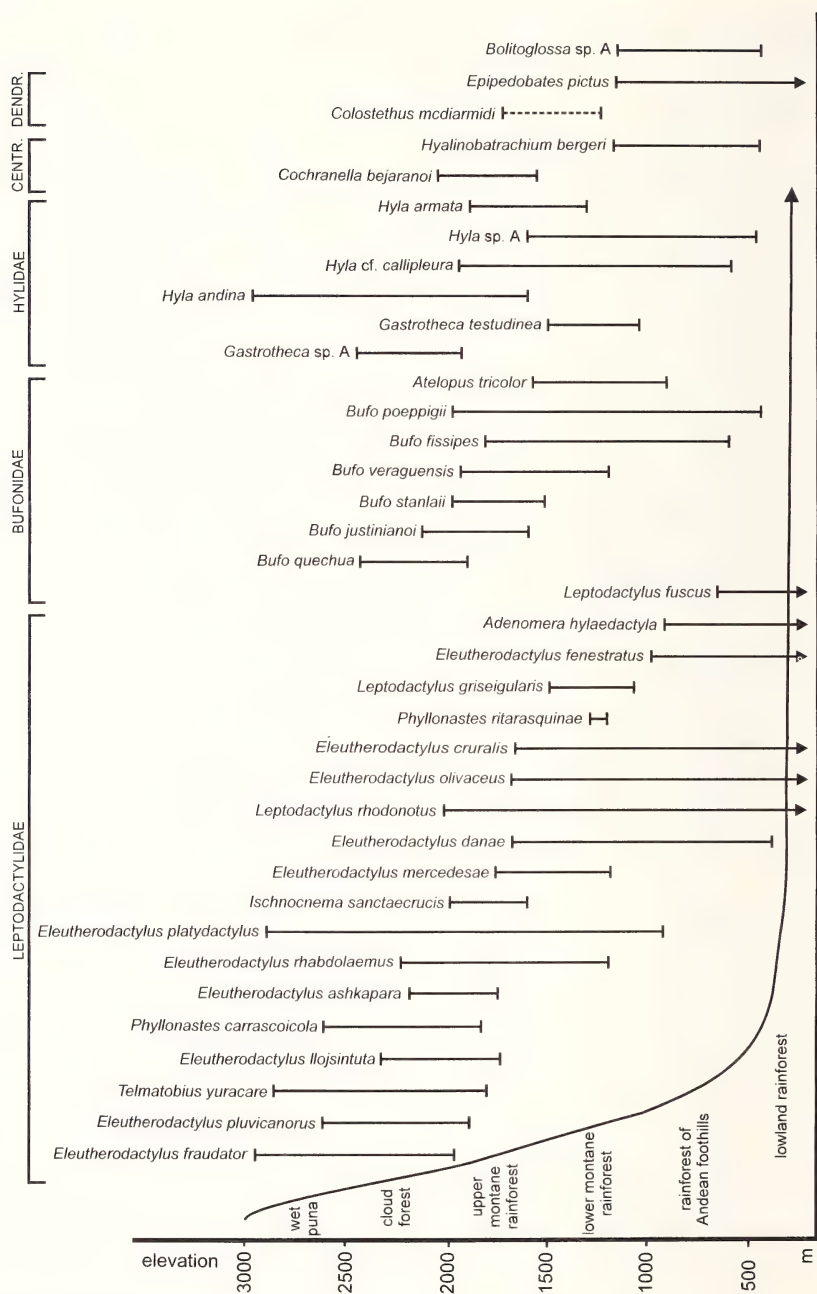
Fig.52: Schematic cross-section diagram of the Chapare transect showing the recorded species and their approximate elevational ranges indicated by vertical bars.

montane rainforests (i.e., *Epipedobates pictus, Adenomera hylaedactyla, Eleutherodactylus fenestratus, Leptodactylus fuscus*). Some species appear to be primarily linked to montane forests but they may partly enter the peri-Andean forests of the lowlands (i.e., *Bufo poeppigii, Hyalinobatrachium bergeri, Hyla* sp. A, *Eleutherodactylus cruralis, E. olivaceus, Leptodactylus rhodonotus*). Of the 32 montane forest species, 13 occur exclusively above 1500 m a.s.l. Eleven of the species seem to have ranges which cover less than 1000 m elevational difference, whereas only three species occur over a range of distinctly more than 1500 m. However, every frog family with the exception of the Dendrobatidae has representative species at almost all elevations between 500 and 2500 m a.s.l. Figure 52 provides a summary of the recorded species and their approximate elevational ranges.
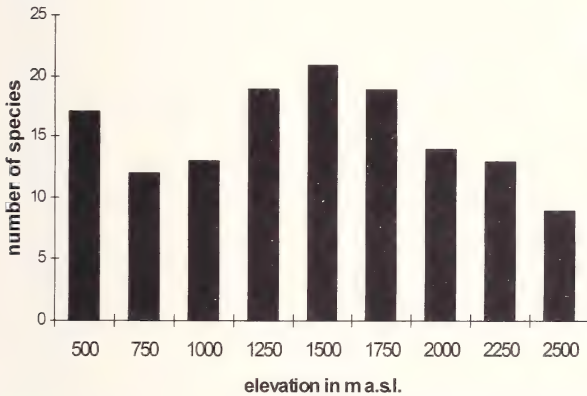
Fig.53: Diagram showing the number of species found at different elevations within the Chapare transect.

The greatest number of species can be found between 1200 and 1700 m a.s.l. (Fig.53), an area where species from upper and lower montane forests meet to form species-rich communities. However, six species seem to be more or less restricted in their occurrence to these mid-elevations. The frog community at approximately 1600 m a.s.l. was composed of 17 species and four more species are highly expectable to occur there as well. This would result in at least 21 species which constitutes a remarkable diversity, especially when considering that at this elevation lentic waters (i.e., ponds and puddles) are lacking. This excludes all amphibian species which are in need for such waterbodies to reproduce. In fact, the species found are either independent from waterbodies and have presumably direct terrestrial development (*Eleutherodactylus, Ischnocnema, Phyllonastes*) or they are able to deposit their eggs in or close to lotic water where the tadpoles develop (bufonids, hylids, and *Leptodactylus*).

Frogs of the genus *Eleutherodactylus* appear not only to be the most species-rich group in the Chapare transect but also the most abundant genus concerning individuals. Species found to be abundant are especially *Eleutherodactylus cruralis, E. danae, E. olivaceus, E. platydactylus*, and *E. rhabdolaemus*, whereas *E. mer-*

cedesae seems to be rather rare (at least during the rainy season). Of the other species, *Bufo veraguensis*, *B. fissipes*, *Hyla* cf. *callipleura*, and *H.* sp. A were commonly observed. Only single specimens were obtained of *Leptodactylus griseigularis*, *Ischnocnema sanctaecrucis*, and *Phyllonastes ritarasquinae*. In general, the trend that species equability is lower at higher elevations seems to be also true for the Chapare transect. At lower elevations, almost all species were observed in similar numbers, whereas above 2000 m a.s.l. one species (*Eleutherodactylus platydactylus*) is clearly dominating (compare Scott 1976).

When looking at the community structure of the different sites within the transect, it becomes obvious that some species are apparently replaced by others when going up or down the elevational gradient. For example, *Gastrotheca* sp. A occurs at elevations approximately between 1800 and 2700 m a.s.l., whereas *Gastrotheca testudinea* occurs at lower elevations (1100–1500 m a.s.l.). Similar cases are probably those of *Phyllonastes carrascoicola* and *P. ritarasquinae*, and *Hyla andina* and *H.* cf. *callipleura*. Although the latter two species occur in sympatry at approximately 1700–1800 m a.s.l., their ranges do not broadly overlap and *H.* cf. *callipleura* was found down to 700 m a.s.l. Summarizing, there is a limited species-turnover along the elevational gradient, although every community studied also contained common species which have large elevational ranges (e.g., *Eleutherodactylus cruralis*, *E. platydactylus*, *E. rhabdolaemus*, *Leptodactylus rhodonotus*), so that differences in community composition at different elevations are not abrupt but sliding.

Amboró transect

In total, 48 amphibian species were considered to be distributed distinctly above 500 m a.s.l. within the Amboró area, with 20 of them being endemic to Bolivia. At the northern boundary of the Parque Nacional Amboró many lowland distributed species enter the lowermost Andean slopes slightly exceeding 500 m a.s.l. (e.g., *Bufo marinus*, *Hyla acreana*, *H. boans*, *H. lanciformis*, *Osteocephalus buckleyi*, *Phyllomedusa vaillanti*, *Eleutherodactylus dundeei*, *Lithodytes lineatus*, *Physalaemus petersi*, *Hamptophryne boliviana*). These species are not included here as montane forest species, but they were considered in the comparative analysis of other sites within the upper Amazon basin (see later). The number of 48 species in this transect is fairly greater than the number of species recorded from the Chapare transect. The difference is at least partly due to the larger number of sites sampled in the Amboró transect as well as to the larger area covered by these sites.

On the other hand there are several arguments supporting real differences in diversity. The Amboró transect covers a very unique area characterized by the presence of contact zones between different ecoregions. At the northern limit of the area, in the lowlands, Amazonian forests contact with semi-deciduous Chiquitanía forests

and at the southern limit humid montane rainforests and cloud forests contact with inter-Andean dry-valleys and semi-humid Tucumanian-Bolivian montane forests. These conditions are responsible for distinctly different species communities which can be found within very short distances and which do partly interdigitate (see also Köhler et al. 1995b, Köhler et al. 1998b). When looking at the elevational distribution of the 48 species, 37 of them occur at 1900–2200 m a.s.l., 27 at 500 m a.s.l., and 22 at 1300–1600 m a.s.l. This is an obviously different situation compared to that in the Chapare transect, where the largest species numbers are present at 1300–1600 m a.s.l. However, as already stated in the introduction, the lacking data from the core area of the Parque Nacional Amboró are undoubtedly responsible for this result which has most probably to be regarded as an artifact. Second, in contrast to the Chapare transect, more sites were sampled at the upper elevations including different ecoregions (only one site at a certain elevation sampled in the Chapare transect). That means, the 37 species found at 1900–2200 m a.s.l. do not occur together at a single site as do the 14 species at 1850 m or the 13 species at 2150 m a.s.l., respectively, in the Chapare transect. The greatest species number found between 1900 and 2200 m a.s.l. at a single site in the Amboró transect is 13 ("El Fuerte" near Samaipata, 1900–2000 m a.s.l.). Following species were recorded: *Bufo veraguensis, Cochranella nola, Hyla andina, H. marianitae, H. minuta, Scinax castroviejoi, Phrynohyas venulosa, Phyllomedusa boliviana, Eleutherodactylus samaipatae, Eleutherodactylus* sp. A, *Leptodactylus gracilis, Pleurodema cinereum,* and *Elachistocleis* cf. *ovalis.* Although showing an almost completely different composition, the alpha diversity equals that of the respective Chapare site.

One important difference is the degree of beta diversity at the upper elevations of the Amboró transect. For example, the humid site "La Yunga" (at 2200 m a.s.l.), about 12 km airline apart from mentioned semi-humid "El Fuerte" has the following species composition: *Bufo veraguensis, Cochranella bejaranoi, Gastrotheca* sp. A, *Hyla marianitae, Eleutherodactylus discoidalis, E. pluvicanorus, E. rhabdolaemus,* and *Ischnocnema sanctaecrucis.* Only two species are shared between these two sites. In other words, species composition of sites varies greatly when moving horizontal in east-west direction along the southern limits of the Parque Nacional Amboró (high beta diversity). Similar situations can be found at the northern limits of the park where sites with semi-humid character (e.g., Macuñucu) which beside others harbor species of Chaco-Cerrado distribution are close to those with strong Amazonian influence. Again, the Chapare transect does not contain such a variety of different eco-geographical zones.

Data about species distribution along an elevational gradient are not complete enough to state something about species-turnover rates. It can be expected that the situation along such a gradient is comparable to that found in the Chapare transect (not abrupt but sliding), because both areas share a large number of montane for-

est species which supposedly have similar elevational ranges in both transects, although they occur at different latitude. That means, the beta diversity is great at the upper elevations of the Amboró transect when considering a certain horizontal expanse, whereas the beta diversity along an elevational gradient within a relatively homogeneous ecoregion is comparatively lower.

The abundance of species highly depended on the kind of habitat and site sampled. At pure montane forest sites, the situation was similar to that in the Chapare transect, with the genus *Eleutherodactylus* clearly dominating the anuran fauna (especially *E. cruralis, E. platydactylus, E. pluvicanorus*, and *E. rhabdolaemus*). At sites closer to the influence of adjacent inter-Andean dry-valleys, species adapted to a distinctly seasonal environment, i.e. by depositing large numbers of eggs in or at temporary ponds, dominated during the rainy season. One of such interesting sites is La Hoyada (1700–1800 m a.s.l.) where the following 15 anuran species were recorded: *Bufo veraguensis, B. stanlaii, Cochranella bejaranoi, C. nola, Hyla armata, H. marianitae, H. minuta, Scinax castroviejoi, Phyllomedusa boliviana, Eleutherodactylus cruralis, E. platydactylus, Ischnocnema sanctaecrucis, Leptodactylus rhodonotus, Pleurodema cinereum*, and *Telmatobius* cf. *simonsi*. Of these, the pond breeders appeared more abundant by far, forming large choruses around ponds or ephemeral puddles.

Such phenomenon was not observed along the Chapare transect, because the steep Río San Mateo valley almost completely lacks lentic waters. In contrast, almost every sampled site in the Amboró transect provided different kinds of freshwater (i.e., ponds, ephemeral puddles, streams, small brooks), resulting in a larger variety of available habitats. On the other side, it is somehow surprising that the larger diversity in available (breeding) habitats is not connected with a higher degree in alpha diversity.

Río Seco transect

In total, 31 amphibian species were considered being distributed distinctly above 500 m a.s.l. along the Río Seco transect. Of these, only three species are currently considered to represent Bolivian endemics. At the upper elevations at the western end of the transect, highland species or more precise those species considered to represent elements of the inter-Andean dry-valleys are dominating. The lower elevations are populated by lowland species which have the ability to enter the Chaco montane forest at the eastern Andean slopes. Species composition at mid-elevations constitutes of species having their main distribution in inter-Andean dry-valleys and species from the arid lowlands, as well as species which are regarded as elements of the Tucumanian-Bolivian montane forests.

Approximate species richness at 500 m a.s.l. is 19 species, 22 species occur at 1100–1600 m a.s.l., and again 19 species at 1900–2200 m a.s.l. That means,

species richness is almost equally distributed along the elevational gradient, with seemingly some emphasize at the mid-elevations (compare Chapare transect).

A remarkable fact is the occurrence of pretended lowland species at the upper limit of the transect. The species *Hyla minuta, Phrynohyas venulosa, Leptodactylus gracilis*, and *Elachistocleis* cf. *ovalis* are known from the Chacoan lowlands, but they also occur in semi-humid and semi-arid climates up to 2000 m a.s.l. in the Bolivian Andes, where they apparently reach their upper limit of vertical distribution (see also Köhler et al. 1995b, Köhler & Lötters 1999c). Moreover, I was a little bit surprised to find other lowland species entering the slopes up to 1000 m a.s.l. (i.e., *Leptodactylus labyrinthicus, Chiasmocleis albopunctata*) or even as high as 1400 m a.s.l. (i.e., *Bufo paracnemis, Leptodactylus chaquensis, Physalaemus albonotatus, P. biligonigerus*). The latter findings argue for close relationships of the Chaco lowland forests and the Chaco montane forests. As long as suitable breeding sites are available, the mentioned lowland species are able to populate at least the Chaco montane forests. Species with an apparently predominant montane forest distribution recorded from the area are *Cochranella bejaranoi, Hyla marianitae, Gastrotheca* sp. A*, Phyllomedusa boliviana, Eleutherodactylus discoidalis, E. samaipatae*, and *Eleutherodactylus* sp. A. When traveling along the elevational gradient, species-turnover is of limited degree. Also at certain horizontal distances the change in species composition is limited. The slopes of the Río Seco transect seem to harbor amphibian faunas being similar in composition over larger distances when compared to those of the other two, more humid transects. Probably, a distinct zonation of climates at different elevations (at least in part responsible for differences in community structure) is more developed in the humid Amboró and Chapare transects than in the more arid region of the southern Río Seco transect (see Study area, climate). Another important factor may be the much stronger influence of cold southern winds ('surazos') at the Río Seco sites. These may be responsible for a less distinctly developed temperature gradient along the slopes, resulting in a more homogeneous environment (which nevertheless is strongly seasonal).

Nearly nothing can be stated about abundance of species. The majority of species is adapted to distinct seasonal differences in rainfall. Usually, individuals appear in large numbers during the first heavy rains of the summer season, aggregating at temporary ponds for reproduction. Mostly, there is very few activity without rainfall. However, a remarkable observation might be that obtained on the 15 December 1997 at an artificial lagoon west of Vaca Guzman, 1360 m a.s.l. At an estimate, the lagoon's surface was approximately 6000 m^2. At this lagoon, I found the following species: *Bufo arenarum, B. paracnemis, Hyla minuta, Scinax fuscovarius, Phrynohyas venulosa, Phyllomedusa boliviana, Leptodactylus chaquensis, Physalaemus albonotatus, P. biligonigerus, Pleurodema cinereum*, and *Elachistocleis* cf. *ovalis*. By far, the most abundant species at that night were *Scinax fuscovarius, Physalaemus biligonigerus* and *Pleurodema cinereum* making

it practically impossible to walk at the lagoon's edge without stepping on frog individuals. Undoubtedly, I observed several thousand individuals at this night, but only one single calling male of *Hyla minuta*. The next morning, I found several dead individuals (most of them *S. fuscovarius* females) floating on the water surface between large masses of eggs (death probably caused by too many males grasping the females). Such a massive appearance of individuals combined with explosive breeding activity may also be caused by the other species which were less abundant during the mentioned observation. The factors leading to such a phenomenon are complex and not predictable (e.g., Schlüter 1984, Duellman 1995).

Ecological comparisons

Beside pure alpha and beta species diversity, ecological diversity is considered another important part of biodiversity. Regarding amphibians, activity patterns (diurnal, nocturnal, or both), habitat use, and reproductive modes have been considered important characters to describe ecological diversity and community structure (e.g., Duellman 1978c, 1989, 1990, Heyer et al. 1990, Hödl 1990). Heyer et al. (1990) defined ecological guilds taking into account the preferred habitat, diurnal or nocturnal activity, and the way how prey is obtained (actively foraging predators versus sit-and-wait predators). The study conducted by Heyer et al. (1990) included long-term fieldwork at a single site, thus many more observations were obtained on the biology of single species than in the present work. Especially, only sparse data whether species are actively foraging or sit-and-wait predators were obtained. Therefore, I do not use the guilds defined by Heyer et al. (1990), but consider activity pattern, habitat use, and reproductive modes separately.

The table 3 provides an overview about ecological categories found in the communities of the three transects. Given are the numbers of species found to fit in certain defined modes, each at the different elevational levels and for the whole transect. At the level of 500 m a.s.l., all the species found in the community were considered, even if not regarded to represent montane forest species. The sums of total numbers given for habitat use are partly larger than the number of species recorded, because some species were not restricted to a single type of habitat. Species considered to have direct terrestrial development include *Adenomera hylaedactyla*, although in contrast to eleutherodactylines and *Gastrotheca testudinea*, the species builds foam nests and has a stage of non-feeding tadpoles. *Adenomera diptyx* was demonstrated to reproduce like members of the *Leptodactylus fuscus* group (De la Riva 1995b).

Activity

In all three transects, species with strictly nocturnal activity are clearly dominating at all elevational levels (Chapare transect: 63%; Amboró transect: 78%; Río

Table 3: An overview about different ecological categories and their distribution within the transects. Species numbers are given for each of the three elevational levels and for the transect in total. The sum of total species numbers for the 500 m level may be greater than the number of species considered in the distribution analysis. Here, all species found at 500 m a.s.l. were considered, even if not distinctly distributed above this elevational level, because all the species are part of the ecological community. For further explanation see text.

Meters above sea level	Chapare transect				Amboró transect				Rio Seco transect			
	500	1300–1600	1900–2200	total	500	1300–1600	1900–2200	total	500	1100–1600	1900–2200	total
Activity												
strictly diurnal	1	3	2	4	2	–	3	5	–	–	–	–
strictly nocturnal	12	16	14	24	25	17	30	52	18	20	15	27
nocturnal, but sometimes diurnal	2	3	6	10	5	5	5	10	1	3	4	6
Habitat Use												
ground	8	9	7	20	17	11	16	29	15	14	8	19
understory	5	11	11	18	12	10	17	31	4	9	11	12
canopy	2	2	1	3	3	2	–	4	–	–	–	–
(semi-)aquatic	–	1	1	2	–	–	3	3	–	–	–	–
Reproductive Modes												
direct terrestrial development	7	12	10	17	8	6	11	16	–	2	3	3
eggs in foam nests, tadpoles in water	2	2	1	3	4	3	4	7	8	8	3	10
egg deposition in lotic water	7	11	9	12	2	6	12	11	–	2	3	4
egg deposition in lentic water	2	–	1	3	13	1	3	13	10	8	8	11
backpack strategy, tadpoles in water	1	–	1	2	1	1	2	3	–	–	1	1
egg deposition above water	1	2	1	2	3	3	3	5	–	1	2	2

Seco transect: 82%). The Río Seco transect completely lacks diurnal species and in all transects species which are mainly nocturnal but also show facultative diurnal activity are more numerous than strictly diurnal species. Facultative diurnal activity, was observed in several species of *Eleutherodactylus* (i.e., *E. cruralis, E. dundeei, E. platydactylus, E. pluvicanorus, E. rhabdolaemus, E. samaipatae, E.* sp. A), *Adenomera* species, and *Bufo quechua*. Whereas males of some species only called in the late afternoon or at dusk, others were observed being active during the whole day (e.g., *Adenomera* spp., *Eleutherodactylus dundeei, E. cruralis, E. rhabdolaemus*). Diurnal activity in anurans is at least partly correlated with the presence of sufficient moisture. During day time, especially within exposed sunlight, the danger of dehydration is undoubtedly higher than during night at lower temperatures and reduced evaporation. This is probably one of the reasons for the lack of diurnal active species in the more arid Río Seco transect, as well as for relatively high degree of diurnal or partly diurnal species in the very humid Chapare transect (37%). In addition, there seems to be a trend of increasing facultative diurnal activity with increasing elevation along the slopes which is possibly correlated with higher amounts of precipitation. The domination of nocturnal species agrees with the results of other studies carried out at lowland sites (e.g., Duellman 1989), although diurnal species of the family Dendrobatidae are usually much more numerous at lowland sites than in the montane forests investigated herein.

Habitat Use

Available habitats are an important resource, especially when considering the need of water bodies for anuran reproduction. Usually, in tropical communities calling male frogs can be found relatively close to the breeding sites where mating takes place. Species independent in their reproduction from water bodies may be distributed more randomly at the sites. So, obviously the reproductive mode often indicates the used habitat, at least during the mating season. However, the distribution of different modes of reproduction is a subject I will refer to later. First, I consider four general categories of habitat use (ground, understory, canopy, and aquatic habitat) to receive an imagination about how species share general habitat resources. Of course, such categories always are accompanied by the problem that certain species do not perfectly fit in only one of them. For example, species primarily inhabiting the forest understory may also be found on the ground during reproduction, canopy species may also be found sometimes in the understory, or ground dwelling species may be found on leaves of the understory while sleeping. Ground dwelling species found on leaves were *Atelopus tricolor, Bufo veraguensis* and *B. stanlaii*. The species *Epipedobates pictus, Hyla andina, H. marianitae, Scinax castroviejoi, S. fuscovarius, Eleutherodactylus rhabdolaemus* and *E. fenestratus* seem to use both, understory and ground, as calling position. However, I here adjoined only one habitat type to a species, namely the one which was used most frequently. In all three transects, at 500 m a.s.l. ground dwelling species con-
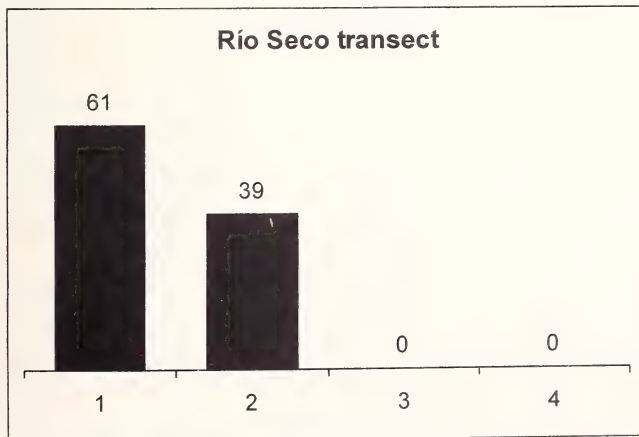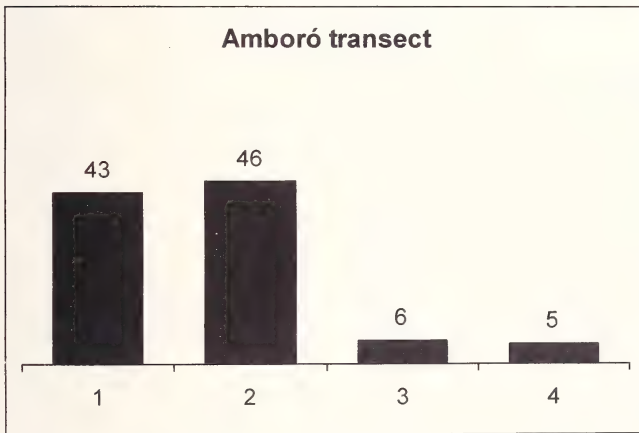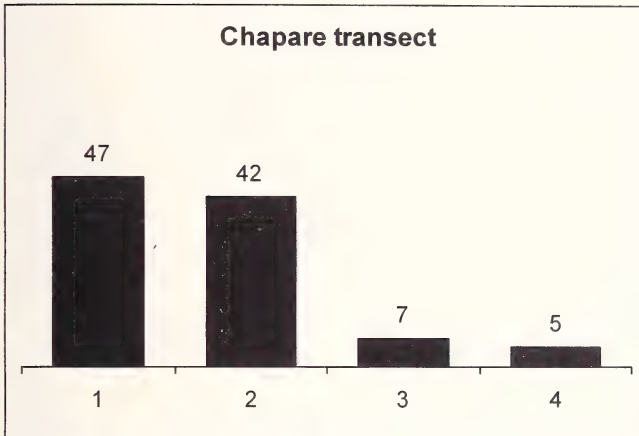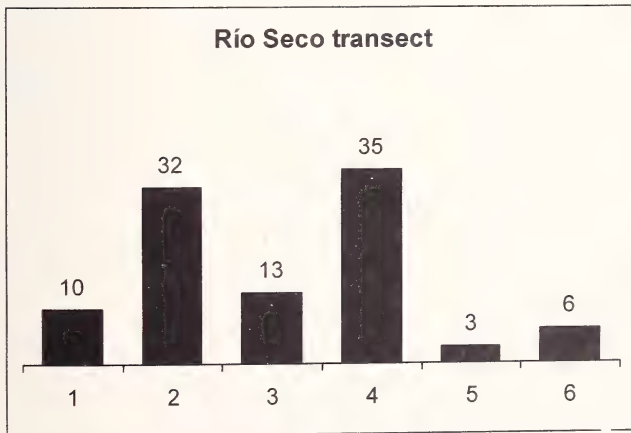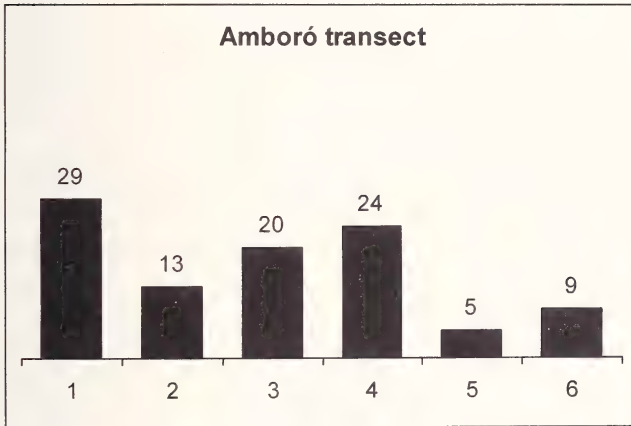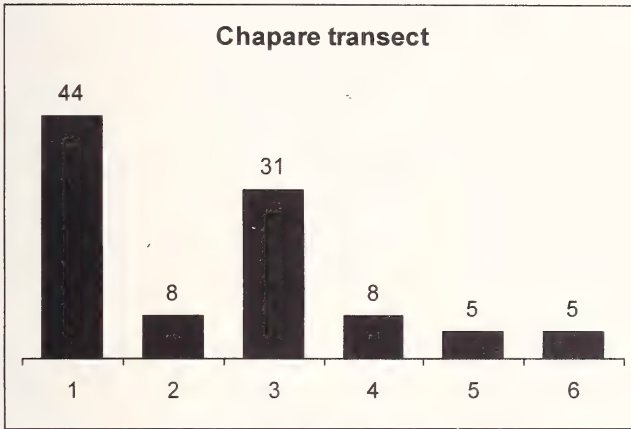
Fig.54: Diagrams showing the distribution of habitat use in the three respective transects. Numbers are values in percent (values rounded).
Habitat use:
1 – ground
2 – understory
3 – canopy
4 – (semi)aquatic

stitute the most numerous group followed by species inhabiting the understory. In the Amboró and Chapare transects, this situation changes when moving up the slopes. At 1300–1600 m a.s.l. ground and understory species are almost equal in numbers, and at 1900–2200 m a.s.l. species inhabiting the understory slightly dominate. In the Río Seco transect, ground dwelling species clearly dominate at 500 m and 1100–1600 m a.s.l., whereas species of the understory dominate the 1900–2200 m a.s.l. elevations. Again, this phenomenon might partly be explained with available humidity. On the ground, the risk of dehydration can be minimized by different behaviors, such as to hide in the moist leaf litter or beneath fallen logs, whereas in the understory (or canopy) the exposure to wind and sunlight supports the possibility of desiccation. Although the lower slopes generally may have a per-humid climate, rainfall can be distributed seasonally, so that there may be also periods with limited access to moisture. The situation at the upper slopes is quite different, because rainfall is more permanent and the frequent occurrence of clouds provides for a continuous irrigation of the forest. When regarding the transects in total, ground dwelling species dominate in the Chapare and Río Seco transects, but understory dwellers do in the Amboró transect. The large number of understory species in the Amboró transect mainly refers to pond-breeding hylids present at 500 m a.s.l. Both, the Amboró and Chapare transects, contain only few canopy species, and the Río Seco transect totally lacks such species. The latter again can be explained with the risk of dehydration in a distinctly seasonal climate. However, some canopy species may remain unnoticed, because of the difficulties to access this habitat. The same is true for aquatic species. Sampling of aquatic habitats requires special techniques. Species found to be aquatic or at least semi-aquatic are *Bufo amboroensis*, *Telmatobius* cf. *simonsi*, and *T. yuracare*. Another species strongly associated with streams is *Hyla armata* which was most frequently found perching on boulders within the water. Undoubtedly, the mentioned species are in need of permanently existing water bodies which apparently do not exist at the investigated sites of the Río Seco transect.

Reproductive modes

Nine out of ten reproductive modes defined by Crump (1974) were reported for Bolivian amphibians (Köhler et al. 1998b). I here refer to somewhat different and more generalized modes, because Crump (1974) did not distinguish between egg deposition in streams and egg deposition in ponds, ditches, or swamps. However, differentiation between egg deposition in lotic or lentic water seems to be appropriate to characterize montane forest communities of amphibians.

In the Chapare transect, the most common mode is direct terrestrial development independent from water bodies (44%) followed by egg deposition in streams with free swimming aquatic larvae (31%). Direct terrestrial development as suspected for almost all species of *Eleutherodactylus* requires permanent availability of moisture during development. The Chapare is supposedly the region with the

Fig.55: Diagrams showing the distribution of reproductive modes in the three respective transects. Numbers are values in percent (values rounded).

Reproductive modes:
1 – direct terrestrial development
2 – eggs in foam nests, tadpoles in water
3 – egg deposition in lotic water
4 – egg deposition in lentic water
5 – backpack strategy, tadpoles in water
6 – egg deposition above water, tadpoles in water

highest amount of precipitation in Bolivia (up to 8000 mm per year, Kessler 1999) and therefore appears to provide ideal conditions for this respective mode. On the other hand, heavy rains bear the risk of destruction of terrestrial egg clutches, but large parts of the annual precipitation is provided directly by clouds (fog), especially at the upper elevations. Only three species deposit eggs in lentic water, two of them occurring only at the lowermost elevations. As already mentioned, the Chapare transect almost completely lacks lentic waters. Only some roadside ditches temporarily have lentic character, but mostly have also recognizable currency. Species depositing eggs in streams are mainly members of the families Bufonidae and Hylidae. Four members of the *Bufo veraguensis* group occur along the transect. Of those, at least *Bufo veraguensis* itself has been demonstrated to have tadpoles which are well-adapted to fast flowing water (Cadle & Altig 1991). The same is true for *Atelopus tricolor* tadpoles (Lavilla et al. 1997) as well as for those of *Hyla armata* (Cadle & Altig 1991, Duellman et al. 1997). Moreover, the two centrolenid species depositing their eggs attached to plants or other structures above the water are also closely linked to streams where the tadpoles complete their metamorphosis. Tadpoles of the foam nest building species *Leptodactylus rhodonotus* and *L. griseigularis* also may develop in lotic water, because the nests and calling activity occurred close to small streams or slow flowing ditches. The two species of *Gastrotheca* have somewhat different modes of reproduction. Whereas in *Gastrotheca* sp. A the tadpoles were released in a certain stage from the females' marsupium into ditches or small streams (see Köhler et al. 1995b), direct development on the females' back occurs in *G. testudinea*. Summarizing, the Chapare transect is clearly dominated by stream breeding species and species independent from water bodies.

In the Amboró transect, the situation is similar with respect to direct terrestrial development being the most common mode (29%). However, this mode is followed in number by species reproducing in lentic water (27%), being more common than those with development in lotic water (20%). As is obvious from the table, the large number of species reproducing in ponds, swamps, or puddles is mainly made up by species at the lowermost elevations of the transect, i.e. hylid frogs. At the upper elevations these species are completely lacking. The higher number of species building foam nests is due to the genera *Leptodactylus* and *Pleurodema*. Species depositing eggs above water are made up by centrolenids (restricted to streams), *Phyllomedusa* species, and *Hyla leucophyllata* (pond

Plate VII: a) *Telmatobius* cf. *simonsi* Parker, 1940, male, La Hoyada, 1750 m; b) *Telmatobius yuracare* De la Riva, 1994, male, Sehuencas, 2150 m; c) *Telmatobius* sp. A, male, Empalme, 2520 m; d) *Physalaemus albonotatus* (Steindachner, 1863), male, Santa Cruz de la Sierra, 400 m; e) *Physalaemus biligonigerus* (Cope, 1861), male, W of Vaca Guzman, 1360 m; f) *Chiasmocleis albopunctata* (Boettger, 1885), male, W of Río Seco, 900 m; g) *Elachistocleis bicolor* (Valenciennes, 1838), male, Cobija, 250 m; h) *Elachistocleis* cf. *ovalis* (Schneider, 1799), male, N of San Juan del Potrero, 2000 m.

Plate VII
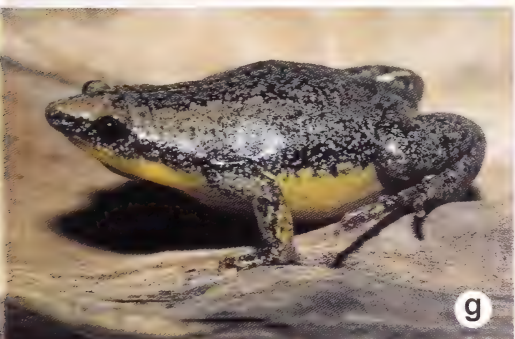
breeders). With the exception of the high number of pond breeders at 500 m a.s.l. (43% of all species recorded from that elevation), the different reproductive modes are slightly more equally distributed among the communities when compared to the Chapare transect. This has two reasons: the larger heterogeneity of sites and habitats in connection with the overall larger availability of lentic waters within the Amboró transect. The heterogeneity of sampled sites is directly connected with the heterogeneity of patterns in reproductive modes found at the respective sites. That means, especially in the uppermost parts of the Amboró transect, distribution of reproductive modes at single sites is not as indicated by table 3. There is large variation in patterns between sites geographically close to each other (see above). However, communities at the steep slopes in the core area of Parque Nacional Amboró most probably exhibit very similar patterns in distribution of reproductive modes when compared to the steep slopes of the Chapare region. In spite of the limited comparability of Amboró and Chapare transects, it is preliminary stated that diversity in reproduction modes is significantly greater in the former.

Completely different patterns occur in the Río Seco transect. There, egg deposition in lentic water is the dominating mode (36%) followed by egg deposition in foam nests with aquatic larvae (32%). Direct terrestrial development and egg deposition in lotic water is of minor importance (10% and 13%, respectively). Only one centrolenid species and one species of *Gastrotheca* (species A?) occur at the uppermost elevations of the transect. The species reproducing in ponds and ditches are almost all more or less explosive breeding species, forming large aggregations at the beginning of the rainy season, mostly laying large numbers of eggs and having fast larval development. The distinctly seasonal environment of the Río Seco transect requires a relatively short period of reproduction and metamorphosis must be completed before the supply of water terminates. Additionally, the Río Seco transect contains larger areas of open habitat bearing a higher risk of desiccation or overheating when eggs or tadpoles are exposed to sunlight. Foam nests have been demonstrated to be an effective protection which enables eggs and tadpoles in seasonal environments to overcome longer periods without rainfall. The availability of permanent streams is low and therefore there are nearly no suitable habitats for stream breeders. On the other hand, during dry periods river beds might be the only habitats providing any water and some species usually breeding at ponds may be found reproducing at the edge of streams (e.g., *Bufo arenarum, B. paracnemis*). In summary, the Río Seco transect is characterized by a large number of species being adapted to distinctly seasonal environments with long dry periods, many of them are also distributed in the Chaco-Cerrado domain of the lowlands. Only few species, considered to represent elements of the Tucumanian-Bolivian montane forests (*Hyla marianitae, Eleutherodactylus discoidalis, E. samaipatae, E.* sp. A), differ in their reproduction by having direct terrestrial development or by egg deposition in streams. However, this strategies probably require a certain use of micro habitat.

Comparisons of diversity and endemism using PAE and NJAE

As already mentioned in the material and methods chapter, parsimony analysis, developed for phylogenetic studies, has been used to determine hierarchical patterns of endemism. This PAE method was first described by Rosen (1988) and was later used also for herpetofaunal analysis (e.g., Raxworthy & Nussbaum 1996, 1997, Harvey 1998). The PAE method is herein completed with NJAE which in almost all cases produced the same dendrograms but different bootstrap values. In the following, I compare the three transects concerning their different elevational levels to answer the question "How are the communities at different elevational levels related to each other within a transect?" and "Is there greater similarity between sites at identical elevations or greater similarity between sites within one transect?" Fig.56 provides a schematic overview of the sites compared with PAE and NJAE.

Comparison of transect sites

First, I compared the three respective elevational levels of each transect (500, 1300–1600, and 1900–2200 m a.s.l.). The figure 57 shows the dendrograms for
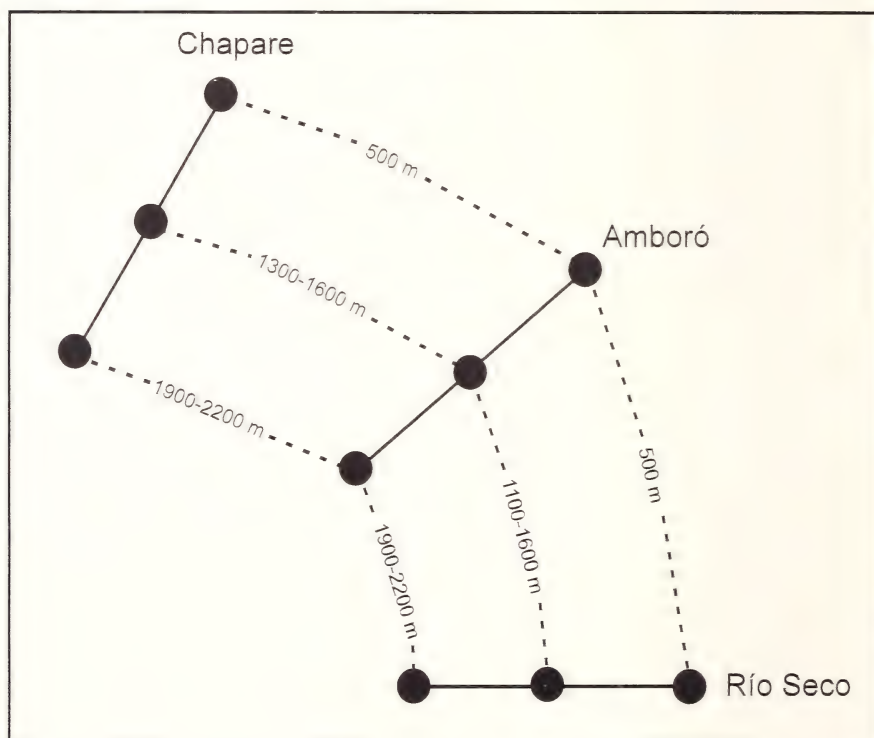
Fig.56: Schematic drawing showing the three transects an the nine elevational levels compared with PAE and NJAE.

each transect resulting from PAE. In all three transects, the two upper elevational levels cluster with relatively high bootstrap values (98/98% and 78/75%) supporting the clades including 1300–1600 m and 1900–2200 m a.s.l. in the Amboró and Chapare transects. This result was expectable, since many species are shared by the uppermost elevational levels and a large number of species occurring at 500 m a.s.l. do not exceed above 900 or 1000 m a.s.l. The situation is similar in all three transects, although bootstrap support is highest in the Amboró transect and significantly lower in the Río Seco transect. The lower support of the clade in the
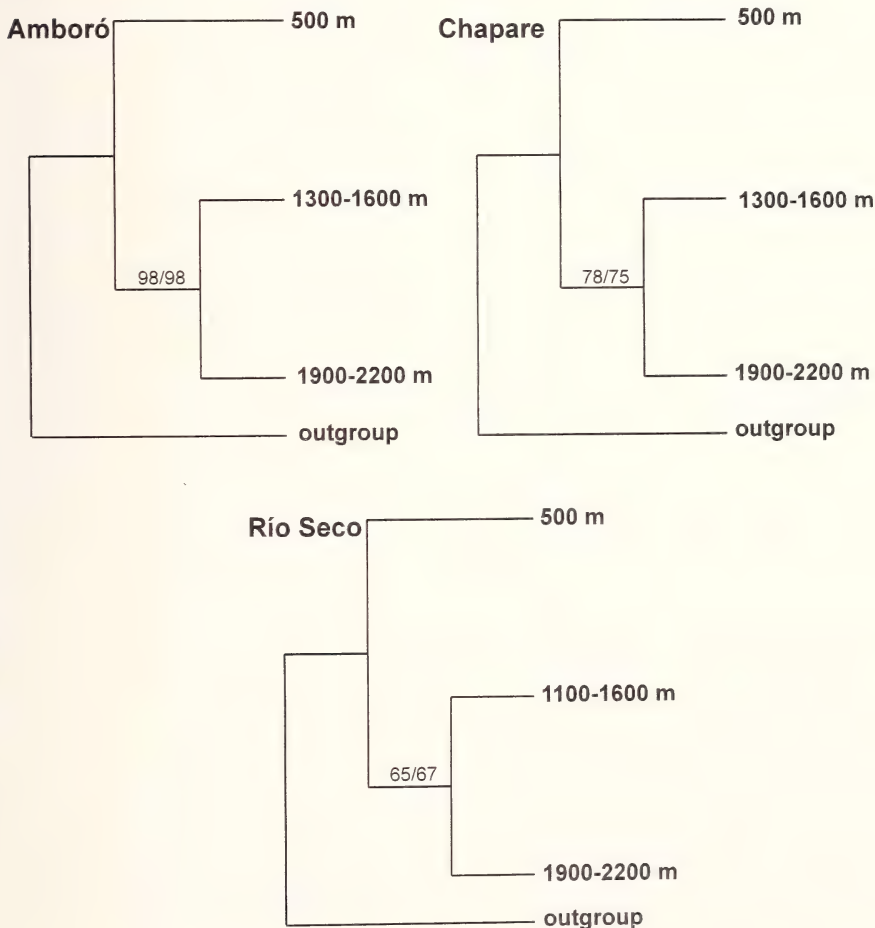
Fig.57: Maximum parsimony dendrograms showing the relationships between sites of different elevation within the respective transects. Eighty-two species considered. Hypothetical outgroup area devoid of all species. Numbers are bootstrap values in percent (500 replicates; PAE/NJAE).

Río Seco transect (bootstrap values 65/67%) is obviously due to the Chaco-Cerrado distributed species which also occur up to the uppermost elevations of the transect (e.g., *Leptodactylus gracilis, Elachistocleis* cf. *ovalis*). Summarizing, faunal relationships between the upper montane forest regions are closer than those to amphibian faunas at the Andean foot where the influence of lowland ecoregions is evident.
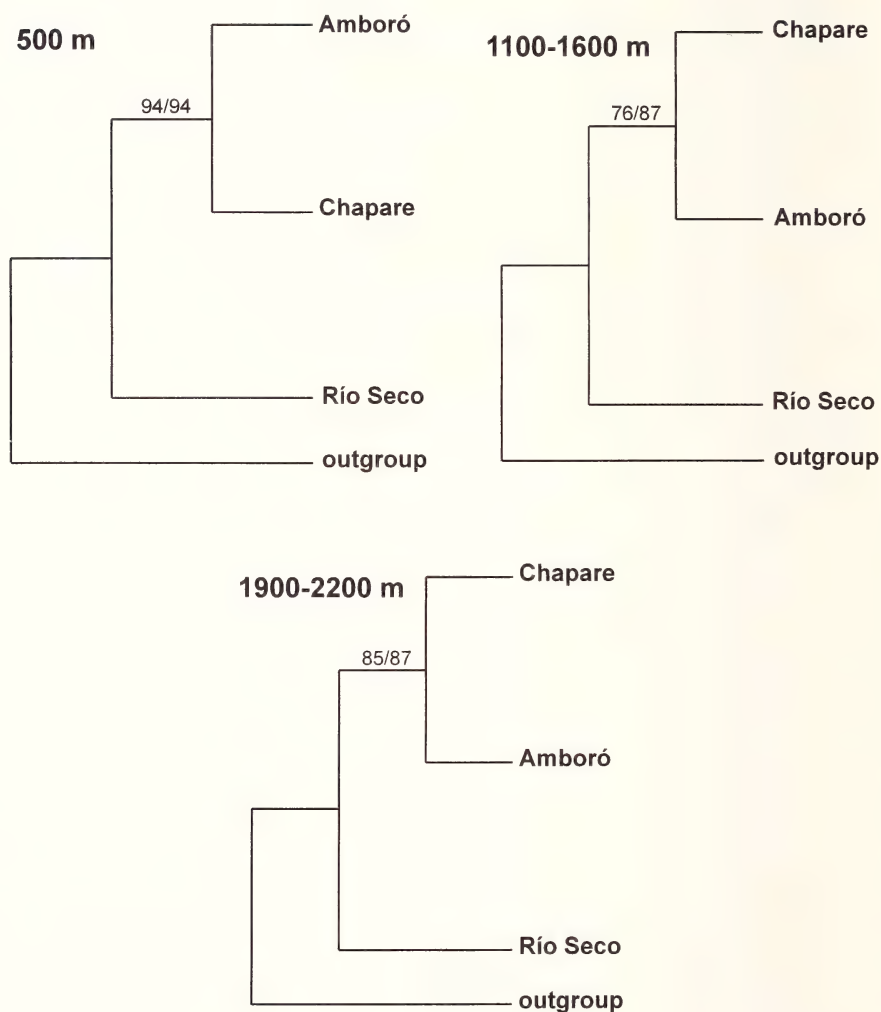
Fig.58: Maximum parsimony dendrograms showing the relationships between sites of similar elevation of the different transects. Eighty-two species considered. Hypothetical outgroup area devoid of all species. Numbers are bootstrap values in percent (500 replicates; PAE/NJAE).

Second, I compared each three sites of one elevational level of the three different transects. The resulting three dendrograms are provided in figure 58. At all three
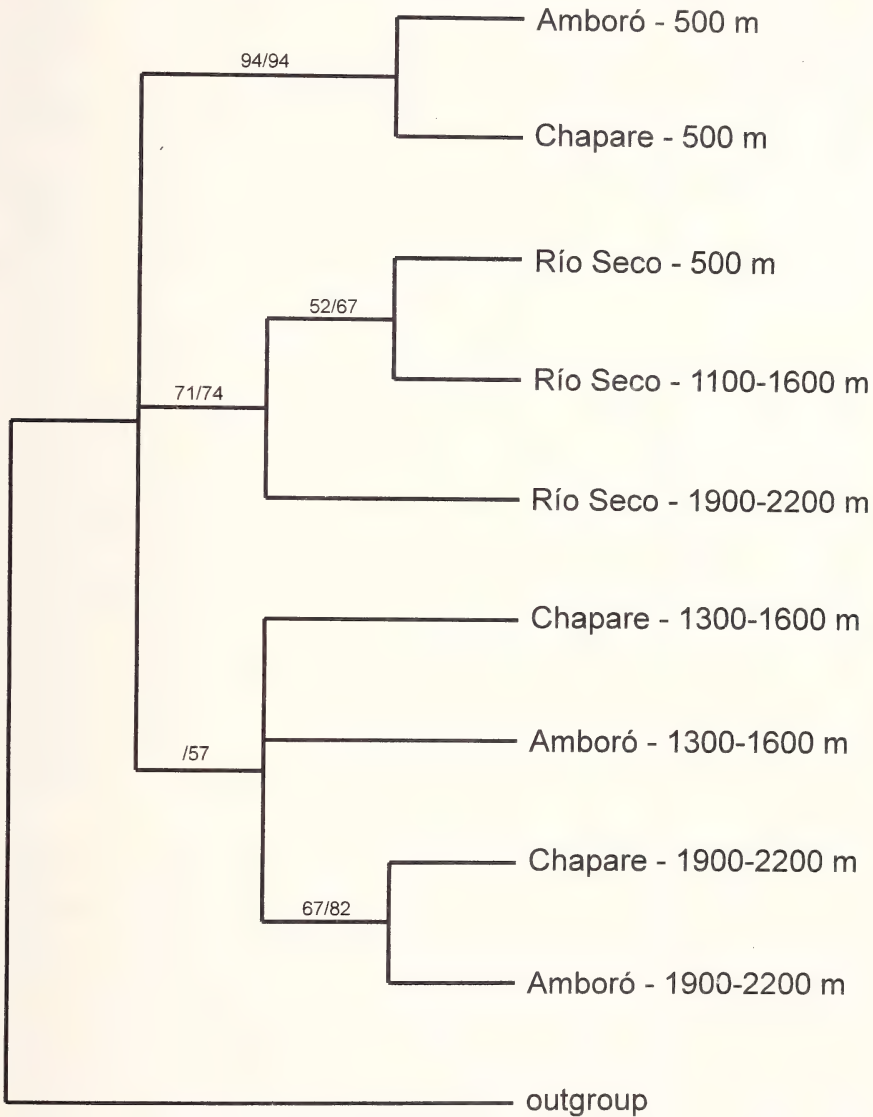
Fig.59: Maximum parsimony dendrogram showing the relationships between nine sites of three different elevational levels within three transects with respect to amphibian species. Eighty-three species considered. Hypothetical outgroup area devoid of all species. Numbers are bootstrap values in percent (500 replicates; PAE/NJAE).

elevational levels the high bootstrap values support a close relationship of the Amboró and Chapare transects. This relation is best supported at 500 m a.s.l. (94/94%) and less at the mid-elevational level (76/87%), but differences in support are not really significant. Although the Amboró transect in part contained semi-humid sites, the PAE and NJAE analyses clearly identify the Amboró area as being dominated by species occurring in a per-humid climate similar to the Chapare. In contrast, at all elevational levels the Río Seco transect harbors a distinctly different amphibian fauna, in the ecological analysis shown to be adapted to a strongly seasonal environment.

Third, I conducted PAE and NJAE analyses using the data sets of all nine transect sites. The resulting dendrogram is provided in figure 59. High bootstrap values (94/94%) support the clade of the Amboró and Chapare 500 m level. Another clade is formed by the three Río Seco sites (bootstrap values 71/74%) supporting the results of the two former analyses. Within the Río Seco clade the elevational levels 500 m and 1100–1600 m a.s.l. form another clade which is in contrast to the former results where the both uppermost levels clustered. However, the bootstrap value for this clade is rather low (52/67%). Another clade is formed by the upper elevations of Amboró and Chapare transects, but bootstrap support is also low. Within this clade, the 1900–2200 m level of Amboró and Chapare group together with relatively high support in the NJAE bootstrap (82%). What becomes clear is that the Río Seco transect is distinguished from the other two, more humid transects. Relationships of the lowermost Río Seco site (500 m a.s.l.) are closer to higher elevations in the same transect than to the respective sites in Amboró and Chapare transects. In contrast, the lowermost sites in the Amboró and Chapare transects have closer relationships to each other than to higher elevations in their respective transect. Regarding these higher elevations in the Amboró and Chapare transects, the PAE and NJAE were not able to resolve the inter-site relationships sufficiently. However, the large similarities between the lowermost elevations of Amboró and Chapare transects argue for the presence of a special ecological region along the Andean foothills.

Comparison to other South American sites and regions

The purpose of the next analysis was to obtain an imagination about the differentiation of diversity and endemism between the investigated transects and other regions along the eastern Andean slopes. Are the differences between the Amboróand Chapare transects of equal value as are differences between the Chapare region and the Yungas de La Paz region or the eastern slopes of southeastern Peru? Distribution data for the Yungas de La Paz region were mainly obtained from museum specimens, whereas data for southeastern Peru were exclusively taken from the available literature. Figure 60 provides the maximum parsimony dendrogram from this analysis. Analogue to the former analysis, the Río Seco transect again builds a clade separated from the more humid regions. These remaining humid regions were grouped together in a well supported clade (bootstrap values 70/89%).
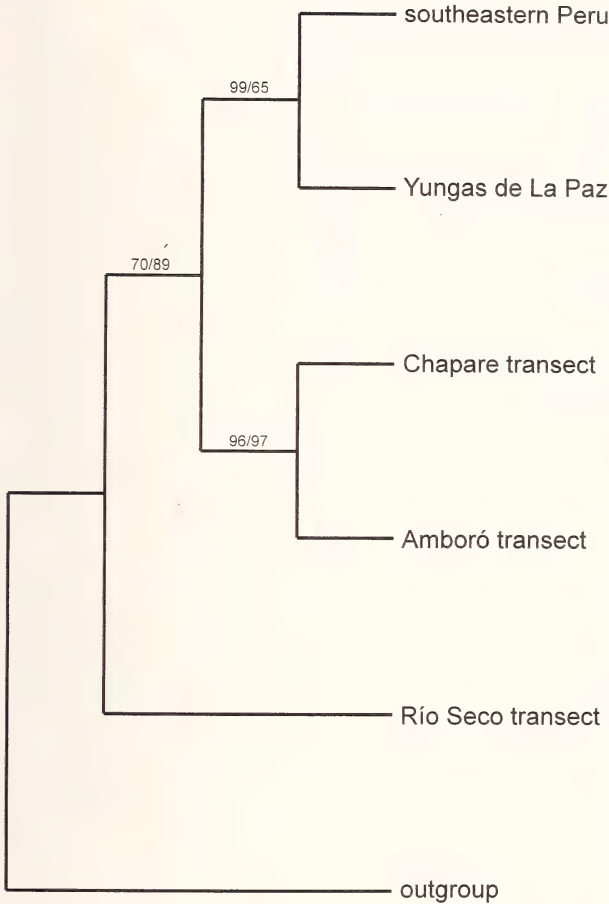
Fig.60: Maximum parsimony dendrogram showing the relationships with respect to amphibian species between the three investigated transects, the Yungas de La Paz region and southeastern Peru close to the Bolivian border. Hypothetical outgroup area devoid of all species. Numbers are bootstrap values in percent (500 replicates; PAE/NJAE).

Within this major clade, the southeastern Peru region and the Yungas de La Paz region cluster with high PAE bootstrap support (99/67%) as do the Amboró and Chapare regions (bootstrap values 96/97%), forming two well differentiated groups. Obviously, there is a significant difference concerning diversity and endemism between the humid montane forest regions of western and central Bolivia.

In the introducing chapters, the inclusion of the peri-Andean forests in the ecoregion humid Amazonian rainforest was already mentioned. Undoubtedly, these very humid forests at the Andean foot contain many Amazonian components which justifies the inclusion in the respective ecoregion. However, the geographic position of these forests is obviously connected with typical climatic conditions, namely higher amount of precipitation when compared to real lowland Amazonian rainforest. In addition, the peri-Andean forests partly border on other ecoregions with very distinct conditions. At the easternmost termination these are
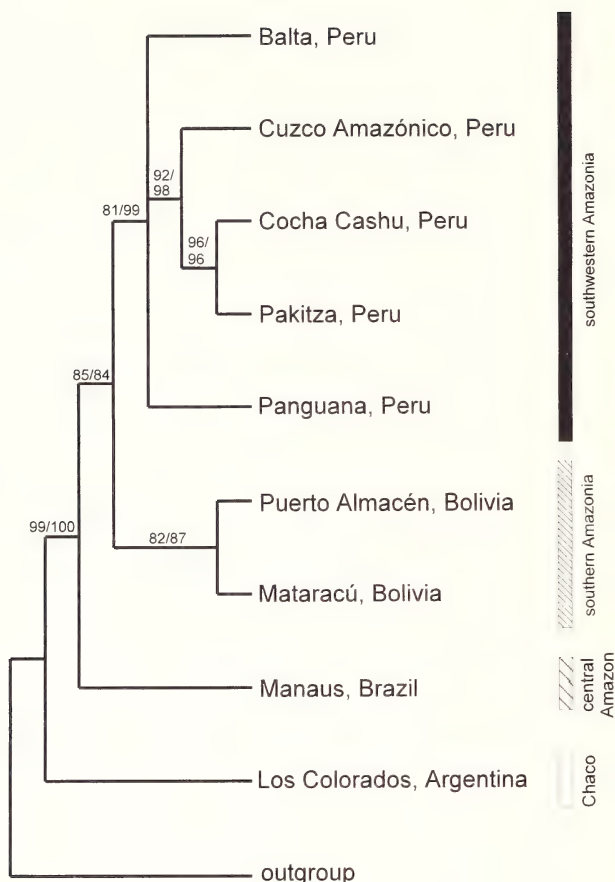
Fig.61: Strict consensus dendrogram showing the relationships between different Neotropical sites with respect to amphibians. Sites here indicated as belonging to the southwestern portion of Amazonia are all located within the upper Amazon basin of Peru. The two Bolivian sites are marked as generally belonging to the southern Amazon, although Mataracú is located at the Andean foot and Puerto Almacén is in northeastern Bolivia within the humid forests of the Pre-Cambrian shield. Hypothetical outgroup area devoid of all species (185 species considered). Numbers are bootstrap values in percent (500 replicates; PAE/NJAE).

the humid transition forests and the semi-deciduous Chiquitanía forests, and even the Chaco dry-forest is very close. Moreover, in the Yungas de La Paz region the peri-Andean forests are very close to wet savannas. Therefore, it might turn out that the relationships of Bolivian peri-Andean forests to lowland Amazonian forests are less evident than per se suspected. With respect to amphibians, I chose the single site Mataracú, located at almost the eastern limit of peri-Andean forest extension (500 m a.s.l.; 17°33' S, 63°52' W), to compare it with other sites of southwestern Amazonia as well as with one site in the central Amazon and one in the dry Chaco. The result is shown in figure 61. In the strict consensus dendrogram, the five Peruvian localities of the upper Amazon basin are grouped together with the two Bolivian sites (including Mataracú) and the central Amazonian Manaus. This group is strongly supported by high bootstrap values (99/100%) and separates the Chacoan site Los Colorados as expected. The Peruvian sites Cuzco Amazonico, Cocha Cashu, and Pakitza form another well supported sub-group

within the major Amazonian clade (bootstrap values 92/98%), with the two latter being more closely related (bootstrap values 96/96%). All three sites are situated in the upper Amazon basin of southeastern Peru, with Cocha Cashu and Pakitza being very close to each other. Although Panguana (central Peru) and Balta (a seasonal rainforest site at about 10°08' S, 78°13' W) are grouped among the other Peruvian sites, relationships are not resolved completely by the consensus tree. Mataracú forms a well supported clade together with the Bolivian Puerto Almacén (bootstrap values 82/87%), a site within the moist forest of the pre-Cambrian shield in the northern Departamento Santa Cruz (15°46' S, 62°15' W). Together, the Peruvian and Bolivian sites form a major clade separated from the central Amazonian Manaus (bootstrap values 85/84%). To summarize, Mataracú is grouped among the sites of the southwestern Amazon basin and has lesser relationships to the central Amazonian site (as does Puerto Almacén). Moreover, relationships of Mataracú to the Bolivian lowland site are stronger than to sites at the foot of the Peruvian Andes. Obviously, the location of Mataracú at the eastern limit of forest strongly influenced by Amazonian elements is responsible for lesser relationships to sites of Peruvian peri-Andean forests than to Puerto Almacén. Amphibian species composition at Puerto Almacén is largely similar to that recorded from Mataracú. However, a remarkable fact is that species compositions from sites located in-between Mataracú and Puerto Almacén are considerably distinct, because the area exhibits a drier and more seasonal climate (see map of ecoregions). Both sites are separated by a distance of approximately 450 km airline and are located in different ecoregions, but conditions for amphibians seem to be largely similar. With respect to amphibians, Mataracú can be regarded as an Amazonian site with significant influence from the Cerrado domain (compare De la Riva 1993d).

Finally, I conducted a NJAE including the three investigated transects as a whole, Andean slopes of southeastern Peru, the Yungas de La Paz region, as well as several Amazonian lowland sites (including Mataracú) and the Chacoan site Los Colorados, Argentina. The resulting dendrogram is shown in figure 62. The Río Seco transect clusters with the Chacoan Los Colorados, corroborating its strong relationships to dry and seasonal environments. The Amboró and Chapare transects are grouped among all other Amazonian sites, including Mataracú and Puerto Almacén. All these four sites or regions form a Bolivian sub-clade, with Mataracú (part of the Amboró transect) being closer related to the two humid transects than to Puerto Almacén (compare to former analysis). All sites of the Peruvian upper Amazon basin form another sub-clade within the Amazonian sites separating again the central Amazonian Manaus. Like in the dendrogram fig.58, Andean slopes of southeastern Peru are grouped with the Yungas de La Paz region, separating these two montane regions from the Amazonian clade. This again supports the distinctness of the Yungas de La Paz region when compared to the Amboró and Chapare regions which clustered within the Amazonian clade.
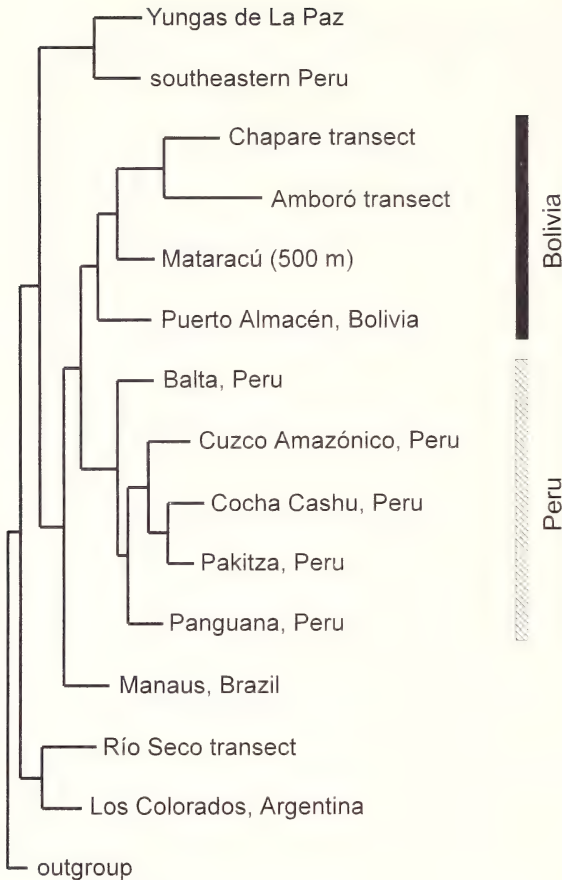
Fig.62: Neighbor-joining dendrogram showing relationships between several Neotropical sites, including the three investigated transects (185 species considered).

To briefly summarize the results obtained from PAE and NJAE analyses: (1) relationships between the Amboró and Chapare transects are stronger than to the Río Seco transect, and this is true for all elevational levels considered; (2) the two upper elevational levels (1100–1600, 1900–2200 m a.s.l.) in all three transects have larger similarities than each of them to the lowermost level (500 m a.s.l.); (3) similarities of the 500 m elevational levels of the Amboró and Chapare transects are larger than those of the upper elevations between the same transects; (4) the humid Amboró and Chapare transects are distinguished from more western Andean slopes, namely the Yungas de La Paz and southeastern Peru; (5) Mataracú as a site at the eastern edge of Bolivian peri-Andean forests can be regarded a Amazonian site with influence from the Cerrado formations. It is more similar to sites of northeastern Bolivia than to sites in the upper Amazon basin of Peru; (6) the Río Seco transect has strong relationships to the dry and seasonal environments of the Chaco; (7) the central Amazonian site Manaus is distinctly distin-

guished from sites in the upper basin of southwestern Amazonia; (8) sites of southeastern Peru are closely related and exhibit distinct differences to sites in central Peru.

Large scale distribution patterns of montane forest species

This chapter refers to large scale distribution patterns of the amphibian species regarded to represent 'real' montane forest species during the present study (this means, I did for example not consider species known from the Yungas de La Paz region, but not ranging in the investigated area; see species accounts). I compiled the known distribution of every species according to literature review, museum specimens, and own findings and I roughly identified twelve general patterns of distribution (shown in Figs.63-74). Of course, not every species fits exactly into one of the suggested patterns and some probably will be changed to another pattern when additional records from field surveys become available. However, several species agree more or less exactly in their known distributions. In the following, the twelve identified patterns are briefly described and commented.

Pattern 1 (Fig.63): species assigned to this pattern are distributed in the upper montane rainforests and cloud forests of the Departamentos Cochabamba and Santa Cruz, mainly between 1600 and 2700 m a.s.l. As a matter of fact, all these species are endemic to Bolivia. Typical representatives are for example *Bufo quechua, Eleutherodactylus fraudator, E. llojsintuta, E. pluvicanorus, Ischnocnema sanctaecrucis, Phyllonastes carrascoicola, Telmatobius yuracare,* and *Telmatobius* sp. A. Some of these species may actually exhibit pattern 2 (see below).

Pattern 2 (Fig.64): this pattern equals pattern 1 with the exception that species' ranges extend also to the Yungas de La Paz region. Again, all species providing this pattern are currently considered Bolivian endemics. Typical representatives
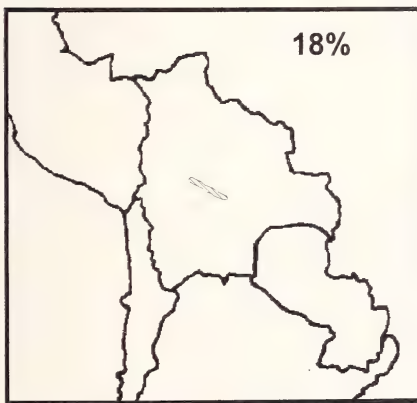
Fig.63: Pattern 1: upper elevations of Yungas de Santa Cruz and Cochabamba.
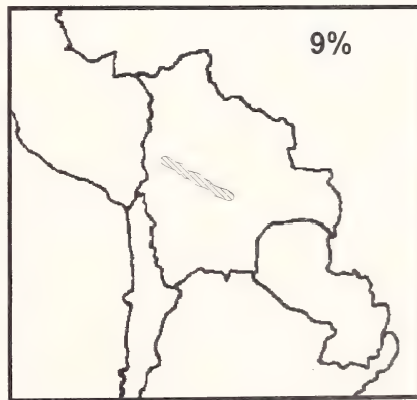
Fig.64: Pattern 2: Yungas de Cochabamba, Santa Cruz and La Paz.

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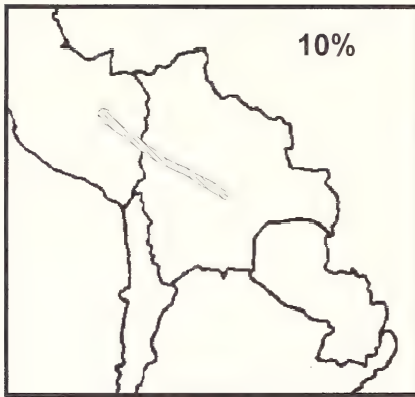
Fig.65: Pattern 3: Bolivian Yunga regions and slopes of southeastern Peru.
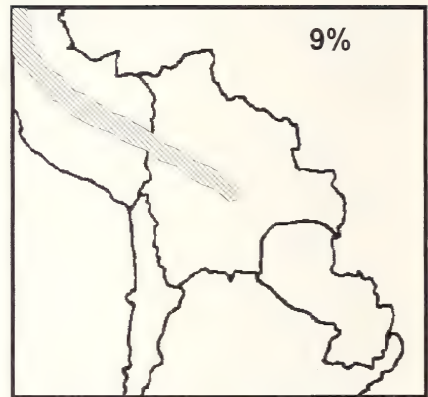
Fig.66: Pattern 4: Bolivian Yunga regions northward to central Peru.

are for example *Bufo justinianoi, B. fissipes, Cochranella bejaranoi,* and *Eleutherodactylus mercedesae.* Some of these species may possibly be less far distributed to the east when compared to species considered in pattern 1.

Pattern 3 (Fig.65): this pattern refers to species distributed in the humid montane rainforests from southeastern Peru along the Andean slopes to the Bolivian Departamentos Cochabamba and Santa Cruz. Some of the species inhabit only the upper forests, whereas others may also occur at the lowermost slopes. None of these species is a Bolivian endemic. Typical representatives are for example *Atelopus tricolor, Hyalinobatrachium bergeri, Hyla armata, Eleutherodactylus cruralis, E. danae, E. olivaceus,* and *E. rhabdolaemus.*

Pattern 4 (Fig.66): this pattern refers to species having a wider range compared to those having pattern 3. Species considered here are distributed on the Andean slopes from Departamento Santa Cruz northward to at least central Peru. Some of the species also occur in northern Peru. In contrast to species exhibiting pattern 3, species of pattern 4 mostly have a greater elevational range. Typical representatives are for example *Bufo poeppigii, Eleutherodactylus platydactylus, Leptodactylus griseigularis,* and *L. rhodonotus.*

Pattern 5 (Fig.67): this pattern most probably does not reflect actual distribution. Here, I considered species currently known only from Bolivia's Chapare region (e.g., *Hyla* cf. *callipleura, H. chlorostea, H.* sp. A, *Eleutherodactylus ashkapara, Phyllonastes ritarasquinae*). In most cases, future findings will probably extend the known distribution of these species. All are preliminary considered being endemic to Bolivia.

Pattern 6 (Fig.68): species considered here have a very limited range in the region called "La Siberia". It is a cloud forest area at the borders of the Departamentos Cochabamba and Santa Cruz from approximately 2000–2800 m a.s.l., character-
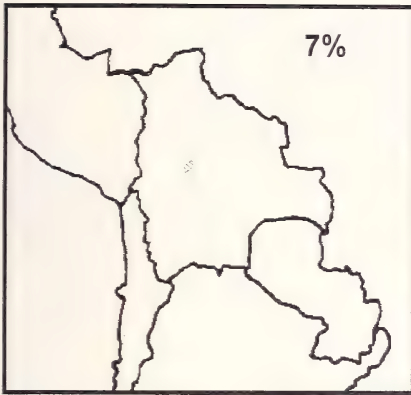
Fig.67: Pattern 5: Bolivian endemics of the Chapare region.
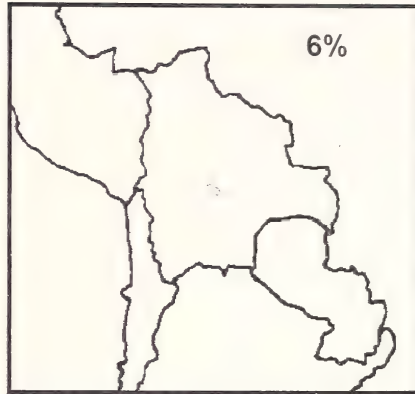
Fig.68: Pattern 6: Bolivian endemics of the "La Siberia" region.

ized by frequent fog and cold winds. Species regarded as "La Siberia" endemics are for example *Gastrotheca lauzuricae, Phrynopus kempffi*, and *Telmatobius edaphonastes*.

Pattern 7 (Fig.69): the two species considered here (*Eleutherodactylus samaipatae* and *Eleutherodactylus* sp. A) are known only from semi-humid montane forests of the Departamentos Santa Cruz and Chuquisaca (and Tarija). Both species may actually exhibit pattern 8 (see below), extending into northern Argentina. However, both are preliminary considered Bolivian endemics.

Pattern 8 (Fig.70): this pattern refers to typical species for the Tucumanian-Bolivian montane forests which are semi-humid with distinct seasonal climate. Their distribution ranges from the Departamento Cochabamba or Santa Cruz
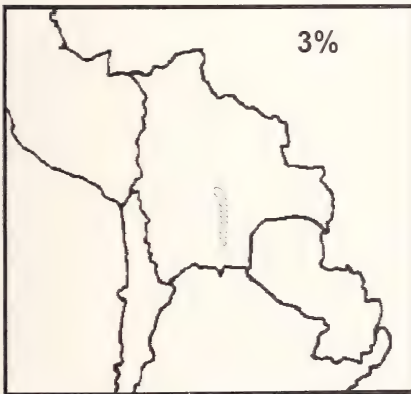
Fig.69: Pattern 7: Bolivian endemics of the semi-humid Tucumanian forests.
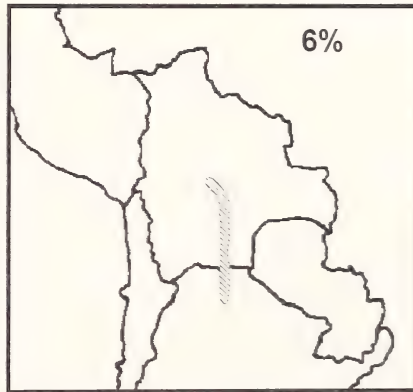
Fig.70: Pattern 8: elements of the semi-humid forests reaching N Argentina.
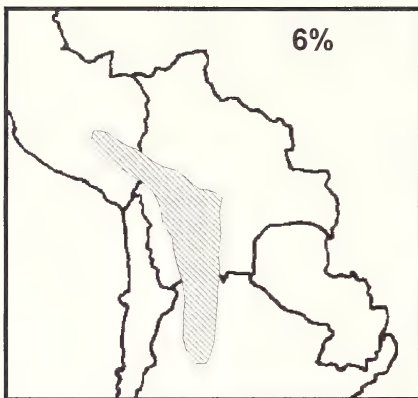
Fig.71: Pattern 9: inter-Andean dry-valleys and adjacent montane forests.
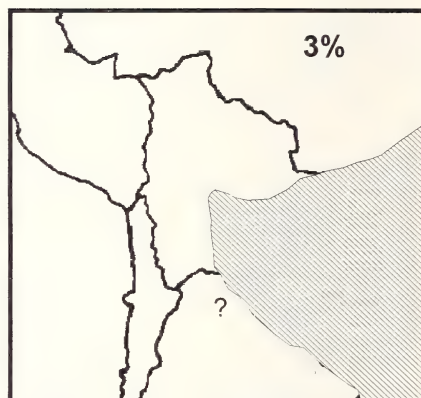
Fig.72: Pattern 10: primarily Chaco-Cerrado distribution to southeastern Brazil.

southward to northern Argentina. Typical representatives are for example *Hyla marianitae, Scinax castroviejoi*, and *Eleutherodactylus discoidalis*.

Pattern 9 (Fig.71): this pattern refers to 'real' Andean elements, distributed in inter-Andean dry-valleys, but also entering upper montane forests. The figure 69 roughly shows the known distribution of *Pleurodema cinereum* as one representative. The other species (*Bufo arenarum, Hyla andina, Telmatobius* cf. *simonsi*) have more restricted or differing ranges, but are also subsumed provisional under this pattern. Only *Telmatobius* cf. *simonsi* is a Bolivian endemic.

Pattern 10 (Fig.72): only two species are considered in this pattern, *Leptodactylus gracilis* and *Physalaemus biligonigerus*. Both species are primarily distributed in the dry lowlands of the Chaco and Cerrado formations and occur also in southeastern Brazil. These species are able to enter montane habitats up to remarkable elevations.

Pattern 11 (Fig.73): the pattern shown in figure 71 equals only roughly the distribution exhibited by the considered species. Considered are for example *Epipedobates pictus, Adenomera hylaedactyla*, and *Eleutherodactylus fenestratus*, occurring in humid but seasonal environments of the lowland forests, and are able to enter the Andean slopes up to considerable elevations.

Pattern 12 (Fig.74): as is obvious from figure 72 this pattern refers to lowland species with wide ranges covering dry to semi-humid and humid forests of eastern Bolivia and adjacent countries (Chiquitanía forests, Chaco, Cerrado, wet savannas, etc.). Such species are for example *Bufo paracnemis, Scinax fuscovarius, Leptodactylus labyrinthicus, Physalaemus albonotatus, Chiasmocleis albopunctata*, and *Elachistocleis* cf. *ovalis*. All of them enter the slopes of the eastern Bolivian Andes.

Actually, few species were not assigned to any of the twelve patterns. These are *Hyla minuta, Phrynohyas venulosa*, and *Leptodactylus fuscus*, which are known
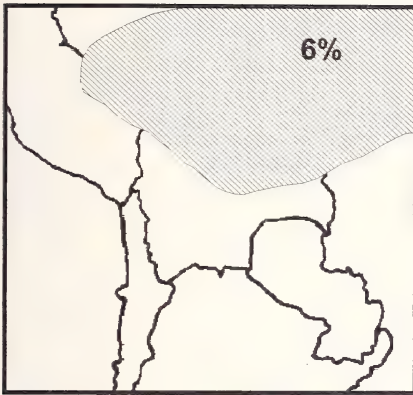
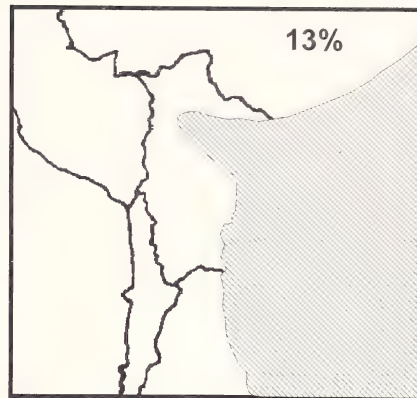Fig.73: Pattern 11: primarily semi-humid lowlands, reaching SW Amazonia.

Fig.74: Pattern 12: wide lowland distribution, seasonal habitats, SE and E Brazil, N Argentina, Paraguay.

from almost the entire South American continent, not only from rainforest areas but also from dry Chaco environments. In addition, all three species are in need of systematic revision. Nevertheless, 96% of the species found fit more or less accurately one of the twelve patterns.

In the figures 63-74 not only the patterns are provided but also the percentages of montane forest species exhibiting the respective pattern. The percentages refer to 68 considered species (i.e., 100%). The pattern 1, endemic species in the upper humid montane forests of the Departamentos Cochabamba and Santa Cruz, is represented by 18% of all montane forest species found during this study. This is a remarkable high value. Additional 9% of the species exhibit pattern 2, being distributed in the whole Bolivian Yungas region including the Yungas de La Paz, and another 6% are considered "La Siberia" endemics (Fig.68), a region located within the upper montane forests of the Departamentos Cochabamba and Santa Cruz. Together, 33% or one third of all recorded species exclusively occur in the humid montane forests of Bolivia. When also including the Chapare endemics (pattern 5; Fig.67), 40% can be considered endemic for the humid Bolivian montane forests! Species distributed exclusively in humid forests along the eastern Andean slopes, although not endemic to Bolivia, exhibit the patterns 3 and 4 (Figs.65-66). Together, both patterns contain 19% of the montane forest species. Species having pattern 3 are more restricted to the southern montane forests and their ranges do not extend very far into southern Peru, whereas species having distribution pattern 4 also occur at the Andean slopes of central or northern Peru and may also range in peri-Andean lowland forests. The patterns 7 and 8 are very similar and refer to the Tucumanian-Bolivian montane forest domain. As already stated, species now considered to have pattern 7 may actually exhibit pattern 8. However, at the present state of knowledge pattern 7 species must regarded to be endemic to

Bolivia. Thus, a total of 43% of the montane forest species occur only in Bolivia. Together, the Tucumanian-Bolivian pattern is represented by 9% of the species. Pattern 9 (6%; Fig.71) reflects a primary distribution in the Andean highlands (e.g., *Pleurodema cinereum*). However, the species considered here frequently enter the upper montane forests and therefore occur in very different habitats. For example, *Hyla andina* is known from dry inter-Andean valleys, wet puna, and very humid montane forests. Often, species occurring in such a variety of habitats are characterized by distinct inter-populational polymorphism (see Duellman et al. 1997) which led to taxonomic confusion in the past. In many cases the taxonomic status of such species is still topic of controversial discussions (see comments on *Pleurodema cinereum* in the species accounts). In the case of *Telmatobius* cf. *simonsi*, montane forest populations seem to be different from the inter-Andean valley populations, but are tentatively regarded a single taxon here. The following patterns 10–12 (Figs.72-74) all refer to lowland species which might enter the Andean slopes up to distinctly more than 500 m a.s.l. Patterns 10 and 12 refer to species occurring in seasonal and dry lowland habitats and together constitute 16% of the montane forest species considered. Almost all of these species exclusively enter the seasonal montane forests south of Santa Cruz de la Sierra and are not found in very humid forests. However, the record of *Elachistocleis* cf. *ovalis* in a cloud forest habitat above 2000 m a.s.l. and that of *Scinax* sp. (cf. *castroviejoi*) within a humid montane forest of the Chapare region (1950 m a.s.l.) are two surprising exceptions which still answer to be clarified. The pattern 11 (6%; Fig.73) includes species which in contrast to pattern 10 and 12 occur in more humid environments of southern Amazonia. A typical example is *Epipedobates pictus* which was recorded at 1300 m a.s.l. in the Yungas de Cochabamba by De la Riva et al. (1996c).

Summarizing, approximately 45% of all species occurring in the investigated montane forests are Bolivian endemics (including *Telmatobius* cf. *simonsi*). Sixty-eight percent are more or less exclusively distributed along the eastern Andean slopes (including Argentina and Peru) and do not significantly enter the lowlands nor the inter-Andean region. These 68% can be regarded as montane forest endemics. Of these, almost one-half (46%) exhibit extremely restricted ranges in the very humid Yungas of the Departamentos Cochabamba and Santa Cruz (patterns 1, 5, and 6). Six percent of the total species number are Andean species which are able to enter montane forests at the eastern slopes and 22% are lowland species entering lower and partly also upper montane forests. Most of the latter (approximately 70%) are restricted to seasonal montane habitats south of Santa Cruz de la Sierra. These results corroborate the statements in the chapter on Species diversity and endemism, identifying the upper elevations of the Bolivian humid montane forests as a region harboring a very diverse and unique amphibian fauna.

DISCUSSION

The degree of amphibian diversity in Bolivia

The total amount of Bolivian amphibians as currently known refers to 200 species. Undoubtedly, this number does not reflect actual diversity. Only ten years of research almost doubled the number of known species and there is apparently no decrease in the rate of discoveries. Many areas remain to be investigated for the first time. When adding the 61 species which were predicted to occur in Bolivia plus a certain number of species new to science, around 350 species would be a more realistic value. With such a number of species, Bolivia would rank among the ten most species-rich countries of the world. However, despite its great diversity in ecoregions, Bolivia will not reach the numbers of other Neotropical countries such as Brazil or Colombia. Brazil is exceptional according to its much larger surface including a great variety not only of ecoregions but also of different major biogeographic domains (e.g., southeastern coastal rainforests, Guianan highlands). Colombia, with currently more than 600 recognized amphibian species, differs from Bolivia in having three parallel mountain ranges as well as trans-Andean lowlands along the Pacific and the Caribbean coast. These conditions constitute a variety of geographically separated regions and strongly support speciation processes.

Nevertheless, Bolivia's amphibian fauna is a diverse and unique one. Its uniqueness might be best described by following main characters: (1) 22.5% of all species are Bolivian endemics; (2) there are certain areas with high degrees in local endemism, containing species with extremely restricted distributions; (3) due to different ecoregions which interdigitate at local scales, Bolivia is rich in areas containing extraordinarily high levels of beta diversity; (4) the close relationships of the inter-Andean region and the dry lowland regions are responsible for exceptional species compositions in the inter-Andean region. One of the most remarkable phenomena is the proximity of very humid and very dry ecoregions in the region of the Andean 'elbow' where slopes turn from west-east direction to a north-south expansion. There are probably very few regions in South America where species from very dry environments and those from very humid environments can be found that close to each other. So, beside levels in alpha diversity that are comparable to neighboring countries, Bolivia's amphibian fauna is characterized by extraordinarily high regional beta diversity and also very high degree in gamma diversity. Especially, the upper parts of the per-humid Yungas forests including the "Ceja" harbor a largely endemic amphibian fauna.

Comparison to other studies

As stated in the introduction, only few studies of elevational transects in the Neotropics are available to compare them to the results of the present work. Another restriction for comparison is the incompleteness of data provided by the

studies (including the present one). Nevertheless, at least basic trends can be drawn from some studies which are worth to be mentioned.

Heyer (1967) investigated the herpetofauna along a transect through the Cordillera de Tilarán in Costa Rica. The transect covered elevations from 88 m to 850 m a.s.l., a relatively narrow range compared to elevations of the South American Andes. On the western slopes of the Cordillera, Heyer (1967) found three distinct herpetofaunal assemblages which largely coincided with the boundaries of vegetation zones. The relationship of herpetofaunal distribution and vegetation zones was suggested to be based on microhabitat conditions and air moisture, rather than on faunal-floral relationships. Thus, environmental conditions obviously constitute the zonal distribution of amphibians and reptiles. Although I would generally agree with the last statement, conditions found on the slopes of the Bolivian Andes appear quite different. The main difference is due to a less distinct vegetational zonation of the humid slopes in Bolivia. As described in chapter 2, the Yungas region can principally divided into four major vegetational zones (peri-Andean forests, lower montane rainforests, upper montane rainforests, and cloud forests). These four zones cover an elevation from approximately 300 m to 3000 m a.s.l. The three vegetation zones present at barely 800 m elevational difference at the western slopes of the Cordillera Tilarán are due to a distinctly seasonal climate with a very pronounced dry season. Thus, ecological boundaries between these zone are relatively well-defined (see also Franzen 1994). It is hardly possible to find a well-defined ecological boundary on the humid Andean slopes of Bolivia within 800 m elevational difference. Also when regarding the total altitudinal expansion of the Bolivian Yungas, a strict relationship of amphibian assemblages to each of the four mentioned zones is not distinctly developed. Most of the species inhabit at least two of the four zones and differences in species composition between different elevations are of sliding character. The same is generally true for the drier Río Seco transect. However, although both situations appear completely different, there is a principal similarity involved. At the Cordillera Tilarán ecological or vegetation zones are well-defined and agree largely with herpetofaunal distribution. In the Bolivian Yungas, boundaries between vegetation zones are less sharply defined (according to generally large amounts of precipitation) as are the distributions of amphibian species. This strongly argues for ecological conditions as a determinant for species distributions. Johnson (1989) investigated herpetofaunal distributions in southern Mexico. In contrast to Heyer's (1967) results, the author did not find any correlation between the herpetofaunal elements and vegetation zones. Johnson (1989) found the assemblages to be associated with 'faunal areas' which are defined by climate, topography, and elevation. However, climate, topography, and elevation usually are also responsible for the zonation of vegetation. When regarding the ten vegetation zones defined by Johnson (1989) and the distribution of species within them, it becomes nevertheless clear that many species are shared between similar vegetation zones,

but none appears to be restricted to one of the zones. Obviously, the results provided by Johnson (1989) would have been more coincident with those of Heyer (1967) through a more generous definition of the vegetational zones.

Lynch (1998) summarized the distribution of 102 species of *Eleutherodactylus* from western Colombia, mainly referring to nine investigated elevational transects. Although considering only a single genus, findings by Lynch (1998) parallel the situation in Bolivia. Lynch (1998) found many lowland species invading the Andean slopes up to considerable elevations (*E. chalceus* up to almost 2000 m a.s.l.), but generally the slopes are inhabited by a larger number of montane species. Great diversity is present at elevations from 1000 m to 2000 m a.s.l. Most species of the lower and mid-elevations are distributed in several parallel transects, whereas cloud forest species tend to have more restricted distributions (see also Peters 1973, Lynch & Duellman 1997). These patterns in distributions of Colombian *Eleutherodactylus* are comparable to patterns found in the anuran fauna of the humid Andean slopes of Bolivia, especially to that of the Chapare region where frogs with terrestrial development are dominating. Similar patterns are also present at the western Andean slopes of Ecuador (Lynch & Duellman 1997), whereas in the *Eleutherodactylus* fauna at the eastern Ecuadorian slopes greatest species numbers were found between 2400 m and 3000 m a.s.l. (Lynch & Duellman 1980, 1997). However, this pattern is restricted when regarding a single transect instead of the whole eastern Andean slopes (Lynch & Duellman 1980: Fig.7).

Cadle & Patton (1988) found an inverse relationship between elevation and species diversity in amphibians and reptiles from the eastern Andean slopes of southern Peru which is in contrast to mammal distribution, where highest diversities were found at lowermost and uppermost elevations. These results argue for the influence of temperature on the diversity of ectothermic organisms. When regarding amphibian distribution only (Cadle & Patton 1988: Fig. 3), it becomes obvious that the elevations between 1000 m and 2000 m a.s.l. contain a greater species diversity than the uppermost elevations of the transect. This is in agreement with own results from humid montane forests in Bolivia. Additionally, other results of Cadle & Patton (1988) coincide with those from Bolivian transects. These are as follows: (1) mid-elevation forested slopes are inhabited by a diversity of leptodactylid frogs (mainly *Eleutherodactylus*), nearly all of them are restricted to forest environments; (2) amphibians do not show distinct species distributional breaks in the intermediate forested elevations; and (3) the amphibian fauna is not very rich in parapatrically distributed species pairs, sympatric congeners in amphibians are common.

Elevational changes in abundance have been noted for forest-floor anurans in Costa Rica by Scott (1976) as well as for anurans in the Philippines (Brown & Alcala 1961). In Costa Rica, the number of individuals increased from 0.12 m² at lowland sites to 0.55/m² at 1200 m a.s.l. Although, no quantitative sampling was

carried out during the present study, the subjective impression agrees with the results by Scott (1976). At upper elevations of the Bolivian Yungas, frogs of the genus *Eleutherodactylus* appear to be extremely abundant and it is easy to find several individuals within a few square meters, whereas at the Andean foot specimens appear to be less common and distributed more scattered within the habitat. Another parameter changing with elevation is the equitability. Usually, there is a decline in species richness but an increase of species abundance with increasing elevation which results in lower equitability at higher elevations. Scott (1976) found the most abundant species to be represented by at least twice the number of the second-most abundant species, and in some cases the most abundant species was represented by more individuals than all of the other species combined. This agrees with the situation at the Bolivian site Sehuencas, 2100 m a.s.l., where Köhler (1995a) found 50% of the individuals represented by *Eleutherodactylus platydactylus* (the actual value is possibly lower because part of the specimens regarded to represent *E. platydactylus* may correspond to the recently described sibling species *E. llojsintuta*).

Summarizing, many results obtained from the few other studies roughly coincide with the findings in Bolivia. However, the particular situation of amphibian distribution along the eastern Bolivian slopes appears complex and is hardly to compare to the mentioned patterns from other geographical regions. There appears to be general coincidence with respect to the change of abundance and equitability with elevation, the presence of greatest species diversity at mid-elevations (ca. 1000–2000 m a.s.l.), and the more restricted distributions of cloud forest species. Some of the Bolivian cloud forest species seem to have very limited distributions, occurring for example only in the "La Siberia" region (e.g., *Bufo amboroensis, Gastrotheca lauzuricae, Phrynopus kempffi, Telmatobius edaphonastes*), or they are very rare species and difficult to discover. Other cloud forest species inhabit a considerably larger area, although they still have a restricted pattern of distribution in the forests of the Departamentos Cochabamba and Santa Cruz (e.g., *Bufo quechua, Eleutherodactylus fraudator, E. pluvicanorus, Telmatobius yuracare, Telmatobius* sp. A). Aquatic species of *Telmatobius* are generally restricted to separate drainage systems and according to the aquatic habit, their possibility to disperse appears to be limited. Thus, it is somehow surprising that *T. yuracare* occurs within an east-west expansion of at least 160 km in the cloud forest belt. A third category refers to more widespread species occurring in the montane rainforests, and a fourth category to widespread lowland species invading the Andean slopes. These four patterns are generally also present in *Eleutherodactylus* distributions in Colombia and Ecuador (Lynch 1998, Lynch & Duellman 1997) and do probably reflect historical events of speciation and dispersal (see later).

In the following, different factors and criteria which might be responsible for the diversity patterns found in Bolivia are questioned and discussed.

Ecological determinism

The ecological determinism model proposes that present-day ecological factors are the major determinant of distributions, regardless of whatever historical changes in distribution have occurred through dispersal or vicariance. Ecological determinism can be regarded at least at two levels. One is the habitat distribution of a species and the other is the ecogeographical distribution of a species. This means, species generally having distinctly different distributions but occur in sympatry at a certain locality inhabit strikingly different habitats. With respect to amphibians this mainly refers to open and forest habitat species. At this level ecological determinism undoubtedly is of major importance. The situation is more complex when regarding ecoregional distribution of species. The Neotropics contain a large variety of environments. Obviously, species are limited in distribution within portions of this environmental gradient. Distribution patterns of amphibian species were shown to fit well into ecogeographical domains (e.g., MacArthur 1972, Heyer & Maxson 1982a) and Vuilleumier & Simberloff (1980) suggested recent ecological factors rather than historical processes to be the determinant for patchy distributions in high-Andean birds. However, the ecological determinism model often is not able to explain restricted distributions within an ecogeographical domain. Nevertheless, in the following amphibian distribution and diversity patterns revealed by the present study are discussed with respect to ecological conditions.

Recent climate

Before discussing different models mainly based on historical climate changes which possibly determined differentiation, it is here focused on recent climate conditions influencing distribution of species. Usually, diversity of biota is limited when certain natural resources are limited. One of these resources is the availability of fresh water. Comparisons of amphibian species richness among various regions in the tropics emphasize the importance of moisture to the richness of the amphibian fauna (Schall & Pianka 1978, Duellman & Trueb 1986). This refers to latitudinal gradients corresponding to decreasing or increasing moisture as well as to moisture gradients at the same latitude. Temperature plays another important role in amphibian distributions. As concluded by Rome et al. (1992), thermal adaptations of tolerance limits commonly is evident in interspecific analyses and is likely to play an important role in setting temporal and distributional limits on amphibians. An aspect which is usually not considered in amphibian biogeography is their reproductive biology, but it has been shown that development of eggs and embryos is closely related with temperature (Moore 1939, Zweifel 1968). Thus, changes in temperature, as well as humidity, most likely play (and have played) an important role in dispersal and differentiation of amphibians (Lynch & Duellman 1997).

When regarding amphibian distribution in Bolivia's lowland ecoregions, the amount of species richness in each ecoregion seems roughly to correlate with the amount of precipitation. The decrease of species richness from the Amazonian lowland rainforests south to the dry Chaco lowland forests fits into this scheme. However, the humid savannas of the Beni have similar amounts of rainfall compared to the surrounding regions, but exhibit an apparently lower species diversity. Biogeographic relationships of the Beni savannas were described and discussed by Hanagarth & Beck (1996) who discovered strong affinities to the Brazilian Pantanal and Campo-Cerrado formations. Thus, the homogeneous open grassland habitat in connection with certain historical factors may constitute relatively small species numbers. Comparatively low species diversity in the Chaco and Chiquitanía forests is obviously due to precipitation as a limited resource. All species occurring in these regions are well-adapted to distinct seasonal environments and a short breeding period. The same is generally true for the southern Andean slopes (Río Seco transect).

Values in species richness are somehow different when regarding the Andean regions. The region with highest amount of precipitation in Bolivia is situated at the eastern Andean slopes of the Departamentos Cochabamba (e.g., Ibisch 1996, Kessler 1999). There, maximum rainfall occurs at elevations between 1500 and 1800 m a.s.l. However, despite containing the highest degree in alpha diversity of all Andean regions, amphibian communities in the Yungas de Cochabamba are not the richest ones when considering total Bolivia (although most species were found at the elevational level of highest precipitation). In other Neotropical regions, anuran communities at 1000–1500 m a.s.l. were also found to be especially diverse, because montane forest species occur together with lowland species entering the slopes (e.g., Duellman 1982b). The decrease of temperatures with altitude is another climatic factor limiting diversity of ectothermic organisms, but might be neglected with respect to the lower montane forests of the Chapare region. This phenomenon is of importance when regarding the upper montane forests and high-Andean regions.

With respect to amphibians, alpha diversity on the slopes of the Yungas de La Paz region is apparently lower than in the adjacent Yungas de Cochabamba. This correlates with distinctly lower amounts of precipitation in the Yungas de La Paz region (about 2000–2500 mm versus 4000–6000 mm/year). In addition, the PAE and NJAE analyses revealed distinct differences between the Yungas de Cochabamba and the Yungas de La Paz supporting the hypothesis that diversity and endemism are correlated with regions of ecoclimatic stability. According to Fjeldså (1995), regions of ecoclimatic stability can be expected where highest amounts of rainfall occur at present-day. Thus, ecological conditions in the Yungas de La Paz region have probably undergone more drastic changes during the Pleistocene than conditions in the Yungas de Cochabamba (see also Simpson 1979). However, sampling efforts in the Yungas de La Paz region are largely

incomplete and by estimates the region covered by the Parque Nacional Madidi was suggested to be one of the most species-rich conservation areas at least in the Neotropics (Remsen & Parker 1995). The high species diversity suggested for the Madidi area might be due to lowland species invading the slopes as well as to greater habitat diversity compared to the Chapare region. Nevertheless, Fjeldså & Rahbeck (1998) pointed out that although rich in species, the Madidi area contains comparatively low rates in endemic species, corroborating their theory of ecoclimatic extremely stable areas.

In high-Andean regions the decline in alpha diversity is probably due to the low temperatures combined with a lower degree of humidity. Temperatures in the Altiplano frequently drop below zero during the night which would restrict anuran activity to daytime. In Bolivia, the species *Pleurodema cinereum* was observed being active in the Altiplano only during the day, whereas at lower altitudes it is almost strictly nocturnal. Even during the day, special adaptations are required allowing activity. Andean anurans were found basking to rise their body temperature (e.g., Sinsch 1989). In addition, rainfall is distinctly seasonal in most regions of the Altiplano and the total amount of precipitation is significantly lower (100–800 mm/year) compared to the eastern slopes.

However, low temperatures do not only influence high-Andean diversity but probably also amphibian diversity at the Andean slopes. The frequent occurrence of Patagonian winds ("surazos") has at least impact on the slopes south of Santa Cruz de la Sierra, but reaches also parts of the cloud forests and upper montane rainforests of the Departamento Santa Cruz and Cochabamba. During own investigations in montane forests, occurrence of "surazos" always resulted in a significant decrease of anuran activity, although sufficient moisture in form of rainfall was present. It might be that localities with exposure to "surazos" generally exhibit a lower degree in alpha diversity. This is partly corroborated by the fact that alpha diversity was similar at humid montane forest sites with high habitat diversity but exposure to "surazos" and sites with low habitat diversity without "surazo" influence.

Recent climate, in connection with historical processes of dispersal, is probably also responsible for the close relationships of the dry Chaco lowlands and the inter-Andean dry-valleys. As emphasized by various authors, both ecoregions share certain faunal and floral elements (e.g., Harvey 1999, Ibisch & Böhme 1993, Ibisch et al. 1996, Köhler et al. 1995b, 1998b, Köhler & Lötters 1999c). The distinctly seasonal and dry climate of the inter-Andean valleys account for the survival of Chacoan species which may have invaded the valleys through orographic depressions at the eastern Andean slopes (e.g., the Río Pirai valley depression) during dry interglacial periods of the Pleistocene. It has already been suggested that physiological adaptations of species from temperate lowlands allow them to invade a wide array of altitudes (Lynch 1986a). That means, mountain passes are 'biologically' higher in the tropic than in temperate zones (Janzen 1967).

Recently, Pounds et al. (1999) found a correlation between mist frequency in trop-
ical montane forests of Costa Rica and population crashes in several anuran
species. In the late 1980s, the total frequency in dry days increased and resulted
in less frequent mist occurrence. Three events of population crashes were corre-
lated with the three years that had maxima in the number of dry days. The results
for anurans are corroborated by parallel effects in populations of anoline lizards
and birds. Amphibian populations are probably sensitive to recent climate changes
and not only their abundance but also their distribution may change considerably
within few years. It has to be shown, if global warming (through the greenhouse
effect) will also affect Bolivian montane forest populations (see Still et al. 1999).

Habitat diversity

Many efforts have been undertaken to explain the coexistence of species in tropi-
cal communities. Community ecologists have emphasized the importance of inter-
specific interaction in the production of patterns of ecological characteristics
among species in assemblages. These theories assume that adaptive selection is
the main force ordering the pattern (see Schoener 1988, Wanntorp et al. 1990).
According to Schoener (1974), resource partitioning is one of the most important
mechanisms regulating the syntopic occurrence of species. The three major ways
in which similar species partition resources were identified as habitat, time, and
diet. The author emphasized that methods of resource partitioning differ notably
between terrestrial ectotherms and endotherms. With respect to anuran communi-
ties, it has been demonstrated that there are distinct differences among the species
regarding feeding ecology (e.g., Toft 1980, Parmelee 1999), general habitat use
and activity pattern (e.g., Toft 1985, Duellman 1990, Rodríguez 1992), as well as
parameters in calls and use of microhabitat for calling (e.g., Hödl 1977, Duellman
& Pyles 1983, Schlüter 1984, Reichle & Köhler 1998). The reproductive mode of
amphibian species is another important component directly connected with the use
of breeding habitat (see Crump 1974, Hödl 1990). In the following, diversity pat-
terns in amphibians inhabiting the Bolivian montane forest regions are discussed
with respect to differences in habitat diversity.

In the results chapter, the heterogeneity in habitat diversity of the sampled sites
was already mentioned. At the upper elevations of the Amboró transect, several
sites contain a mosaic of different habitats (e.g., open grasslands, semi-humid
forests, humid forests, secondary growth, deciduous forests) including the pres-
ence of different types of water bodies for reproduction (compare also Köhler et
al. 1995b). However, alpha diversity at a certain site of limited expanse is compa-
rable to that at sites with more homogeneous habitat structures. The communities
found at single sites within the upper Amboró transect contained approximately
the same numbers of species as sites in the Chapare transect where only a limited
diversity of habitats occurs. When considering a slightly larger expanse of the
Amboró sites, notable differences in beta diversity are obvious. The species-

turnover rate is remarkably higher in the upper Amboró region. That means, species are linked to certain habitat structures and the mosaic of habitats is reflected by a distributional mosaic of distinct amphibian communities. Although some single Amboró sites apparently provide greater habitat diversity, alpha diversity appears to be limited through other factors (i.e., climate). In the case of the Bolivia's Chapare region, one important factor is the availability of breeding habitats. The orographic conditions at upper elevations of the Chapare region largely prevent the presence of lentic water bodies as an important breeding habitat for anurans. Thus, communities are dominated by species with terrestrial development or reproduction in lotic water. Species restricted to lentic water for reproduction are completely lacking. Nevertheless, the permanent humidity and the dense vegetation provide excellent conditions to harbor well-differentiated communities.

Nevertheless, habitat diversity (or habitat fragmentation) apparently does determine alpha diversity when climatic conditions are similar. When comparing the lowermost elevations (500 m a.s.l.) of the Amboró and Chapare transects, differences in alpha diversity are tremendous. Whereas only 17 species occur at 500 m a.s.l. in the Chapare transect, about 50 species occur in sympatry at the Amboró site Mataracú. Climatic conditions at both sites can be regarded as similar, with the exception that the absolute amount of rainfall is greater at the Chapare site. The site Mataracú comprises a variety of habitat types (i.e., streams, swamps, temporal ponds, open grassland, disturbed primary forest, secondary growth, scrub), providing suitable conditions for forest and open habitat species as well as for pond breeding species. The mosaic of habitat types concentrates on much smaller scales compared to habitat distribution at the upper elevations of the transect. Therefore, most of the species occur together within very short distances or even in micro sympatry. Only two open habitat species (*Adenomera hylaedactyla* and *Leptodactylus fuscus*) occur at the Chapare site where they are restricted to disturbed roadside habitats. Greater habitat diversity at the Chapare site would probably result in greater alpha diversity in amphibians (especially in pond breeding hylids), because many more species than present are generally distributed in the peri-Andean forests of the Departamento Cochabamba.

At the sampled sites of the drier Río Seco transect, habitat structures are considerably less diverse than in certain Amboró sites, but apparently more diverse than in the Chapare sites. However, alpha diversity in the Río Seco transect is the lowest of all three regions. Thus, recent climate, i.e. the amount of precipitation, generally appears to be a stronger determinant than diversity of habitat types.

In a recent paper, Zimmerman & Simberloff (1996) questioned the assumption that the distribution of habitat use in anuran assemblages is only due to interspecific interactions, environmental disturbance, and resulting adaptive selection. From their studies of Central Amazonian rainforests, the authors concluded that

the use of general breeding habitat (stream, pool, terrestrial) is probably determined by phylogenetic lineage, because reproductive mode and developmental habitat are strongly associated with species' systematic position (family or generic level). Additionally, Zimmerman & Simberloff (1996) found only few stream-breeding species, although streams were common in the study area. This parallels the situation in other Amazonian communities (e.g., Duellman 1978c, 1990, Rodríguez & Cadle 1990). In contrast, about half of the anuran species at a Bornean site with similar habitat structures were found to be stream breeders (Inger 1969). These results support the assumption of Ricklefs (1987) that historical events of species production are often overlooked when regarding the ecological distribution of species within communities. Related species may share behavioral and physiological traits, because they are descended from a common ancestor, not because of similar selection pressures and convergent evolution (e.g., Gittleman 1986). Thus, possibly few riparian taxa colonized South America and/or those that did never radiated extensively for reasons not related directly to their reproductive mode. On the other hand, Zimmerman & Simberloff (1996) found close relationships of species and subhabitat (or microhabitat) use at the local level, suggesting that adaptive selection is the determinant of narrow distributions within major habitat types.

The scarcity of stream breeding species is also evident at several Bolivian lowland sites. At the Andean slopes, very few hylid frogs are restricted to stream habitats (e.g., *Hyla armata*), whereas others appear primarily riparian but reproduce in streams and lentic water (e.g., *Hyla andina, H. marianitae*). Other stream breeding species on the slopes mainly refer to the Bufonidae (e.g., *Atelopus tricolor, Bufo veraguensis* group), Leptodactylidae (*Telmatobius* spp.), and Centrolenidae (*Cochranella* spp., *Hyalinobatrachium bergeri*). At least within the Hylidae, Bufonidae, and Leptodactylidae reproduction in streams has evolved convergently. Thus, the situation at the humid Andean slopes does not completely agree with those at Neotropical lowland sites. However, the adaptive ability of hylid frogs to develop in lotic water indeed appears to be limited. Generally, there seem to be significant differences in portions of stream breeding species in Neotropical versus Asian (e.g., Inger 1969) and Madagascan communities (Glaw & Vences 1994). These differences are hardly to explain with ecological conditions, supporting the suggestions by Zimmerman & Simberloff (1996).

Ritchie & Olff (1999) developed another hypothesis for mechanisms which determine species diversity. The authors employed spatial scaling laws to describe how species with different body sizes find resources in space, and how limits to the similarity in body size between any two species predicts the potential number of species in a community. Ritchie & Olff (1999) predicted that body size determines the abundance of food and resources that a species perceives. Their following analytical approach is supported by extant species richness–body size distributions in East African herbivores and Minnesota plants. The analysis formalizes the idea

that diversity depends on the number of spatial niches (e.g., Morse et al. 1985), and indicates that coexisting species cannot infinitely partition space (see Rosenzweig 1995). However, the model of Ritchie & Olff (1999) refers to simplified relationships only and may not explain diversity in communities including species that use different resources and different habitats. In addition, other factors like colonization limitation and biogeographical history are neglected by the model. Thus, spatial scaling laws may be applicable to the distribution of herbivorous mammals in East African savannas, but they appear largely inappropriate to explain species diversity in tropical amphibian assemblages.

The relationships of amphibian diversity in Bolivian montane forest regions to climate and habitat diversity generally agree with the observation of Duellman (1989) that in areas of higher climatic stability and vegetational heterogeneity there is a greater number of species than in less stable and less heterogeneous areas. Stability of climates and vegetation creates a stable environment for animals and allow them to specialize on food and microhabitat. Thus, regions with stable climates permit the evolution of finer specializations than do regions with more erratic climates.

Historical perspectives

In the foregoing chapters, principal determinants of diversity and distribution were discussed largely excluding historical perspectives. However, there remain the basic questions "Where do all the species come from?", "What are the mechanisms of speciation?", and "Where were the centers of speciation?". But discussing these questions in absence of precise phylogenetic hypotheses is a waste of time (Ball 1975), because this would never approach reality. Another point is that it should not be searched for a singular mechanism responsible for speciation events. Speciation (and also extinction) is a still ongoing process. There are young and old species, and the processes that have produced these species might be different. In spite of the complexity of the subject and the lack of required data for a well-founded discussion, several biogeographical aspects and hypotheses are considered in the following with respect to montane forest amphibians of Bolivia.

Various models have been developed to explain speciation, differentiation, and biogeographic patterns of organisms (see e.g., Endler 1977, Rosenzweig 1995). One of the most influencing insight has been the recognition that tropical regions have undergone recent and dramatic physiogeographic and climatic changes, rather than having a long history of ecological stability. This realization led to the theory that forest fragmentation was directly responsible for the diversification of tropical forest biota via allopatric speciation in isolated refuges during dry periods of the Pleistocene (the refuge theory; e.g., Haffer 1969, 1979, Simpson 1979, Simpson & Haffer 1978). It has been argued that the best supporting evidence for distributions correlating with refugia is current distribution which coincides with the proposed location of refugia. Distribution data for several groups of organisms

were used to support the refuge theory: birds (Haffer 1974); butterflies (Brown 1976, 1982); bees (Carmago 1978); lizards (Vanzolini 1970, Vanzolini & Williams 1981); frogs (Lynch 1979, Duellman 1979b, 1982a); scorpions (Lourenço & Florez 1991); and plants (Prance 1982, 1987). The argumentation that current centers of endemism and diversity reflect Pleistocene refugia is based on the presumption that species are still in progress of dispersal from these refuges. Ideally, refugia should be based on geomorphological data rather than on biotic distribution patterns. Rosen (1978) identified areas of endemism by mapping areas of geographical activity (events which might produce range disjunctions) and then selecting the undisturbed areas as potential areas of endemism. Evidence for the loss of rainforests during Pleistocene dry cycles was provided through the discovery of xeric fossil soils within existing rainforests (Ab'Saber 1977). However, the Pleistocene forest refuge hypothesis has been doubted by other authors. Endler (1977, 1982a, b) demonstrated that present-day ecological conditions may also be the primary determinants of patterns of differentiation. In addition, biochemical studies of species of the genus *Leptodactylus* in the Amazon basin suggest that speciation in this group were Tertiary rather than Quaternary events (Heyer & Maxson 1982a). Lynch (1988) discussed the problems accompanying Haffer's (1969) theory circumstantially and finally stated that no amount of corroboration serves to test the model nor does it improve its scientific credibility.

More recently, the refuge theory experienced a differentiated interpretation in that refuges were regarded areas with extremely stable ecological conditions, independent from their type of vegetation (Fjeldså 1994, 1995). Thus, this new interpretation does not necessarily imply that continuous rainforests were divided into patchy rainforest refuges. Rather, it is suggested that in certain areas ecological conditions were highly variable over time, so that some species survived these disadvantageous periods exclusively in zones with extremely stable climatic conditions. However, extremely stable ecoclimatic conditions were suggested to have occurred in areas with present-day high amounts of precipitation. Remote sensing techniques revealed that hotspots in diversity and endemism correlate with the suggested stable areas (Fjeldså et al. 1999). By using DNA hybridization data to identify the ages of species, Fjeldså & Lovett (1997) pointed out that some current distribution patterns are probably the result of post-speciation redistribution events during the Pleistocene.

The foregoing paragraphs demonstrate the difficulties connected with a historical interpretation of recent distributions. What at least appears to be true is that several speciation events occurred before the Pleistocene age, that Pleistocene events influenced distribution of organisms, and that orographic isolation also played an important role for speciation. With respect to Bolivian montane forest species, the situation is further complicated by the lack of phylogenetic data. Relationships between amphibian taxa are suggested only according to morphological similarities (which indeed might reflect phylogenetic relationships); genetic data provid-

ing insight to the age of species are almost completely lacking. Nevertheless, some recent patterns of Bolivian amphibian distribution are in the following compared with respect to their coincidence with proposed models.
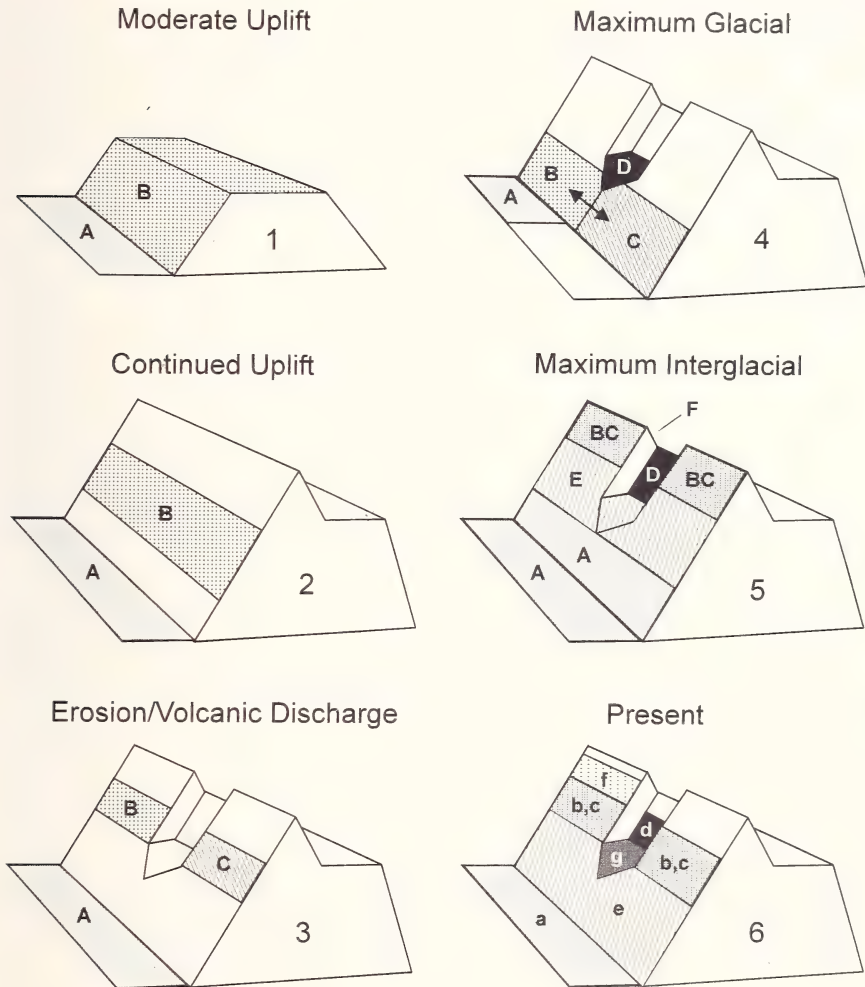

Fig.75: Speciation model for taxa with respect to uplift and erosion events in the Bolivian Andes, followed by Quaternary climate changes. Lineage A is restricted to humid areas in the lowlands; continued uplift results in uninhabitable elevations that fragment the range of lineage B; depression distributions of lineages B and C results in their dispersal into the areas previously occupied by only one of the lineages. Lower case letters identify derived lineages that are products of lineages from earlier times (upper case letters). "La Siberia" endemics would correspond to f. Modified after Lynch & Duellman (1997).

Speciation models of Andean anurans based on vicariance events resulting from alternating climatic depression and elevation were proposed by Duellman (1982b) and Lynch (1986a). In combining data on orogenetic history and climatic changes, Lynch & Duellman (1997) proposed a vicariance speciation model for anurans in western Ecuador. The authors suggested that primary speciation events were connected with the initial Andean uplift (fossil records provided evidence for many amphibian groups were established before most of the Andean uplift occurred – e.g., Báez & de Gasparini 1979). During the uplift, anuran species adapted to changing climates and speciated in connection with the orographic fragmentation of the once contiguous lowlands. With continuing uplift, upland species would be subject to vicariance events (erosional fragmentation of elevational zones, deposition of volcanic discharge resulting in unsuitable habitat). Subsequently, glacial stages would further fragment lower elevational zones, whereas interglacial stages would have the effect of additional vertical slicing of distributions on Andean slopes (Lynch & Duellman 1997). This model emphasizes climatic compression and vertical up and downshift of vegetational zones during Pleistocene times, which possibly could result in a mixture of species from the uplands and lowlands. This model incorporates most extensive distributions of lowland species and narrow but elongated distributions on the slopes (Fig.75). The final drawing provided by Lynch & Duellman (1997: Fig.86), reflecting present-day pattern, largely coincides with Bolivian patterns (Fig.75:6). Bolivian species invading the slopes but have extensive distribution along the Andean foot are for example *Bufo poeppigii, Eleutherodactylus cruralis, E. olivaceus,* and *Leptodactylus rhodonotus.* These species may regarded as derived from lowland species during the Pleistocene, because all of them have relatives with extensive distributions in the Amazon basin (see Lynch & Duellman 1997 and Fig.75:6,e). Species on the slopes with latitudinally elongated but more restricted distributions refer to species occurring in upper montane rainforests and cloud forests (e.g., *Bufo quechua, B. justinianoi, B. stanlaii, Eleutherodactylus fraudator* group, *Ischnocnema sanctaecrucis, Phrynopus* spp., *Phyllonastes carrascoicola, Telmatobius yuracare*). The model by Lynch & Duellman (1997) predicts that related species evolved through vicariance events previous to the Pleistocene, at present occur together in sympatry at the same elevational level (see also Peters 1973, Lynch & Duellman 1980). This is possibly true for Bolivian species of the *Eleutherodactylus fraudator* group, *Bufo veraguensis* group, and the *Hyla pulchella* group. Moreover, the model predicts that some species at the upper forested edge of the slopes remain isolated and distinctly restricted in their distribution due to limited possibilities to disperse because of orographic barriers (i.e., deep Andean valleys). This would possibly explain the presence of species endemic to the "La Siberia" region. Another prediction is the presence of species restricted to certain incisions within the slopes (i.e., deep valleys). The findings suggesting cer-

tain Bolivian species to be restricted to the Chapare region would corroborate this prediction, but, however, there is the chance that these species will be discovered in adjacent regions, if further sampling efforts take place. However, the coincidence of Lynch & Duellman's (1997) model with the Bolivian pattern would be somehow less convincing, if the assumption is true that the genus *Eleutherodactylus* invaded the central Andes from Amazonian lowlands subsequent to the uplift (Duellman 1979c).

Another vicariance event possibly took place when glaciers partly covered the Yungas de La Paz region during glacial periods of the Pleistocene (see Simpson 1979). This assumption is congruent with the predictions of the hypothesis of eco-climatic stable areas (see Fjeldså & Rahbeck 1998) as well as with the results of the PAE and NJAE analyses for amphibians, separating the amphibian faunas of the Amboró and Chapare regions from those of the Yungas de La Paz and the slopes of southeastern Peru. It might be suspected that the Yungas de La Paz region was alternately invaded by lowland forms subsequent to glacial periods. The distributional boundary between the Yungas de Cochabamba and La Paz also correlates with the so-called Ichilo Fault, a line where the eastern Cordilleras narrow in response of the Cretaceous collision of the Nazca and South American plates (James 1971, Simpson 1979).

Besides the different forms of vicariant speciation models (allopatric speciation), a gradient model (parapatric speciation) has been developed (Endler 1977, 1982a, b). The differences in the historical sequence of population divergence and resulting phyletic patterns between the vicariant and gradient models projected on two adjacent valleys on the Andean slopes are shown in figure 76. The diagram incorporates the elevational distribution of a species within a single drainage system as well as latitudinal distributions among different drainages. The allopatric pattern of divergence predicts that adjacent taxa at the same elevation, but in different drainages, should be more closely related to one another than to adjacent taxa in the same drainage but at different elevations (Fig.76 A). The parapatric speciation model predicts that the ancestral species has sufficient dispersal potential to become widespread across a range of habitats. Such environmental variation would provide a sufficiently strong gradient of selection pressures to produce divergence between populations that potentially remain in contact. The predicted phyletic relationships of species differentiated through this model are opposite to those of the allopatric model (Fig.76 B). The ancestral taxa A and A' are not each other's closest relatives, but are individually closest relatives of each of the derived taxa B and B'.

Although no genetic data are available to discover actual phylogenetic relationships of the amphibian taxa occurring on Bolivian slopes, currently suggested relationships seem to support the allopatric speciation model. As mentioned above for Bolivian montane forest amphibians, seemingly related species occur together
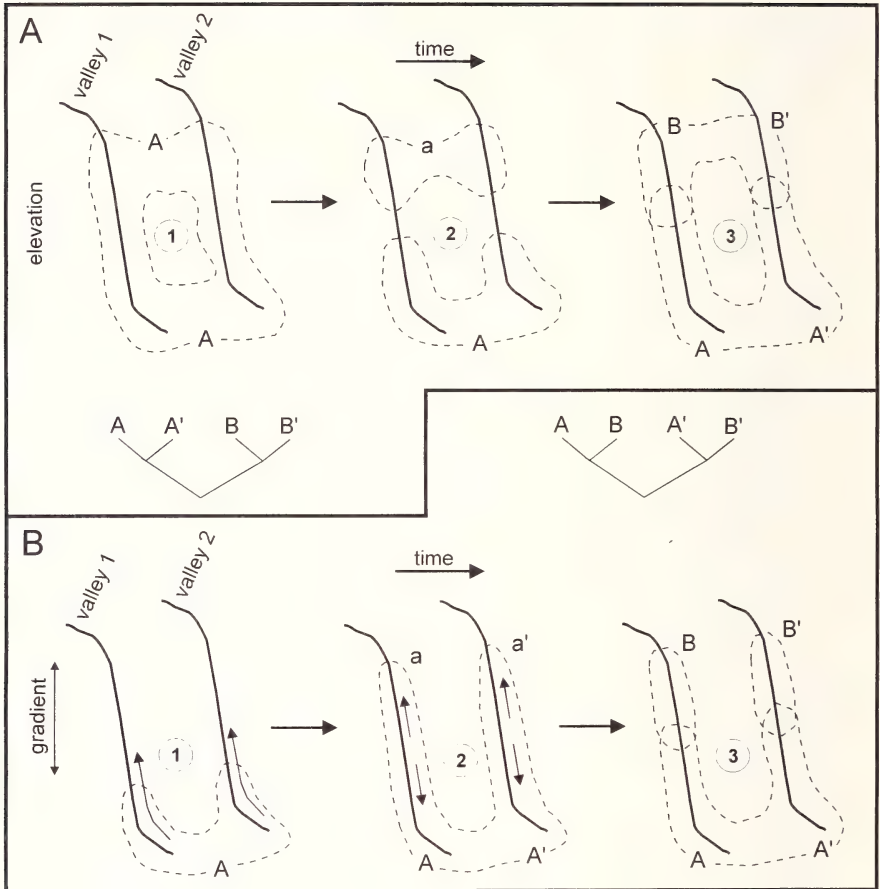
Fig.76: Schematic representation of sequential patterns of differentiation among populations of an ancestral species that diverges by (A) the allopatric speciation model, and by (B) the gradient, or parapatric speciation, model. Time is on the horizontal axis, elevational gradient on the vertical axis. The distribution of populations across two adjacent river valleys is indicated. The cladograms show the predicted phylogenetic relationships among extant taxa that have speciated by these two models. Redrawn from Cadle & Patton (1988).

at similar elevations in adjacent drainage systems of the Amboró and Chapare regions (e.g., species of the *Eleutherodactylus fraudator* and *Bufo veraguensis* groups). Seemingly, only very few parapatrically distributed species pairs occur within the same drainage system which should be more common, if species differentiated through processes postulated by the gradient model. Biogeographical analyses of anuran distribution patterns in the Andes of Colombia and Ecuador also support an allopatric speciation model (Lynch 1998, Lynch & Duellman

1980, 1997). Also the investigations of elevational transects in southeastern Peru by Cadle & Patton (1988), which were accompanied by genetic studies, argue for vicariance events. At the current state, the vicariant model provided by Lynch & Duellman (1997) appears to be the most suitable one to explain the distribution patterns of Bolivian montane forest amphibians.

However, the knowledge of amphibian distribution and phylogenetic relationships still is in such a fetal stage that parapatric or even sympatric speciation events due to selection pressures might often be underestimated or neglected. Evidence for sympatric speciation has been provided by genetic analyses suggesting monophyly of cichlids occurring in isolated crater lakes (Schliewen et al. 1994). There is no reason to believe a priori that amphibians do not speciate sympatrically. The use of methods such as the molecular clock in closely related and syntopically occurring anuran sibling species (some of them are apparently distinguished only by advertisement call characteristics) would probably be helpful to throw some light on the age of species and the mechanisms of their genesis.

Another mostly disregarded question in discussions on historical biogeography concerns the speed and ability of organisms to disperse. Usually, dispersal speed in amphibians is suggested to be significantly slower than in birds or larger mammals. This might obviously be true, but the question is, if these differences in dispersal speed are of any significance when considering periods of several 10,000 years. Observations on open habitat anuran species invading large disturbed areas shortly after the clearing of forests suggest that amphibians have the ability to occupy previously uninhabited areas promptly and to disperse through them, if habitat conditions agree with ecological preadaptations. Principally, there is no reason to beleive that forest species have more limited dispersal capabilities to enter suitable habitats. Thus, discussions should probably focus more on the distributions of habitats instead of generally predicting limited dispersal capabilities.

Recommended conservation priorities

Nowadays, it is becoming clear that human impact accounts for environmental changes which probably exceed those by natural causes during the Pleistocene. Besides the interests which should further focus on biogeographic history and phylogeny, the rapidly vanishing forests in the Neotropics urgently call for quick inventories of the present fauna as a basis for well-managed conservation projects. In a recent paper, Pimm & Raven (2000) estimated the current number of species disappearing every decade by extinction to be 24,000 per million existing species. If we assume the existence of only 10 million species on earth, than these 24,000 species go extinct every year. Several efforts have been undertaken to find the most effective way how to preserve diversity in certain groups of organisms (e.g., Sayer et al. 1990, Da Silva & Sites 1995). One promising approach is the identification of diversity hotspots. The hypothesis presumes that the majority of the earth's biota can be protected through the conservation of areas where high num-

bers of species concentrate (e.g., Pimm et al. 1995). Myers et al. (2000) identified 25 hotspots on earth, 17 of them being tropical forest areas. They considered the tropical Andes to harbor 6.7% of all global plants and 5.7% of all global vertebrates, both representing the highest values of all considered hotspots. However, the same authors stated that the tropical Andes have already lost 75% of their primary vegetation. Considering the whole tropical Andes as a diversity hotspot is probably not wrong, but the possibility to protect this vast area in total is absolutely not realistic, because conservation policy occurs at a more regional level. In practice, there is the need to identify hotspots on a finer scale. A useful tool for this purpose seems to be remote sensing technique in combination with Geographical Information Systems (GIS) (e.g., Fjeldså et al. 1999, Kress et al. 1998). However, the use of this techniques and the analyses for amphibians are still in progress in Bolivia, and it is therefore not possible to refer to respective results.

As far as known, no Bolivian amphibian species has become extinct hitherto. This is probably in contrast to the Andes of northern South America, where population declines due to the clearing of pristine montane forests have been recognized. However, as already pointed out, several Bolivian species have extremely restricted distributions in regions highly endangered by habitat destruction and therefore must be considered vulnerable. These species mainly inhabit cloud forests and upper montane rainforests and most of them are Bolivian endemics. Thus, the protection of upper montane forests and "Ceja" forests (only barely included in existent conservation areas) appears to deserve highest priority. Especially the "La Siberia" region, subsequently excluded from the Parque Nacional Amboró, is of very limited expanse and harbors a highly endemic anuran fauna. The same might be true for the uppermost elevations of the Chapare region (not investigated during the present study) (compare Fjeldså & Rahbeck 1998). Although less rich in endemic species, the humid forests along the Andean foot harbor the greatest species numbers. At least two regions seem to deserve the status of local hotspots: (1) the lowermost slopes and Serranias of the Yungas de La Paz, already covered by the Parques Nacionales Madidi and Pilon Lajas, and (2) the peri-Andean forests of the northern Amboró area. Successful protection of these two areas would probably cover more than half of Bolivia's amphibian fauna. However, most of these species have wide ranges and also occur in adjacent Peru, so they would not considered endangered. In contrast, the vanishing of Bolivian cloud forests would definitely result in extinction of many species. The species-rich mid-elevations of the humid Andean slopes are less endangered due to very steep slopes which make access to and exploitation of the forests more difficult. Thus, conservation efforts should focus on the upper and lowermost edges of humid montane forests, because these regions are endangered by good accessibility and high population pressures.

Future research

Like many other studies on tropical biota, this study demonstrates that we are far from understanding the evolution of organisms that led to current distribution, diversity, and ecological communities. Sometimes, it appears that any further work will only reveal that much more than presumed remains to be known. The remarkable increase of amphibian species recorded from Bolivia during the past decade (De la Riva et al. 2000) gives certainty that we are still in an initial phase of inventory. For the majority of species few or nothing is known about their biology and/or phylogenetic relationships. So, future research on Bolivia's amphibians is urgently needed to receive a more accurate imagination of its real diversity. These research projects should first focus on faunistic surveys of previously uninvestigated areas as well as on already investigated sites, because species inventories are of basic importance for the proposal of new conservation areas. These surveys should cover the most threatened regions first, like for example the cloud forests. Second, long term monitoring is required to estimate the influence of habitat destruction and climatic changes on amphibian populations. Amphibian decline has been noted for several regions in the northern Andes as well as in lower Central America and it has to be shown, if similar phenomena also occur in Bolivian populations. Again, attention should be drawn to upper montane forest and cloud forest communities, because they were demonstrated to react sensitively in response to climatic changes (Pounds et al. 1999). If we manage to realize these efforts, much would be done not only for the understanding of Bolivia's amphibian diversity but also for its preservation. In this sense, I hope that the present study will contribute to stimulate further research.

SUMMARY

Amphibian diversity in Bolivia: a study with special reference to montane forest regions

With respect to faunistic studies, Bolivia still has to be regarded one of the least explored countries in South America. Intensified investigations on Bolivian amphibians during the past decade led to an enormous increase of knowledge. However, the still ongoing discoveries of new taxa and biological phenomena clearly demonstrate the defectiveness of this knowledge. The present study provides a first comprehensive analysis of amphibian diversity in Bolivia. Distribution and ecology of species as important components of biodiversity are analyzed. Special emphasize is set on montane forest regions along the eastern Andean slopes (humid Yungas of the Departamentos Cochabamba and Santa Cruz, semi-humid montane forests in southern Departamento Santa Cruz). Fieldwork in the respective regions was conducted during the rainy seasons 1997/98 and 1998/99. In addition, data from museum collections and the literature, as well as from own investigations in 1994 were included in the analysis.

An updated checklist of Bolivian amphibians is provided. The known and expected distributions in Bolivia's Departamentos and twelve defined ecoregions are given for all 200 species. Forty-five species are considered Bolivian endemics (= 22.5%). The provided checklist is commented concerning taxonomic problems and miscellaneous notes. *Eleutherodactylus peruvianus* is deleted from the list, *Eleutherodactylus dundeei* is added, and *Eleutherodactylus bisignatus* is resurrected from synonymy. In addition, 61 species predicted to occur on Bolivian territory are listed.

The spatial distribution of species diversity within Bolivia is analyzed and figured with respect to the distribution in twelve ecoregions. The Amazonian lowland rainforests harbor the largest portion of Bolivian Amphibians (45.1%), followed by the moist forest of the pre-Cambrian shield (35.4%) and the humid transition lowland forests (34.9%). The drier Chiquitanía and Chaco forests contain dis-

tinctly lower species numbers. Species diversity in the Bolivian lowlands is decreasing when traveling the ecoregions from the north to the south. This general trend is interrupted by the Beni wet savannas exhibiting comparatively low species diversity (15.4%). The per-humid Yungas montane forests harbor the greatest species diversity of all Andean regions by far (32.0%). Regarding political endemism, 69.6% of all species occurring in the cloud forests ("Ceja") are restricted to Bolivia. The per-humid Yungas follow with 54.0% endemic species. In both ecoregions, endemism is distinctly over-represented, whereas political endemism is practically absent in lowland ecoregions. Only the Amazonian rainforests contain 4.5% endemic species. This value is due to species distributed in the humid peri-Andean forests. Ecoregion endemism is great in the lower Yungas forests and the peri-Andean forests (together 51.6%) extending into southern and central Peru, as well as in the upper Yungas montane forests and cloud forests (together 55.7%). Approximately one-fourth of all Bolivian Chaco inhabiting species are restricted to this region which extends to northern Argentina and Paraguay. Besides the total region of humid eastern Andean slopes, four hotspots of diversity are tentatively identified: Alto Madidi region, "La Siberia" region, Samaipata region, and eastern parts of the lower elevations of the Parque Nacional Amboró.

The diverse montane forest regions in the Departamentos Cochabamba and Santa Cruz were investigated more detailed. An overview about all 70 montane forest species found in the study area is provided (only species distinctly exceeding 500 m a.s.l. are regarded montane forest species). For every species, information on distribution, natural history, and vocalization is given, as well as notes on its taxonomy, if necessary. The advertisement calls of 33 species are described and figured, many of them for the first time. A brief diagnosis is provided for the unnamed species included.

A model of three more or less 'virtual' transects is established to compare and estimate the diversity patterns in montane forests: 1– Chapare transect (roughly equals the old road connecting Paractito and Cochabamba along the Río San Mateo valley); 2 – Amboró transect (approximately equaling a line from the Samaipata area northeastward to the lowlands); 3 – Río Seco transect (equaling a line with east-west expansion from Provincia Vallegrande to the village Río Seco). The transects are described with respect to their alpha and beta diversity. Ecological comparison include activity patterns, habitat use, and reproductive modes for each of three elevational levels per transect.

Thirty-six species are recorded from the Chapare transect, with greatest species diversity found between 1300–1700 m a.s.l. Communities are dominated by frogs of the genus *Eleutherodactylus*. The most common reproductive mode is direct terrestrial development (44%) followed by tadpole development in lotic water (31%). Lentic water bodies are practically absent. Beta diversity along the elevational gradient is limited, but gamma diversity is exceptional high. Species with

restricted montane rainforest distributions are clearly dominating, and 53% of the recorded species are Bolivian endemics. With 48 species, the Amboró transect appears more diverse. However, this number is partly due to the larger number of sites sampled covering also a larger variety of habitats. Of the recorded species, 42% are Bolivian endemics. Exceptional high beta diversity is present at the upper elevations of the transect (1700–2300 m a.s.l.). The degree of alpha diversity is comparable to that of the Chapare transect. Direct terrestrial development is the dominating reproductive mode (29%), followed by egg deposition in lentic water (24%). The latter value is mainly due to hylid frogs at the lowermost elevational level (500 m a.s.l.). Thirty-one species are recorded from the Río Seco transect, distributed at different elevational levels without significant differences in alpha diversity. In total, alpha diversity of investigated sites is lower when compared to the former transects. Beta diversity also is limited. Reproductive modes adapted to dry and distinctly seasonal environments (explosive breeding at temporary ponds, 35%; foam nest production, 32%) are dominant within the recorded communities. Many lowland species of the Chaco-Cerrado domain enter the Andean slopes up to remarkable elevations, reaching their upper limit of vertical distribution in the transect area. The results support close relationships of inter-Andean dry-valleys and Chaco-Cerrado formations in the lowlands.

With help of "Parsimony Analysis of Endemism" (PAE) and "Neighbor Joining Analysis of Endemism" (NJAE), amphibian communities of three elevational levels (500, 1300–1600, 1900–2200 m a.s.l.) in each transect are compared to each other as well as to other sites along the eastern Andean slopes and the southwestern Amazon basin. The PAE and NJAE analyses revealed the following results: (1) relationships between the Amboró and Chapare transects are stronger than to the Río Seco transect; this is true for all elevational levels considered; (2) the two upper elevational levels of all three transects have larger similarities than each of them to the lowermost level; (3) similarities of the 500 m elevational levels of the Amboró and Chapare transects are larger than those of upper elevations between the same transects; (4) the Amboró and Chapare transects are distinguished from more western Andean slopes, namely the Yungas de La Paz and southeastern Peru; (5) the Río Seco transect has close relationships to the dry and seasonal environments of the Chaco; (6) Mataracú, a site at the eastern edge of Bolivian peri-Andean forests (17°33'S, 63°52'W, 500 m a.s.l.), is closer related to sites in northeastern Bolivia than to sites in peri-Andean forests of Peru.

Findings on amphibian diversity are estimated and classified. Identified patterns are discussed with respect to possible determinants, including ecological determinism and historical perspectives. The patterns seem to agree best with vicariant speciation models. Recommendations for conservation priorities and future research are given.

RESUMEN

Diversidad de anfibios en Bolivia: un estudio considerando especialmente las regiones de los bosques montanos

Con relación a estudios faunísticos, Bolivia se puede considerar como uno de los países menos investigados de América del Sur. La investigación intensificada sobre los anfibios durante los últimos 10 años ha causado un enorme incremento de conocimiento. Los permanentes descubrimientos de nuevas taxas y fenómenos demuestran ilustrativamente cuan incompleto es nuestro conocimiento. El presente estudio significa una contribución exhaustiva al conocimiento de los patrones de diversidad de los anfibios bolivianos. El análisis de la diversidad está complementado con datos sobre la distribución y ecología. Un peso especial se da a las regiones de los bosques montanos de las laderas andinas nor-orientales (Yungas húmedos de los departamentos Cochabamba y Santa Cruz, bosques montanos semihúmedos del sur del departamento Santa Cruz). Para este fin se realizaron estudios de campo en tales regiones en las épocas de lluvia 1997/1998 y 1998/1999. Adicionalmente se tomaron en cuenta datos bibliográficos, de las colecciones de diferentes museos y de anteriores estudios realizados por el autor en el año 1994. Se presenta una lista preliminar de los anfibios de Bolivia. Para todas las 200 especies se dan a conocer datos sobre su distribución conocida y esperada en los departamentos y doce ecoregiones de Bolivia. 45 especies son endémicas para Bolivia (= 22,5%). La lista de especies se comenta analizando ciertos problemas taxonómicos: *Eleutherodactylus peruvianus* se elimina de la lista, se añade *Eleutherodactylus dundeei* y se revalida *Eleutherodactylus bisignatus*. Además se mencionan 61 especies que con cierta probabilidad existen en el territorio boliviano. La distribución espacial de la diversidad de especies y del endemismo en Bolivia se ilustra según las doce ecoregiones definidas. Los bosques amazónicos albergan el mayor porcentaje de las especies bolivianas (45,1%); siguen los bosques húmedos de transición de las tierras bajas (34,9%) y el bosque húmedo del escudo pre-cámbrico (35,4%). Los bosques más secos de la Chiquitanía y del Chaco tienen una diversidad claramente más baja. La diversidad de especies, en las tierras bajas, en general disminuye del norte hacía el sur. Las sabanas del Beni significan una excepción de esta regla teniendo un porcentaje relativamente bajo (15,4%). Considerando las ecoregiones andinas, los bosques montanos perhúmedos de los Yungas albergan muy claramente la mayor diversidad de especies (32,0%). Analizando el endemismo político resulta que un 69,9% de todas las especies que ocurren en los bosques de neblina ("ceja"; 69,9%) son endémicas para Bolivia. En los Yungas el porcentaje de endemismo es 54,0%. Las dos regiones mencionadas muestran un porcentaje de endemismo desproporcionalmente alto. En contraposición a este hecho, en las ecoregiones de las tierras bajas, con excepción de los bosques amazónicos (4,5%), no se registran especies endémicas; en los bosques amazónicos las especies endémicas se concentran en

los bosques pre-andinos. También el así llamado endemismo ecoregional es especialmente alto en los Yungas y en los bosques húmedos pre-andinos (conjuntamente 51,6%) que se alargan hasta el sur o el centro de Perú, y en los bosques montanos superiores más los bosques de neblina (55,7%). proximadamente un cuarto de las especies de los anfibios del Chaco boliviano es endémico de esta región que llega hasta el norte de Argentina y Paraguay. Aparte de las enteras laderas húmedas nororientales de los Andes (Yungas y ceja) se identifican de manera preliminar cuatro centros de diversidad ('hotspots'): región de Alto Madidi, región de "La Siberia", región de Samaipata y las partes orientales del Parque Nacional Amboró.

Los bosques montanos de los departamentos de Cochabamba y Santa Cruz fueron investigados más detalladamente. Se caracterizan todas las 70 especies encontradas. El criterio aplicado para considerar una especie como especie de los bosques montanos es su distribución principalmente encima de los 500 m.s.n.m. Para cada especie se presentan datos sobre su distribución, ecología y llamadas de apareamiento. Además es discuten aspectos taxonómicos. Nuevas especies que aún no tienen nombre científico se diferencian brevemente. Se describen e ilustran las llamadas de apareamiento de 33 especies, muchas de ellas por primera vez.

Para poder evaluar y comparar los patrones de diversidad en los bosques montanos se definen en un modelo tres transectos, que son más o menos virtuales. 1 – Transecto del Chapare (coincide más o menos con la carretera antigua de Paractito a Cochabamba siguiendo el valle del Río San Mateo; 500–2300 m.s.n.m.); 2 – Transecto del Amboró (más o menos una linea recta de la región de Samaipata bajando hacía las tierras bajas en el noreste; aproximadamente 500–2600 m.s.n.m.); 3 – Transecto del Río Seco (más o menos la línea del este al oeste saliendo de la provincia Vallegrande al pueblo Río Seco; aproximadamente 500–2100 m.s.n.m.). Se describen los transectos referente a su diversidad alfa y beta. Una comparación ecológica toma en cuenta patrones de actividad de especies, utilización del hábitat y estilos de reproducción, analizados según tres pisos altitudinales en cada transecto.

En el transecto del Chapare se registraron 36 especies, con un máximo de diversidad entre los 1300 y 1700 m. Las comunidades están dominadas por ranas del género *Eleutherodactylus*. La reproducción de la mayoría de las especies pertenece a los estilos de desarrollo directo (44%) o desarrollo en aguas turbias (31%). Aguas estancadas práticamente no existen. La diversidad beta a lo largo del transecto altitudinal es limitada. La diversidad gamma es alta. Especies típicas de los bosques montanos húmedos predominan; un 53% de las especies son endémicas de Bolivia. Con 48 especies registradas el transecto del Amboró parece más diverso pero cabe mencionar que se estudiaron más localidades que además involucran una diversidad más alta de hábitats. Un 42% de las especies pertenece a las especies endémicas de Bolivia. En la parte superior del transecto (1700–2300 m) se encuentra una diversidad beta muy alta. La diversidad alfa es comparable

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con la del Chapare. Predomina el desarrollo directo (29%) y sigue la reproducción en aguas estancadas (24%). El porcentaje anteriomente mencionado principalmente se debe a un porcentaje alto de Hylidae en el piso altitudinal más bajo (500 m.s.n.m.). En el transecto de Río Seco se registraron 31 especies; ningún piso sobresalió referente a la diversidad de especies. La diversidad alfa, en comparación con los otros dos transectos, es más baja como también la diversidad beta. Predominan estilos de reproducción adaptados a un clima muy estacional (reproducción explosiva en aguas temporales 35%; nidos de espuma 32%). Muchas especies de las tierras bajas de la región Chaco-Cerrado colonizan las laderas andinas de esta región hasta en altitudes muy destacables llegando a su límite superior de su distribución vertical. Los resultados confirman una relación íntima entre los valles secos y las formaciones del Chaco y del Cerrado.

Aplicando un análisis parsimónico de endemismo ("Parsimony Analysis of Endemism" - PAE) y un análisis de endemismo "juntando vecinos" ("Neighbor Joining Analysis of Endemism" - NJAE) se comparan las faunas anfíbicas de los diferentes pisos altitudinales entre ellas y con otras localidades de las laderas orientales de los Andes y de la región sudoeste de la Amazonía. El PAE y el NJAE tienen los siguientes resultados: (1) Las relaciones entre Amboró y Chapare son más estrechas que de cada uno con Río Seco. Esto es válido en el caso de todos los pisos altitudinales. (2) Las similitudes entre los pisos superiores de los diferentes transectos son más grandes que las similitudes entre los superiores y los más inferiores. (3) Las relaciones entre los pisos bajos de los transectos Chapare y Amboró son más estrechas que entre los pisos más medianos y altos. (4) Amboró y Chapare se diferencian claramente de los Yungas de La Paz y de las laderas andinas del Perú. (5) El transecto de Río Seco tiene relaciones con regiones áridas y estacionales del Chaco. (6) La localidad Mataracú (17°33'S, 63°52'W, 500 m) tiene relaciones más estrechas con el noreste de Bolivia que con los bosques preandinos del Perú.

La diversidad observada se evalúa ante posibles causas recientes e históricas. Se manifiestan recomendaciones con respecto a prioridades para la conservación y investigaciones del futuro.

ZUSAMMENFASSUNG

Amphibien-Diversität in Bolivien: eine Studie mit spezieller Berücksichtigung der Bergwaldregionen

Bolivien kann im Hinblick auf faunistische Studien als eines der am wenigsten untersuchten Länder Südamerikas gelten. Eine intensivierte Erforschung der bolivianischen Amphibienfauna innerhalb der letzten Dekade führte zu einem enormen Kenntniszuwachs. Die anhaltende Entdeckung neuer Taxa und Phänomene demonstriert jedoch die Unvollständigkeit unseres Wissens. Die vorliegende Studie leistet einen ersten umfassenden Beitrag zur Kenntnis von Diversitäts-

mustern bolivianischer Amphibien. Dabei werden neben der Diversität auch Daten zur Verbreitung und Ökologie analysiert. Besonderes Gewicht liegt dabei auf den Bergwaldregionen des östlichen Andenabhangs (humide Yungas der Departamentos Cochabamba und Santa Cruz, semi-humide Bergwälder im südlichen Departamento Santa Cruz). Zu diesem Zweck wurden Feldarbeiten in den Regenzeiten 1997/1998 und 1998/1999 in entsprechenden Gebieten durchgeführt. Zusätzlich flossen Daten aus Literatur und Museumssammlungen sowie einer vorangegangenen Untersuchung im Jahr 1994 in die Analyse ein.

Es wird eine vorläufige Checkliste der Amphibien Boliviens präsentiert. Zu allen 200 Arten werden Angaben zur bekannten und der zu erwartenden Verbreitung in den bolivianischen Departamentos und zwölf definierten Ökoregionen gemacht. Fünfundvierzig Arten sind endemisch für Bolivien (22,5%). Die Checkliste wird nachfolgend kommentiert: u.a. werden taxonomische Probleme einiger Arten geschildert, *Eleutherodactylus peruvianus* wird von der Bolivienliste entfernt, *Eleutherodactylus dundeei* wird hinzugefügt und *Eleutherodactylus bisignatus* wird revalidiert. Es werden zudem 61 Arten genannt, für die ein Vorkommen in Bolivien wahrscheinlich ist.

Die räumliche Verteilung der Artendiversität und des Endemismus innerhalb Boliviens wird anhand der Verbreitung in zwölf Ökoregionen dargestellt. Die amazonischen Regenwälder beherbergen den größten Anteil der bolivianischen Arten (45,1%), gefolgt von dem Feuchtwald des Prä-Kambrischen Schildes (35,4%) und den humiden Übergangswäldern des Tieflandes (34,9%). Die trockeneren Wälder der Chiquitanía-Region und des Chacos weisen eine deutlich geringere Artenvielfalt auf. Die Artenvielfalt innerhalb der Tiefland-Ökoregionen nimmt generell von Norden nach Süden ab. Die Beni-Savannen unterbrechen diesen allgemeinen Gradienten, indem sie eine verhältnismäßig niedrige Artenvielfalt (15,4%) aufweisen. Unter den andinen Ökoregionen beherbergen die immerfeuchten Bergregenwälder der Yungas mit Abstand die größte Artenvielfalt (32,0%). Betrachtet man politischen Endemismus, so zeigt sich, daß 69,6% aller Arten, die in den Nebelwäldern ("Ceja") vorkommen, bolivianische Endemiten sind. Die Yungas-Bergregenwälder folgen mit einen Endemitenanteil von 54,0%. Beide Regionen zeigen somit einen stark überproportionalen Anteil endemischer Arten. Dagegen ist politischer Endemismus in den Ökoregionen des Tieflandes, mit Ausnahme der amazonischen Regenwälder (4,5%), nicht zu finden. Der geringe Prozentsatz in letztgenannter Region ist auf Arten der amazonisch geprägten peri-andinen Wälder zurückzuführen. Sogenannter Ökoregionen-Endemismus ist besonders hoch in den Yungas-Bergregenwäldern und den humiden peri-andinen Wäldern (zusammen 51,6%), die sich bis Süd- bzw. Zentral-Peru erstecken, sowie in den oberen Bergregenwäldern und den Nebelwäldern (zusammen 55,7%). Ungefähr ein Viertel aller Amphibienarten des bolivianischen Chaco ist endemisch für diese Region, die sich über Nord-Argentinien und Paraguay erstreckt. Neben dem gesamten perhumiden östlichen Andenabhang (Yungas und Ceja) werden vorläufig vier Diversitätszentren ('hotspots') identifiziert: Alto

Madidi-Region, "La Siberia"-Region, Samaipata-Region und östliche Teile des unteren Amboró-Nationalparks.

Die Bergwaldregionen der Departamentos Cochabamba und Santa Cruz wurden detaillierter untersucht. Es wird ein Überblick über alle 70 Bergwaldarten gegeben, die im Untersuchungsgebiet gefunden wurden. Kriterium für eine Bergwaldart ist hierbei eine deutliche Verbreitung oberhalb von 500 m ü.NN. Für jede Art werden Angaben zur Verbreitung, Ökologie und dem Anzeigeruf gemacht, sowie ggf. taxonomische Aspekte erläutert. Neue Arten, die bisher noch unbenannt sind, werden kurz diagnostiziert. Die Anzeigerufe von insgesamt 33 Arten werden beschrieben und abgebildet, viele davon erstmalig.

Um die Diversitätsmuster innerhalb der Bergwälder beurteilen und vergleichen zu können, werden als Modell drei mehr oder weniger 'virtuelle' Transekte definiert: 1 – Chapare-Transekt (entspricht in etwa der 'alten' Straße von Paractito nach Cochabamba entlang des Río San Mateo-Tals; 500–2300 m ü.NN); 2 – Amboró-Transekt (entspricht etwa einer Linie von der Samaipata-Region nach Nordosten ins Tiefland; ca. 500–2600 m ü.NN); 3 – Río Seco-Transekt (entspricht etwa einer Linie in Ost-West-Richtung von der Provincia Vallegrande zum Ort Río Seco; ca. 500–2100 m ü.NN). Die Transekte werden bezüglich ihrer alpha- und beta-Diversität beschrieben. Ein ökologischer Vergleich berücksichtigt Aktivitäts-muster, Habitatnutzung und Reproduktionsmodi der gefundenen Arten auf jeweils drei exemplarischen Höhenstufen der Transekte.

Im Chapare-Transekt konnten 36 Arten nachgewiesen werden, wobei sich die größte Artenvielfalt zwischen 1300–1700 m ü.NN konzentriert. Die Zönosen werden von Fröschen der Gattung *Eleutherodactylus* dominiert. Die Fortpflanzung der meisten Arten geschieht durch Direktentwicklung (44%) oder Entwicklung in Fließgewässern (31%). Stehende Gewässer sind praktisch nicht vorhanden. Die beta-Diversität entlang des Höhengradienten ist begrenzt. Die gamma-Diversität ist hoch. Reine Bergregenwaldarten dominieren und 53% der Arten sind endemisch für Bolivien. Mit 48 Arten erscheint der Amboró-Transekt artenreich-er, doch wurde eine größere Anzahl von Lokalitäten untersucht, die zudem eine größere Variation von Habitaten einschloß. 42% der Arten sind bolivianische Endemiten. Im oberen Bereich des Transekts (1700–2300 m ü.NN) findet sich eine extrem hohe beta-Diversität. Die alpha-Diversität ist vergleichbar mit der des Chapare-Transekts. Direktentwicklung dominiert (29%) gefolgt von Reproduktion in stehenden Gewässern (24%). Der letztgenannte hohe Anteil ist vorallem auf die Präsenz von Hyliden auf der niedrigsten Höhenstufe (500 m a.s.l.) zurückzuführen. Im Río Seco-Transekt waren 31 Arten zu finden, wobei keine Höhenstufe signifikant bezüglich der Artenvielfalt dominierte. Die alpha-Diversität ist im Vergleich zu beiden anderen Transekten geringer, die beta-Diver-sität ist ebenfalls beschränkt. Es dominieren an stark saisonales Klima adaptierte Reproduktionsmodi (Explosivlaichen in temporäre Gewässer 35%; Schaumnester 32%). Viele Tieflandarten des Chaco-Cerrado-Bereichs besiedeln die Andenhänge in dieser Zone bis in bemerkenswerte Höhen und erreichen dort die Obergrenze

ihrer Vertikalverbreitung. Eine enge Beziehung innerandiner Trockentäler zu den Chaco-Cerrado-Formationen wird durch die Ergebnisse bestätigt.

Mittels "Parsimony Analysis of Endemism" (PAE) und "Neighbor Joining Analysis of Endemism" (NJAE) werden die Amphibienfaunen der verschiedenen Höhenstufen je Transekt (500, 1300–1600, 1900–2200 m ü.NN) untereinander sowie mit anderen Lokalitäten des östlichen Andenabhangs und des südwestlichen Amazonasbeckens verglichen. Die PAE und NJAE-Analysen ergeben folgende Ergebnisse: (1) Die Beziehungen zwischen Amboró und Chapare-Transekt untereinander sind enger als jeweils zum Río Seco-Transekt; dies gilt für alle Höhenstufen. (2) Die Ähnlichkeiten zwischen den oberen beiden Höhenstufen sind in allen drei Transekten größer, als jeweils zur unteren Höhenstufe. (3) Die Beziehungen zwischen den unteren Ebenen des Amboró- und Chapare-Transekts sind enger, als die zwischen den mittleren und hohen Ebenen. (4) Amboró- und Chapare-Transekt unterscheiden sich beide deutlich von der Yungas de La Paz-Region und den Andenhängen Südost-Perus. (5) Der Río Seco-Transekt hat starke Beziehungen zu trockenen und saisonalen Regionen des Chaco. (6) Die Lokalität Mataracú (17°33'S, 63°52'W, 500 m ü.NN) hat stärkere Beziehungen zu Nordost-Bolivien als zu Lokalitäten im peri-andinen Bereich Perus.

Die vorgefundene Diversität wird zusammenfassend beurteilt und eingeordnet. Identifizierte Muster werden bezüglich möglicher Determinanten diskutiert, die ökologischen Determinismus sowie historische Vorgänge einschließen. Allopatrische Artbildungsmodelle scheinen die Muster am besten zu erklären. Es werden Empfehlungen für Schutzprioritäten und zukünftige Forschungsmaßnahmen ausgesprochen.

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APPENDIX
Voucher Specimens

The following account lists only specimens collected in montane forest regions during this study. The first entry of every record refers to the Departamento. The list of specimens deposited in the Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK) can be regarded as being complete. The account of specimens deposited in the Colección Boliviana de Fauna (CBF) lists only the most important specimens. The collection numbers of specimens deposited in the Museo de Historia Natural "Noel Kempff Mercado" (NKA) are not available yet.

Bufonidae

Atelopus tricolor: Cochabamba: "Old" Chapare road, 1200 m, ZFMK 69919-20.

Bufo arenarum: Chuquisaca: W of Vaca Guzman, 1360 m, ZFMK 67026-28.

Bufo fissipes: Cochabamba: "Old" Chapare road, 1300 m, ZFMK 66985; 1400 m, 72668-71 + additional specimens.

Bufo justinianoi: Cochabamba: "Old" Chapare road, 1650 m, ZFMK 72600-02; 2250 m, ZFMK 72621; Karahuasi, 1800 m, ZFMK 72657.

Bufo paracnemis: Santa Cruz: W of Río Seco, 900 m, ZFMK 67061-63.

Bufo poeppigii: Cochabamba: "Old" Chapare road, 500 m, ZFMK 72530; Karahuasi, 1800 m, ZFMK 72654.

Bufo quechua: Cochabamba: Sehuencas, 2200 m, ZFMK 60255-74, 60276-82 and 66835-36; Incachaca, 2300 m, ZFMK 66939-41; "Old" Chapare road, 2250 m, ZFMK 72622.

Bufo stanlaii: Cochabamba: road Villa Tunari-Cochabamba, 1850 m, ZFMK 60464; road to San Onofre, 1900 m, CBF 3346 and ZFMK 67097; "Old" Chapare road, 1400 m, ZFMK 67096.

Bufo veraguensis: Cochabamba: "Old" Chapare road, 1250 m, ZFMK 72555-58; 1300-1500 m, ZFMK 72574-75; 1650 m, ZFMK 72590-92; Karahuasi, 1800 m, ZFMK 72658; Santa Cruz: 29 km SE of Guadalupe; 1600 m, ZFMK 66850-51; La Yunga, 2300 m, ZFMK 66880; "El Fuerte" Samaipata, 1750 m, ZFMK 66884; W of Río Seco, 1100 m, ZFMK 67077-78.

Centrolenidae

Cochranella bejaranoi: Cochabamba: Sehuencas, 2150 m, ZFMK 66830-34; Incachaca, 2300 m, ZFMK 66946; road Karahuasi-Empalme, 2300 m, ZFMK 66889-90; "Old" Chapare road, 1650 m, ZFMK 72586; Santa Cruz: N of San Juan del Potrero (Remates), 2080 m, ZFMK 66862-63.

Cochranella nola: Santa Cruz: Mataracú, 500 m, ZFMK 66376; "El Fuerte", Samaipata, 1700 m, ZFMK 66377-78; La Hoyada, 1750 m, ZFMK 72636.

Hyalinobatrachium bergeri: Cochabamba: "Old" Chapare road, 500 m, ZFMK 72538.

Dendrobatidae

Epipedobates pictus: Cochabamba: "Old" Chapare road, 550 m, ZFMK 66962-63; 900 m, ZFMK 66984; Santa Cruz: Mataracú, 500 m, ZFMK 66854-59.

Hylidae

Gastrotheca cf. *testudinea*: Cochabamba: "Old" Chapare road, 1300 m, CBF 3338-40 and ZFMK 66977, 70316.

Gastrotheca sp. A: Cochabamba: Sehuencas, 2200 m, ZFMK 60275, 60283-302 and 66837-40; Incachaca, 2300 m, ZFMK 66954; road Karahuasi-Empalme, 2300 m, ZFMK 66893; Santa Cruz: N of San Juan del Potrero (Remates), 2080 m, ZFMK 66868.

Hyla andina: Cochabamba: Sehuencas, 2150 m, ZFMK 66828; Incachaca, 2300 m, ZFMK 66947-52; road Karahuasi-Empalme, 2300 m, ZFMK 66891-92; "Old" Chapare road, 1300-1500 m, ZFMK 72580; 1650 m, ZFMK 72605; Santa Cruz: "El Fuerte" Samaipata, 1750 m, ZFMK 60420-21.

Hyla armata: Cochabamba: Río Roncito, 1800 m, ZFMK 67088-90; "Old" Chapare road, 1300-1500 m, ZFMK 72581; Karahuasi, 1800 m, ZFMK 72648-50; Santa Cruz: La Hoyada, 1700 m, ZFMK 72637.

Hyla cf. *callipleura*: Cochabamba: Incachaca, 2300 m, ZFMK 66942-45 and 66953; "Old" Chapare road, 700 m, ZFMK 72544; 950 m, ZFMK 72547-48; 1300 m, ZFMK 66967 and 72554; 1650 m, ZFMK 72583-85 and 72603-04; 1850 m, ZFMK 72613.

Hyla marianitae: Cochabamba: Karahuasi, 1800 m, ZFMK 67103 and 72651-52; Santa Cruz: "El Fuerte" Samaipata, 1900 m, ZFMK 60412-18 and 66886-87, Samaipata, 1600 m, ZFMK 60419; S of Cuevas, 1400 m, ZFMK 66379-86 and 66881, N of San Juan del Potrero (Remates), 2080 m, ZFMK 66869-70; W of Río Seco, 900 m, ZFMK 67059-60; 1100 m, ZFMK 67073-76; La Hoyada, 1700 m, ZFMK 72634-35.

Hyla minuta: Chuquisaca: W of Vaca Guzman, 1360 m, ZFMK 66045; Santa Cruz: "El Fuerte" Samaipata, 1900 m, ZFMK 60403-07, Laguna de Bermejo, 1130 m, ZFMK 60440, W of Río Seco, 900 m, ZFMK 67053-55; La Hoyada, 1900 m, ZFMK 72630-31.

Hyla sp. A: Cochabamba: "Old" Chapare road, 500 m, ZFMK 72526-28; 650 m, CBF 3332 and ZFMK 67139-42; 950 m, CBF 3331 and 3336-37 and ZFMK 68658; 1500 m, ZFMK 70317.

Phrynohyas venulosa: Chuquisaca: W of Vaca Guzman, 1360 m, ZFMK 67035-36; Santa Cruz: Samaipata, 1600 m, ZFMK 60422.

Phyllomedusa boliviana: Chuquisaca: W of Vaca Guzman, 1360 m, ZFMK 67029-34; Santa Cruz: Samaipata, 1600 m, ZFMK 60423-24; 29 km SE of Guadalupe, 1600 m, ZFMK 66842; La Hoyada, 1750 m, ZFMK 72639-43.

Scinax castroviejoi: Cochabamba: road to San Onofre, 1900 m, ZFMK 67093-95 (cf. *castroviejoi*); Santa Cruz: Samaipata, 1600 m, ZFMK 60425-26; Laguna de Bermejo, 1130 m, ZFMK 60428-32; La Hoyada, 1700, ZFMK 72632-33 and 72645.

Scinax fuscovarius: Chuquisaca: W of Vaca Guzman, 1360 m, ZFMK 67037-43; Santa Cruz: 29 km SE of Guadalupe, 1600 m, ZFMK 66846-49; W of Río Seco, 900 m, ZFMK 67057-58.

Leptodactylidae

Adenomera hylaedactyla: Cochabamba: "Old" Chapare road, 550 m, ZFMK 66989.

Eleutherodactylus ashkapara: Cochabamba: "Old" Chapare road, 2100 m, CBF 3344 and ZFMK 70318.

Eleutherodactylus cruralis: Cochabamba: "Old" Chapare road, 550 m, ZFMK 66964, 72532 and 72541-43; 800 m, CBF 3347; 1300 m, ZFMK 66971-72; 1300-1500 m, ZFMK 72570; Santa Cruz: La Hoyada, 1800 m, ZFMK 72644; S of Cuevas, 1100 m, CBF 3348-49.

Eleutherodactylus danae: Cochabamba: S of Villa Tunari, 500 m, ZFMK 59574; "Old" Chapare road, 550 m, ZFMK 66988 and 72537; 1300 m, ZFMK 66973-76 and 72564-65; 1650 m, ZFMK 72587-89.

Eleutherodactylus dundeei: Santa Cruz, Mataracú, 500 m, ZFMK 66861.

Eleutherodactylus fenestratus: Cochabamba: "Old" Chapare road, 550 m, ZFMK 66965-66 and 72536; 700 m, ZFMK 72545-46.

Eleutherodactylus fraudator: Cochabamba, Sehuencas, 2200 m, ZFMK 60244-54; Santa Cruz: "La Siberia", 2600 m, ZFMK 72660-62.

Eleutherodactylus llojsintuta: Cochabamba, Sehuencas, 2200 m, CBF 3300-01 and ZFMK 60216-17, 60219, and 66387-89.

Eleutherodactylus mercedesae: "Old" Chapare road, 1300-1500 m, ZFMK 72571-73; 1650 m, ZFMK 72597-99.

Eleutherodactylus olivaceus: Cochabamba: "Old" Chapare road, 500 m, ZFMK 72533-34; 700 m, CBF 3329-30 and ZFMK 67133; 950 m, ZFMK 72549-50; 1300 m, ZFMK 67132, 72553, and 72568; 1300-1500 m, ZFMK 72578-79.

Eleutherodactylus platydactylus: Cochabamba, Sehuencas, 2200 m, ZFMK 60205-15, 60218, 60220-43, and 67153-61; road Villa Tunari-Cochabamba, 1850 m, ZFMK 60465; road Karahuasi-Empalme, 2300 m, ZFMK 66894-96 and 72655-56, "La Siberia", 3200 m, ZFMK 66897-99; "Old" Chapare road, 900 m, ZFMK 66981-83 and 72551; 1300 m, ZFMK 66978-80, 72566-67, and 72576; 1650 m, ZFMK 72595-96; 1850 m, ZFMK 72606-12; 2200 m, ZFMK 66993 and 72623-28; Incachaca, 2300 m, ZFMK 67129-31; Santa Cruz: La Yunga, 2300 m, ZFMK 66877-79; La Hoyada, 1800 m, ZFMK 72646; "La Siberia", 2600 m, ZFMK 72665-67.

Eleutherodactylus pluvicanorus: Cochabamba: Sehuencas, 2200 m, ZFMK 60186-204; Incachaca, 2300 m, ZFMK 66938, "Old" Chapare road, 2250 m, ZFMK 72619-20; Santa Cruz: La Yunga, 2300 m, ZFMK 66872-75, "La Siberia", 2600 m, ZFMK 72663-64.

Eleutherodactylus rhabdolaemus: Cochabamba: P.N. Carrasco, 1900 m, ZFMK 60388; road Villa Tunari- Cochabamba, 1850 m, ZFMK 60466-70; "Old" Chapare road, 1250 m, ZFMK 72552; 1650 m, ZFMK 72593-94; 1850 m, ZFMK 72614; 2200 m, ZFMK 66994 and 72615-18; Río Roncito, 1800 m, ZFMK 67091-92; road to San Onofre, 1700 m, ZFMK 67134; Karahuasi, 1800 m, 72659; Santa Cruz: La Yunga, 2300 m, ZFMK 66876.

Eleutherodactylus samaipatae: Santa Cruz: "El Fuerte" Samaipata, 1850 m, ZFMK 59600; S of Cuevas, 1300 m, ZFMK 66882-83; W of Río Seco, 900 m, ZFMK 67064; 1100 m, ZFMK 67071-72.

Eleutherodactylus sp. A: Santa Cruz: "El Fuerte" Samaipata, 1900 m, ZFMK 60402; E of Bermejo, 750 m, CBF 3341.

Ischnocnema sanctaecrucis: Cochabamba: "Old" Chapare road, 1300-1500 m, ZFMK 72569; Karahuasi, 2200 m, ZFMK 72647.

Leptodactylus chaquensis: Chuquisaca: W of Vaca Guzman, 1360 m, ZFMK 67005-06.

Leptodactylus fuscus: Cochabamba: "Old" Chapare road, 500 m, ZFMK 72531.

Leptodactylus gracilis: Santa Cruz: "El Fuerte" Samaipata, 1900 m, ZFMK 60399-401; 29 km SE of Guadalupe, 1600 m, ZFMK 66841.

Leptodactylus griseigularis: Cochabamba: "Old" Chapare road, 1300 m, ZFMK 66968.

Leptodactylus leptodactyloides: Santa Cruz: Laguna de Bermejo, 1130 m, ZFMK 60427.

Leptodactylus rhodonotus: Cochabamba: road Villa Tunari-Cochabamba, 1850 m, ZFMK 60463; "Old" Chapare road, 750 m, ZFMK 66905-09; 1250 m, ZFMK 72559-63 and 72577 (cf. *rhodonotus*); road to San Onofre, 1900 m, ZFMK 67135-38; Karahuasi, 1800 m, ZFMK 72653; Santa Cruz: La Hoyada, 1800 m, ZFMK 72629.

Phyllonastes carrascoicola: Cochabamba: Sehuencas, 2150-2230 m, ZFMK 59569-73 and 66829; "Old" Chapare road, 2200 m, ZFMK 66991 and 71643-44.

Phyllonastes ritarasquinae: Cochabamba: "Old" Chapare road, 1250 m, CBF 3350.

Physalaemus albonotatus: Chuquisaca: W of Vaca Guzman, 1360 m, ZFMK 67044.

Physalaemus biligonigerus: Chuquisaca: W of Vaca Guzman, 1360 m, ZFMK 67016-25.

Pleurodema cinereum: Chuquisaca: W of Vaca Guzman, 1360 m, ZFMK 67007-15; Santa Cruz: "El Fuerte" Samaipata, 1900 m, ZFMK 60408-11; 29 km SE of Guadalupe, 1600 m, ZFMK 66843-44 and 66852-53; La Hoyada, 1750 m, ZFMK 72638.

Telmatobius edaphonastes: Cochabamba: "La Siberia", 2900 m, ZFMK 66900.

Telmatobius cf. *simonsi*: Santa Cruz: La Hoyada, 1750 m, ZFMK 69922-23.

Telmatobius yuracare: Cochabamba: Sehuencas, 2200 m, ZFMK 60185; "Old" Chapare road, 2200 m, CBF 3335 and ZFMK 66990.

Telmatobius sp. A: Santa Cruz: N of San Juan del Potrero (Remates), 2080 m, ZFMK 66871; Empalme, 2630 m, ZFMK 70315.

Microhylidae

Chiasmocleis albopunctata: Santa Cruz: W of Río Seco, 900 m, ZFMK 67056.

Elachistocleis bicolor: Santa Cruz: Laguna de Bermejo, 1130 m, ZFMK 60433-39.

Elachistocleis ovalis: Santa Cruz: N of San Juan del Potrero (Remates), 2150 m, ZFMK 66865-67; "El Fuerte" Samaipata, 1900 m, ZFMK 66888; W of Río Seco, 900 m, ZFMK 67065-66.

Plethodontidae

Bolitoglossa sp. A: Cochabamba: "Old" Chapare road, 500 m, CBF 3334.

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