To the Graduate Council:

I am submitting herewith a dissertation written by Monique Halloy de Grosse entitled "Sand Burying Behavior in Neotropical Species of Lizards, Liolaemus, Tropiduridae: a Phylogeny of the boulengeri group." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Life Sciences.

Gordon M. Burghardt

Dr. Gordon Burghardt, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

C.W. Minkel

Associate Vice Chancellor and
Dean of the Graduate School

SAND BURYING BEHAVIOR IN NEOTROPICAL SPECIES OF LIZARDS, *LIOLAEMUS*, TROPIDURIDAE: A PHYLOGENY OF THE *BOULENGERI* GROUP

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Monique Halloy de Grosse
December 1995

DEDICATION

This dissertation is dedicated

to the many many lizards
without whom all that follows
would not be,

and to Anne and Paul,
two very special people

ACKNOWLEDGMENTS

This dissertation is the end product of many years of research conducted partly in Argentina and partly in the United States. Many people from both countries went out of their way to make this major undertaking in my life arrive at good port. I will always be grateful to all of them.

I am especially grateful to Dr. G. M. Burghardt, my major advisor, for his continuous and much appreciated guidance, for his many suggestions and enlightening ideas, and for caring.

I am very grateful to Dr. R. Etheridge for suggesting the original idea which embarked me on this long and beautiful journey and for his much appreciated guidance throughout the project.

I am grateful to my committee members, Dr. A. Echternacht, Dr. R. Etheridge, Dr. J. Gittleman, Dr. R. Saudargas, for inspiring discussions, for their careful reading of the manuscript and for many valuable suggestions.

In addition, I would like to thank all the following people who each and everyone of them contributed in their own way to make this dissertation a better product:

- to Drs. R. Laurent, P. Goloboff and F. Lobo for commenting on an initial version of the dissertation,

- to Constantin, Anne, and Paul Grosse, to Richard Etheridge, Lee Grismer, Jimmy McGuire, and to Omar Pagaburo and Juan Bracamonte for collection of the many lizards used in this study,

- to Philippe, Nadine and Juliette Halloy for kindly bringing me a Liolaemus scapularis from Cafayate, Salta,

- to Lee Grismer for lending me a specimen of Phrynosoma douglassii from northeast Colorado for observation,

- to Drs. R. Laurent and R. Etheridge for identifying many of the species I used,

- to Drs. S. Halloy and F. Vervoorst, and Lic. N. Muruaga, Lic. A. Slanis, and Lic. A. M. Türpe for identifying the plants listed in Appendix B,

- to Dr. R. Lech for identifying soil types, shown in Appendix B,

- to Lic. J. G. Sanagua for a mechanical analysis of soil texture of two types of sand, used to generate Figure 14,

- to Stéphan Halloy for revising in great detail Appendices B and C (any error being my responsibility),

- to Ing. Ramón Fernandez and Mr. Eduardo Fernandez for providing fruit flies (Ceratitis capitata) for the lizards,

- to Dr. C. Grosse for setting up the video equipment, for computer and statistical advice, and for most of the pictures (some pictures were taken by P. Grosse and S. Castro),

- to Drs. F. Lobo and P. Goloboff for advice on use of Hennig86 and discussions on phylogeny,

- to Paul Grosse for being a cheerful and willing participant in the interobserver reliability test,

- to Felix Cruz for his help in creating the graphs for figures 14, 15, and 16,

- to Patricia Vince for drawings of burying lizards shown in figures 20 and 21,

- to the services provided by Interlibrary Services of the University of Tennessee, Knoxville, and to Marty Courtois for a literature search which provided many needed references which would have been otherwise inaccessible,

- to C. Grosse for taking the time to translate from Russian the article by Shammakov et al. 1981,

- to G. Thor for locating hard to find Australian references and for sending them to me,

- to P. Andreadis and D. Layne for helping me whenever I needed assistance and for locating many references,

- to Christian Halloy for giving me a "home" during the last two months of writing, for computer advice, and for his enthusiasm and his encouragement,

- to friends and fellow graduate students, particularly to Paul Andreadis, Dan Cunningham, Donna Layne, Jesus Rivas, and Mark Waters, for lively discussions, for their companionship, and for sharing my enthusiasm in animal behavior,

- to all my friends of the "Segundo" at the Fundacion Miguel Lillo, Virginia Abdala, Cristina Buti, Felix Cruz, Liliana Ferrari, Esteban Lavilla, Fernando Lobo, Adriana Manzano, Alicia Marcus, Marta and Ricardo Montero, Silvia Moro, Gabriela Pierotti, Sonia and Gustavo Scrocchi, for being such a great bunch of people and for conveying the special feeling of a big caring and joyful Herp family,

- to my family, C., A., and P. Grosse, and to R. Etheridge, L. Grismer and J. McGuire for sharing many wonderful and unique moments during various field trips,

- to Dr. A. Haedo Rossi, Director of the Fundación Miguel Lillo, and to Lic. J. de Herrera, Director of the Zoology Department of the Fundación Miguel Lillo, for believing in me and for being supportive in all my projects,

- to the Fundación Miguel Lillo for giving me a leave of absence during two years and two months, which enabled me to conclude this project,

- to the Programa de Investigación y Desarrollo (PID n° 3556/88 and 3722/92) for providing the terraria needed in the study, and for helping with films and gas used during field trips,

- to the Psychology Department of the University of Tennessee, Knoxville, for an assistantship and a tuition waiver that supported me and allowed me to take many excellent courses,

- to my parents, L. and R. Laurent, for going out of their way to help me in every way they could, for their unconditional support and for their encouragement throughout this project,

- to my brothers, Philippe, Christian and Stéphan, for their wonderful companionship in a somewhat unusual life, and for helping out whenever I needed it,

- and to my husband and two children for believing in me and for their understanding, but especially for just being there.

ABSTRACT

Sand burying behavior has been reported in many species of lizards spanning several taxonomic families. Burying behavior has been linked to possible functions such as predator escape, avoidance of extreme temperatures, or as an effective means of spending the inactive part of the daily or seasonal cycle. Rarely is the behavior itself described or, even more unusually, referred to in a historical context. This is understandable in light of a resistance to consider behavioral patterns stable enough within a species to be meaningful in an evolutionary setting. Nevertheless, many authors have verified the conclusion of early ethologists that behavioral characters are species-characteristic and are as useful in phylogenetic reconstructions as are morphological characters.

In the present study, sand burying behavior was investigated in a group of species belonging to the genus Liolaemus, Tropiduridae. The main objectives were to describe the behavior, determine the amount of variation within species, and to use the obtained information to construct a phylogenetic hypothesis of the relationship among the species under study.

The genus Liolaemus contains more than 150 species that occupy a wide variety of habitats over a range that extends

from Peru and Bolivia in the North to Tierra del Fuego in the South. Within this large genus, certain groups of species have been identified, among them the monophyletic boulengeri group which is diagnosed on the basis of morphological evidence. Of the 26 known species belonging to this group, many have been reported to bury in sand. The relationships among these species are largely unresolved. Sand burying behavior was considered a potential, even critical, phylogenetic tool in helping clarify these relationships. This behavior appeared to be species specific and variation among species was suspected. Furthermore, sand burying arose in conjunction with living into more extreme type habitats characterized by the presence of a loose sandy substrate and little vegetation available for cover. This situation triggered a series of adaptive changes in the organism, among them behavioral changes such as sand burying.

Nineteen species of the boulengeri group formed the ingroup. Another four species of Liolaemus, which did not belong to the boulengeri group, constituted the functional outgroup. Lizards were tested at least twice on two types of loose sand, one somewhat coarser than the other. Their behavior was videotaped and later analyzed. Descriptions of burying behavior were based on movements prior to entering the sand, movements of the head upon entering the sand, movements of the tail, location on body where the lizard

first stopped, whether a lizard ended up totally covered or only partially covered, total number of stops made by the lizard before settling down for the night, and time recordings of the burying. These formed 7 character subsets, each containing various behavioral characters, totalling 26.

In an attempt to establish the stability and stereotypy of sand burying within species, 5 character subsets were compared in different situations: intra-individual variability; context variability; variability between males and females; variability among populations within a species; and variability between adults and neonates. Most of the results of the various statistical tests were non-significant indicating that the behavioral characters involved in sand burying were species-specific and, thus, appropriate for use in a phylogenetic analysis.

The four species of the functional outgroup and one of the 19 species of the boulengeri group, L. ornatus, did not bury. Within the remaining 18 species, 3 burying modes were observed:

1. Species that dug or burrowed their way into sand, keeping their head straight as they entered and keeping their tail straight throughout. They often were not completely covered.
2. Species that entered loose sand by generally using a lateral movement of the head and by retrieving or pulling in their tail to get completely covered.

3. Species that dove or plunged into sand, often back stepping prior to entering sand, thrusting their head forward into sand, and lashing their tail to get completely covered.

A cladistic analysis of 26 behavioral characters supported the observed burying modes within the boulengeri group. The consensus tree gave three main branches, each branch representing a different type of sand burying behavior. In addition, the results generally agreed with what is known for this group based on morphological evidence and they further discriminated among species.

This study indicates how behavior can clarify the phylogenetic relationships among species while suggesting a hypothesis that may later be confirmed or refuted by additional behavioral, morphological, ecological, or molecular data. Different burying styles do not seem to reflect different mechanical problems that lizards may encounter. In fact, the sand in which lizards bury is very similar across geographical regions. Instead, these different burying modes seem to reflect the history of lizard species in the form of lineage constraints which may limit or expand available options when confronted with a specific situation.

TABLE OF CONTENTS

PART III: RESULTS

PART IV: DISCUSSION

LIST OF TABLES

LIST OF FIGURES

PART I

GENERAL INTRODUCTION AND OVERVIEW

CHAPTER 1

INTRODUCTION

The comparative study of behavioral patterns among related species can give insight into their evolutionary history. Behavioral characters have been used and have proved useful in the reconstruction of phylogenies (e.g., McLennan et al., 1988; de Queiroz and Wimberger, 1993; Greene, 1994). To be useful for phylogenetic analysis at the species level, a behavior has to have heritable components and show variation among species. Sand burying behavior in a group of lizard species belonging to the Neotropical genus Liolaemus, Tropiduridae, seems a likely candidate for this type of analysis. Burying in loose sand in species of this genus appears to be stereotyped and it shows discernible variations among species.

Burying into loose sand by lizards appears to have originated, in some cases, as an adaptation for escape from predators (e.g., in Meroles, Lacertidae), and in others, as an adaptation for concealment at the end of activity periods (e.g., in Ophisops elegans, Lacertidae; Arnold, 1994a). In O. elegans burying into sand is characterized by long pauses, possibly an adaptation to the substrate mixed with roots in which it typically buries. In this species, slow burial may be advantageous (Arnold, 1994a). The movements used in sand

burying are believed to be a modification of the normal running motions used when escaping (Arnold, 1994a).

Arnold (1994a:126) considers adaptation to be "produced or at least promoted by natural selection for the use that it has at a specified time". He adds that the ability to enter loose sand as an adaptation for escaping from predators may become an exaptation for night burying, exaptation being understood as "a trait of a population, or larger taxonomic unit, that confers performance advantage in a particular way at a specific time but was not produced by natural selection directly for that use".

Although information on the phylogeny of a group of species may help determine whether a trait is an adaptation or exaptation, as in the above examples, the boundary between these concepts is not always clear. In Phrynocephalus (Chamaeleonidae, Agaminae), for instance, it is unclear which arose first: diving to escape predators or burying for the night and, therefore, which function is possibly the result of adaptation (Arnold, 1994a). Moreover, exaptations are often complex and may arise through several evolutionary events (e.g., sand diving in the phrynosomatid lizard, Uma, Arnold, 1994a).

Arnold (1994a:154-155) describes several modes of submerging into sand in different lizard families. These may be summarized as follows:

- Lizards that "dive head first into the sand using all their limbs, and flexing the head and body laterally into serpentine waves, the tail being buried by broad whip-like sweeps" (e.g., Meroles).

- Lizards that submerge into sand vertically using oscillating lateral movements of the limbs and later of the head and tail (e.g., Phrynocephalus).

- Lizards, such as Uma, that "dive" head first into sand but the way they bury is different from that of Meroles, "Initially the head is twisted rapidly about its sagittal axis like an awl and forward motion is largely produced by the hindlimbs, the forelimbs being quickly laid back along the flanks." Towards the end, the end of the tail is vibrated or "shymmied" and the lizard is concealed.

- Another type of burying in lizards seems to be a combination of head first diving and vertical sinking. This is the case of Phrynosoma (Phrynosomatidae). Here, the head is "swung from side to side and then pushed under the surface, the forelimbs again being soon laid along the flanks.... Once the foreparts are buried the hind quarters are rapidly oscillated from side to side, so that they sink vertically."

- Finally, lizards that swim their way into sand. An example is Scincus (Scincidae) which enters the sand "head first, rapidly laying both pairs of hind legs along the

flanks. After this they progress by rapid high-amplitude sinusoidal movement of the body, and swim through the sand rather like a fish in water." According to Arnold (1994a), Angolosaurus skoogi (Cordylidae, Gerrhosaurinae) from southwest Africa, appears to bury in a similar way.

Arnold (1994a, 1995) tends to generalize results from a few species to the genus and even to the family. This is possibly based on his assumption that sand burying is a very stereotyped and plesiomorphic behavior (i.e., once the behavior appears in an ancestor it tends to be present in all or most of its descendents). This has not been established, however, and such a generalization may be premature. Nevertheless, Arnold (1994a, 1995) makes a crucial point in underscoring the importance of historical constraints or lineage effects on the type of burying mode observed in a particular lineage. A good example is Phrynocephalus, which evolved a very blunt snout prior to developing burying behavior. This effectively eliminated, for species of this genus, the possibility of entering sand head first. When burying behavior did appear, the genus opted for an alternative solution, which was to submerge into sand vertically with its entire body.

The focus of the present study will be on the evolutionary history of a group of lizards based on their sand burying behavior. To provide a context to the study, a

brief historical and theoretical account of the use of behavioral patterns in understanding the evolution of a group of species follows.

The Relationship of Behavior Patterns and Phylogeny

In his "On the Origin of Species", Darwin (1859) argued that the behavior patterns of animals could reveal information about their evolutionary history. For instance, he compared the behaviors of species of slave-making ants with non-slave making ants. Based on his observations, he proposed a probable evolutionary trend for these species, suggesting that the species that was most dependent on its slaves, Formica rufescens, was the most derived.

At the beginning of this century, Whitman (1898/1985) and Heinroth (1911/1985), observing the behaviors of pigeons and doves (Columbidae) and geese and swans (Anatidae), respectively, concluded that discrete behavioral patterns were as suitable for systematic analysis as morphological characters. For instance, Heinroth used wing position in swans to discriminate among species.

Lorenz (1941, in Lorenz, 1971; 1981) maintained that behavior patterns were equivalent to morphological structures and could be as informative when considering the phylogeny of a group of species. This author compared the motor patterns of about 20 different species of Anatinae

(1941, in Lorenz 1971). Based on his results, he was able to elaborate a figure in which he proposed a phylogeny for this group.

Tinbergen (1951) believed firmly that it was not only possible but necessary to do comparative studies of behaviors in interpreting the evolutionary history of closely related species. He demonstrated this both in his research on closely related species of sticklebacks (Gasterosteidae) with respect to their courtship behaviors (1951), and in his comparisons of communication displays of different species of gulls (1960). In the latter case, he was able to conclude that these species form a monophyletic group.

In their review of reptile behavior patterns, Carpenter and Ferguson (1977:336) concluded that these provided "a critical tool for describing and comparing systems to gain insight into evolutionary derivations and origins of particular movements and postures". Carpenter (e.g., 1963, 1967a, 1978) and others (Hunsaker, 1962; Lynn, 1965; Ferguson, 1971; Carpenter and Ferguson, 1977) have shown that many species of lizards have distinctive species characteristic head bobbing displays. Although phylogenetic trees were not constructed in these studies, they were often implied and reference to more primitive and more derived species was made (e.g., Lynn, 1965; Ferguson, 1971). As a

way of conclusion, Cogger (1978:665) states that, "Recent studies have found that many innate behaviour patterns are species-specific and that such patterns are valuable in establishing systematic affinites and evolutionary histories."

However, there were skeptics (e.g., Klopfer, 1969, 1975; Atz, 1970). Klopfer and Atz argued that behavior would not evolve along phyletic lines, mainly because it was a process and not a structure. Because of this it would be difficult to determine behavioral homologies, a necessary step in establishing phylogenetic relationships. As a result, they considered attempts to compare behavioral traits among taxa undesirable (reviews in Burghardt and Gittleman, 1990; Brooks and McLennan, 1991; and Gittleman and Decker, 1994).

Yet early on, Mayr (1958) and later Hinde (1966) had pointed out that genetic variability is universal whether it is related to morphology or to behavior. Hinde and Tinbergen had written (1958:263), "In spite of their ephemeral nature, characters of behavior have been used successfully in studies of the systematics of a number of groups. The problems involved are parallel to those entailed in the use of morphological characters." These authors emphasized the importance of knowing the natural history of the animal as well as the causation and function of the behavior to avoid

some of the difficulties involved in the use of behavioral characters in systematics. Brown (1975:19) is impressed by the correspondence between "natural groupings of species suggested by behavioral traits and those suggested by morphological and other nonbehavioral traits" and cites numerous examples. He concludes that, "the behavior of every species of animal, including man, has been profoundly influenced by its evolutionary history even down to seemingly insignificant details of behavior."

De Queiroz and Wimberger (1993) found, in an analysis that compared data sets that contained both morphological and behavioral characters, no significant differences between mean consistency indices (which measure homoplasies) within data sets for the two types of characters. Their results support the view that behavioral characters are just as useful as morphological characters for the estimation of phylogeny and that these can help confirm existing phylogenies. Nevertheless, Gittleman et al. (1996) caution that their usefulness may depend on the taxon, the behavior and the morphology involved.

Greene (1994) argues that behavior is not necessarily more variable nor more difficult to describe than morphology. Actually, the distinctions between behavior and other phenotypic traits are "fuzzy" (Greene, 1994:378). Greene explains, "Enzyme-substrate reactions and other fast

molecular events are referred to as biochemical or physiological, somewhat slower responses are called behavior, and features that appear stable over long periods are known as morphology. All these phenomena are outcomes of genetic, developmental, and control processes". Greene (1994) concludes that behavior should be no more difficult to homologize than any other attribute of an organism. Thus, behavior patterns can provide information that may be useful in the study of the evolutionary history of a group of taxa in conjunction with other traits, morphological, biochemical or ecological (Gittleman, 1981; McLennan et al., 1988; Burghardt and Gittleman, 1990; Brooks and McLennan, 1991; de Queiroz and Wimberger, 1993; McLennan, 1993; Greene, 1994).

Critics raised another difficulty, that behaviors rarely leave any fossil record (e.g., Atz, 1970; but see Seilacher, 1967, and Boucot, 1990, for numerous examples). This could have been a serious problem for estimating behavioral homology if it was understood that extinct taxa were the direct common ancestors of the taxa that are being studied which is generally not the case. As Greene (1994:380) points out, fossils provide additional taxa for analysis, "not proof per se of ancestral traits and thus of homology".

In any case, many morphological traits do not leave any fossil traces either. Nevertheless, they are no less useful

in a phylogenetic reconstruction because of it. Greene (1994) notes that the homology of vertebrate hearts, for instance, has not been questioned for lack of a fossil record (also see Gittleman et al., 1996). Furthermore, one of the major advantages of the cladistic method is that the distinction between similarities due to common ancestry and those due to homoplasy does not necessarily require fossil records (Etheridge, pers. comm.).

Although the concept of homology (shared similarity due to shared history) can be applied to behavioral studies, care must be taken in using the best supported phylogeny from the systematic literature to test the historical origin of behavioral traits (Dobson, 1985; Lauder, 1986; Brooks and McLennan, 1991). These authors suggest using taxonomies that were established following a cladistic methodology (e.g., Wiley, 1981). By using this type of methodology, it is possible to obtain taxonomies that give better estimates of phylogeny due to its concern for accurate inference of patterns that share a common history.

Today it is well accepted that the comparative study of behavioral patterns among taxa can often clarify, confirm or hypothesize their evolutionary history. To conclude this section, a few examples taken randomly from the literature are given.

Greene (1977) and Greene and Burghardt (1978) observed constriction in 48 species of snakes (26 genera in 4 primitive families). They found that despite differences in prior experience, size, shape, habitat, and diet, the snakes used a single pattern of constriction indicating that this pattern was probably used by their common ancestor.

In amphibians, Duellman (1985) defined 29 reproductive modes in anurans and used this information to construct a phylogeny. The results showed that shared derived reproductive modes could be useful in phylogenetic analyses. Duellman concluded that modes of anuran reproduction accompanied by their morphological, physiological and/or behavioral modifications in the adults have great phylogenetic significance and should be used whenever possible in reconstructing phylogenies.

McLennan et al. (1988) and McLennan (1993) used information on courtship and nesting behavior in 6 species of sticklebacks to determine phylogenetic relationships among these species. They arrived at the conclusion that the behavioral data provided a less ambiguous picture than the available morphological data.

Prum (1990) used behavioral characters of manakins (Aves: Pipridae) to construct a phylogenetic hypothesis for this group of birds. He used 44 display characters. Prum found that the results were highly consistent with an

independent hypothesis of phylogeny based on 57 morphological syringeal characters and that, therefore, behavioral characters could be used in accurately reconstructing phylogeny.

CHAPTER 2

OVERVIEW OF SAND BURYING IN LIZARDS OF THE WORLD

Burying behavior has been noted in many lizards that live on loose, aeolian sand, but the details of this behavior have been documented for only a few. Nevertheless, it is a behavior worth looking into because it may be phylogenetically informative. Sand burying seems to be a species specific behavior and variation among species may occur. Moreover, sand burying behavior appears when lizards occupy more extreme type habitats characterized by the presence of a loose sandy substrate where little vegetation is available for cover. This situation may trigger a series of adaptive changes in an organism, among them behavioral changes such as sand burying.

I will attempt a survey of the literature of what is known of burying behavior in the different families of lizards (Table 1). Here "burying" is used in the large sense of the word to include sand burying into loose soil but also sand swimming in loose soil and digging in hard soil with the construction of a burrow and/or tunnel. Specific use of the word "burying" will be explained in the next two sections (in particular p. 26-27).

Table 1 - Burying in different lizard families.

Family	Example	Location	Mode	Function	Reference
Anniellidae	Anniella	California & NW Mexico	DB?		Mosauer, 1932
			SB/DB?		Carr, 1963
			SB, SS?		Pough et al., 1978
	A. pulchra	California	SS		Gans et al., 1992
Chamaeleonidae (Agaminae)	Agama hispida makarikarica (now Agama etoshae, Arnold 1995)	Namibia	SB	IP, PA	Steyn et al., 1963
	Amphibolurus barbatus (now Pogona barbata, Cogger, 1994)	Australia	DB	IP	Rankin, 1977
	A. clayi (now Ctenophorus clayi, Cogger, 1994)	Australia	SB?		Storr, 1966
	A. cristatus (now Ctenophorus cristatus, Cogger, 1994)	Australia	DB		Houston, 1978
	A. decresi (now Ctenophorus decresii, Cogger, 1994)	South Australia	DB?	IP	Armstrong, 1979
	A. gibba (now Ctenophorus gibba, Cogger, 1994)	Australia	DB	TE	Houston, 1978
	A. inermis	Australia	DB		Storr, 1966
				TE	Bradshaw & Main, 1968
				PA	Davey, 1970
				IP, TE	Heatwole, 1970
				IP	Houston, 1978
	A. maculosus (now Ctenophorus maculosus, Cogger, 1994)	Australia	DB	IP, TE	Houston, 1978
	A. nuchalis (now Ctenophorus nuchalis, Cogger, 1994)	Australia	DB	IP, PA, TE	Rankin, 1977
	A. pictus (now Ctenophorus pictus, Cogger, 1994)	Australia	DB		Mayhew, 1963; Bustard, 1965
					Storr, 1966; Houston, 1978
	Bufoniceps laungwalaensis	NW India	SB	IP, PA	Prakash, 1972, & Sharma, 1978, (in Arnold, 1992)
	Ctenophorus clayi	Australia	DB	IP, PA, TE	Greer, 1989 & references therein
	C. cristatus	Australia	DB	IP, PA, TE	Greer, 1989 & references therein
	C. gibba	Australia	DB	IP, PA, TE	Greer, 1989 & references therein
	C. nuchalis	Australia	DB	IP, PA, TE	Greer, 1989 & references therein
	C. pictus	Australia	DB	IP, PA, TE	Greer, 1989 & references therein
	C. reticulatus	Australia	DB	IP, PA, TE	Greer, 1989 & references therein
	C. salinarum	Australia	DB	IP, PA, TE	Greer, 1989 & references therein
	C. scutulatus	Australia	DB	IP, PA, TE	Greer, 1989 & references therein
	Diporiphora linga	Australia	SB	IP	Houston, 1978

Table 1 (continued)

Family	Example	Location	Mode	Function	Reference
Chamaeleonidae (Agaminae)	Phrynocephalus	Central & SW Asia	SB		Schmidt & Inger, 1957
				IP, PA	Carr, 1963
				IP, PA	Arnold, 1994a
	P. arabicus	Middle East	SB	PA	Arnold, 1984
	P. reticulatus	----	SB	PA	Arnold, 1995
	Rankinia adelaidensis	Australia	DB/SB	PA	H. Ehmann, pers. comm. to Greer, 1989
	Uromastyx aegyptius	Israel	DB		Schmidt & Inger, 1957
					Bouskila, 1987
	U. hardwicki	NW India	DB	IP, TE	Murthy & Arockiasamy, 1977
Cordylidae (Gerrhosaurinae)	Angolosaurus skoogi	SW Africa	SS	PA	Steyn, 1963
				IP, PA	Hamilton & Coetzee, 1969
					Mitchell et al., 1987
				IP, PA	Arnold 1994a
	Zonosaurus laticaudatus	Madagascar	SS	IP	Arnold, 1995
Gekkonidae	(psammophilous gekkonids)	SW Africa	DB		Werner, 1977
					Carrillo de Espinoza et al., 1990
					Bauer & Russell, 1991
	Chondrodactylus angulifer	SW Africa	DB		Haacke, 1976b
	Coleonyx variegatus	SW USA	DB		Klauber, 1939
				IP	Cowles, 1941
	Kaokogecko	SW Africa	DB		Bauer & Russell, 1991
	K. vanzyli	SW Africa	DB		Haacke, 1976a
	Nephrurus stellatus	South Australia	DB	TE	Galliford, 1978
	Palmatogecko rangei	SW Africa	DB	IP, TE	Haacke, 1976a
					Russell & Bauer, 1990
					Bauer & Russell, 1991
	Ptenopus	Southern Africa	DB		Haacke, 1964 (in Werner, 1977)
					Bauer & Russell, 1991
	P. carpi	SW Africa	DB		Haacke, 1975
	P. garrulus	Southern Africa	DB		Haacke, 1975
	P. g. garrulus	Southern Africa	DB	IP, PA, TE	Haacke, 1975
	P. g. maculatus	Southern Africa	DB		Haacke, 1975
	P. kochi	SW Africa	DB	PA	Haacke, 1975
	Teratoscincus S. scincus	Karakum, Central Asia	DB		Shammakov et al., 1981
Hoplocercidae	Hoplocercus spinosus	Brazil	DB		Schmidt & Inger, 1957
Iguanidae	Dipsosaurus dorsalis	SW North America	DB	IP	Cowles, 1941
					Norris, 1953; Mayhew, 1963

Table 1 (continued)

Family	Example	Location	Mode	Function	Reference
Lacertidae	Acanthodactylus schmidti	North Africa	DB	PA	Arnold, 1984, 1994a
	Aporosaura anchietae	Namib Desert	SB	PA, TE, IP	Louw and Holm, 1972
	Eremias (some)	Central & SW Asia	SB		Arnold, 1994b
	E. acutirostris	Central Asia	SB		Arnold, 1995
	Meroles	SW Africa	SB	IP, PA	Arnold, 1994a, 1995
	M. anchietae	SW Africa	SB	IP, PA	Arnold, 1995
	M. ctenodactylus	SW Africa	SB	IP, PA	Arnold, 1995
	M. cuneirostris	SW Africa	SB		Mitchell and Steyn, 1967
				IP, PA	Arnold, 1995
	M. knoxii	SW Africa	DB	IP, PA	Arnold, 1995
	M. micropholidotus	SW Africa	SB	IP, PA	Arnold, 1995
	M. reticulatus	SW Africa	DB, SB	IP, PA	Arnold, 1995
	M. suborbitalis	SW Africa	DB	IP, PA	Arnold, 1995
	Mesalina adramitana	North Africa	DB	PA	Arnold, 1984
	Ophisops elegans	Middle East	SB	IP	Arnold, 1994a
	Psammodromus hispanicus	Spain	SB		Arnold, 1994a
Phrynosomatidae	Callisaurus	SW North America	SB		Pough, 1969a
					Pough et al., 1978
	C. crinitus	Vizcaino Desert,			
		Baja California	SB		Mosauer, 1936
	C. draconoides	SW North America	SB	IP, PA	Arnold, 1995
					pers. obs., 1993
	Cophosaurus	----	SB	IP, PA	Arnold, 1995
	C. texanus	----	SB	IP	Arnold, 1995
	Holbrookia	Mid West USA &	SB		Pough et al., 1978
		North Mexico		IP, PA	Arnold, 1995
	H. lacerata		SB	IP, PA	Axtell, 1956
	H. maculata		SB	IP, PA	Axtell, 1956
					Clarke, 1965
	H. propinqua		SB	IP, PA	Axtell, 1956
	H. texana		SB	IP, PA	Axtell, 1956
	Phrynosoma	Central & West			
		North America	SB		Mosauer, 1932
					Schmidt & Inger, 1957
					Tanner & Krogh, 1975
					Pough et al., 1978
			SB	IP, PA	Arnold, 1995
	P. coronatum	California &			
		Baja California	SB	IP, TE	Heath, 1965
	P. cornutum	Mid North America	SB	IP, TE	Heath, 1965
	P. douglassi	West North America	SB	IP, TE	Heath, 1965
					pers. obs., 1993

Table 1 (continued)

Family	Example	Location	Mode	Function	Reference
Phrynosomatidae	Phrynosoma m'calli	Arizona	SB	IP, PA, TE	Norris, 1949
				TE	Reeve, 1952
					Mayhew, 1963
				IP, TE	Heath, 1965
	P. modestum	North America	SB	IP, TE	Heath, 1965
					Arnold, 1994a
	P. orbiculare spp.	SW USA	SB		Klauber, 1939
	P. platyrhinos	West North America	SB	IP	Klauber, 1939
				TE	Reeve, 1952
				IP, TE	Heath, 1965
					Pough, 1969b
				IP, TE	Tanner & Krogh, 1973
					pers. obs., 1993
	P. solare	Arizona & Mexico	SB	IP, TE	Heath, 1965
	Sceloporus arenicolous	Texas	SB		Etheridge, pers. comm., 1993
	S. clarki	Arizona	SB		Etheridge, pers. comm., 1993
	S. graciosus	California	SB		Etheridge, pers. comm., 1993
	S. magister	California	SB		Cowles, 1941; Arnold, 1995
					Etheridge, pers. comm., 1993
	S. occidentalis	Western USA	SB		McGinnis, 1966; Pough, 1969b
				IP	Arnold, 1995
					Etheridge, pers. comm., 1993
					pers. obs., 1993
	S. olivaceous	Texas	SB		Etheridge, pers. comm., 1993
	S. orcutti	California	SB	IP	Arnold, 1995
					Etheridge, pers. comm., 1993
	S. rufidorsum	Mexico	SB		Etheridge, pers. comm., 1993
	S. variabilis	Texas	SB		Etheridge, pers. comm., 1993
	S. virgatus	North America	SB		Stebbins, 1963
	Uma	North America	SB	TE	Stebbins, 1944; Mayhew, 1964
					Norris, 1958
				PA	Pough, 1969a, 1970
			SB	IP, PA	Arnold, 1994a, 1995
	U. exsul	Mexico	SB	IP	Carpenter, 1967a
			DB?, SB	IP, PA	Pough et al., 1978
	U. notata	California	SB		Mosauer, 1932
				PA, TE	Klauber, 1939
				IP	Cowles, 1941
				IP, PA	Carpenter, 1963
					Mayhew, 1963
					pers. obs., 1993
	U. n. inornata	California	SB	IP, PA	Carpenter, 1963; Pough, 1970

Table 1 (continued)

Family	Example	Location	Mode	Function	Reference
Phrynosomatidae	Uma paraphygas	Mexico	SB	IP	Carpenter, 1967a
	U. scoparia	California	SB	IP, PA	Carpenter, 1963; Mayhew, 1966
				IP, PA	Pough, 1970
					Arnold, 1995
	Urosaurus microscutatus	Mexico	SB		Arnold, 1995
	U. nigricaudus	----	SB		Etheridge, pers. comm., 1993
	Uta	Mexico	SB		Tanner & Krogh, 1975
	U. squamata	----	SB		Etheridge, pers. comm., 1993
	U. stansburiana	California	SB	IP	Arnold, 1995
					Etheridge, pers. comm., 1993
					pers. obs., 1993
	U. tumidarostra	Mexico	SB		Etheridge, pers. comm., 1993
Polychrotidae	Pristidactylus casuhatiensis	Buenos Aires	DB?		Gallardo, 1977; Cei, 1993
	P. fasciatus	Central Argentina	DB?		Cei, 1993
Pygopodidae	flap-footed lizards	Australia & New Guinea	DB		Schmidt & Inger, 1957
Scincidae	Ablepharus kitaibelii	----	SS	IP	Arnold, 1995
	Acontias	Africa	DB, SS?		Schmidt & Inger, 1957
	Anomalopus leuckartii	Australia	SS		Ehmann & Swan, 1987
	A. swansoni	Australia	SS		Ehmann & Swan, 1987
	Brachymeles	Philippines	DB, SS?		Schmidt & Inger, 1957
	Chalcides	South Europe & North Africa	SS		Schmidt & Inger, 1957
					Pough, 1970
	C. ocellatus	----	SS	IP	Arnold, 1995
	C. sepsoides	North Africa & Near East	SS		Mosauer, 1932
	Ctenotus robustus	South Australia	DB?	IP	Armstrong, 1979
	C. storri	Australia	DB?	PA	Rankin, 1978
	C. taeniolatus	Australia	DB	PA, IP	Davey, 1970
					Taylor, 1984
				IP	Greer, 1989 & references therein
	Egernia bos	Australia	DB		Storr, 1960; Ford, 1963
	E. coventryi	Australia	DB		Greer, 1989 & references therein
	E. inornata	Australia	DB		Davey, 1970
				PA, TE	Webber, 1979
					Coventry & Robertson, 1980
				PA, IP, TE	Pianka & Giles, 1982
					Pianka, 1986
					Greer, 1989 & references therein

Table 1 (continued)

Family	Example	Location	Mode	Function	Reference
Scincidae	Egernia kintorei	Australia	DB		Greer, 1989 & references therein Cogger, 1994
	E. luctuosa	Australia	DB		Greer, 1989 & references therein
	E. multiscutata	Australia	DB		Coventry & Robertson, 1980 Greer, 1989 & references therein
	E. striata	Australia	DB	PA, IP, TE	Pianka & Giles, 1982 Pianka, 1986 Greer, 1989 & references therein
	E. whitii	Australia	DB		Hickman, 1960 Greer, 1989 & references therein
	Eremiascincus fasciolatus	Australia	SS	PA	Greer, 1989 & references therein Andrews & Kenney, 1990 James & Losos, 1991 Cogger, 1994
	E. richardsonii	Australia	SS		James & Losos, 1991
	Eumeces fasciatus	----	DB		Pough, 1969b
	E. schneideri	----	SS	IP	Arnold, 1995
	Hemiergis decresiensis	Australia	SS?		Jenkins & Bartell, 1979
			DB?		Cogger, 1994
	Lerista	Australia	SS		Greer, 1989 & references therein Cogger, 1994
	L. bipes	Australia	SS?		Davey, 1970; Smith, 1976
	L. bougainvillii	Australia	SB?		Armstrong, 1979
			SS?		Jenkins & Bartell, 1979
	L. macropisthopus	Australia	SS?		Davey, 1970
	L. muelleri	Australia	SS?		Smith, 1976
	Lygosoma fernandi	Africa	DB		Schmidt & Inger, 1957
	Mabuya acutilabris	SW Africa	SB	IP, PA	Arnold, 1995
	M. brevirostris	SW Africa	SS	IP	Arnold, 1995
	M. variegata	SW Africa	SB	IP	Arnold, 1995
	M. vittatus	SW Africa	SS	IP	Arnold, 1995
	Neoseps	Florida	SS		Schmidt & Inger, 1957
	N. reynoldsi	Florida	SS		Telford, 1959 Andrews, 1994
	Nessia	Ceylon	DB, SS?		Schmidt & Inger, 1957
	Ophiomorus	Asia	SS		Schmidt & Inger, 1957 Pough, 1970
	O. blanfordi	Asia	SS		Schmidt & Inger, 1957
	Ophioscincus	SE Asia	DB, SS?		Schmidt & Inger, 1957
	Rhodona punctatovittata	Australia	DB		Bustard, 1968
	Scelotes	Africa	DB, SS?		Schmidt & Inger, 1957

Table 1 (continued)

Family	Example	Location	Mode	Function	Reference
Scincidae	Scincus	North Africa & SW Asia	SS		Schmidt & Inger, 1957
					Pough, 1970
			SS		Arnold, 1994a, 1995
	S. mitranus	North Africa	SS	PA	Arnold, 1984, 1995
	S. officinalis	North Africa	SS		Mosauer, 1932, 1936
	S. scincus	Sahara Desert	SS		Hetherington, 1989
	Siaphos aqualis	Australia	SS?	PA	Davey, 1970
	Sphenomorphus richardsonii	Australia	DB?		Smith, 1976
	Sphenops sepsoides	North Africa	SS		Andrews & Kenney, 1990
					Andrews, 1994
	Typhlacontias	Africa	DB, SS?		Schmidt & Inger, 1957
	Typhlosaurus	S Africa	DB, SS?		Schmidt & Inger, 1957
	T. gariepensis	Kalahari Desert	SS		Huey et al., 1974
	T. lineatus	Kalahari Desert	SS		Huey et al., 1974
	Australian sandfish?	Australia	SS		Carr, 1963
Teiidae	Ameiva ameiva	North Argentina	DB		Vanzolini et al., 1980 (in Cei, 1993)
	Cnemidophorus lacertoides	Argentina & Uruguay	DB		Gallardo, 1977
	C. longicaudus	Central Argentina	SB, DB?		Cei, 1986, 1993
	Teius oculatus	Central Argentina	DB		Cei, 1993
	T. teyou	Argentina	DB, SB?		Cei, 1986, 1993
	T. oculatus	Central Argentina	DB		Cei, 1986
Tropiduridae	Leiocephalus	West Indies	SB?		Arnold 1994b
	Liolaemus anomalus	Central Argentina	DB		Cei, 1986
	L. boulengeri	South Central Argentina	DB, SB?		Cei, 1986
	L. canqueli	Chubut, Argentina	DB, SB?		Cei, 1986
	L. cuyanus	Central Argentina	SB		Cei, 1993
	L. fitzingerii	Central Argentina	DB		Donoso-Barros, 1966
			DB, SB?		Cei, 1986
	L. kuhlmani	Coastal Chile	SB		pers. obs., 1991
	L. lutzae	n/Rio de Janeiro	SB		Rocha, 1993
	L. melanops	Chubut, Argentina	DB, SB?		Cei, 1986
	L. multimaculatus	Buenos Aires coast	SB		Gallardo, 1977
				TE	Cei, 1979, 1986, 1993
	L. nigromaculatus	Coastal Chile	SB	IP, PA, TE	Simonetti, 1984
			SB		pers. obs., 1991
	L. occipitalis	Southern coast of Brazil & Uruguay	SB		Keller & Krause, 1986
					L. Verrastro, pers. comm., 1995

Table 1 (continued)

Family	Example	Location	Mode	Function	Reference
Tropiduridae	Liolaemus rabinoi	Mendoza, Argentina	SB	TE	Cei, 1979, 1986
	L. riojanus	Central Argentina	SB		Cei, 1986, 1993
	L. salinicola	Central Argentina	SB		Cei, 1993
	L. wiegmannii	Argentina	SB		Cei, 1993
	L. zapallarensis	Coastal Chile	SB		pers. obs., 1991
	Stenocercus doellojuradoi	NW Argentina	SB		pers. obs., 1995
Varanidae	Varanus bengalensis	North India & Sri Lanka	DB	IP, PA, TE	Auffenberg, 1983
	V. brevicauda	Australia	DB		Schmida, 1975 (in Greer, 1989)
	Varanus gouldii	Australia	DB	IP, TE	Schmidt & Inger, 1957 Houston, 1978 Cogger, 1994
	V. komodoensis	Indonesia	DB	TE	Auffenberg, 1981
	V. storri	Australia	DB		Bartlett, 1982

Notes: The new partition into 8 families by Frost and Etheridge (1989) is recognized for the old family Iguanidae. In the "Location" column is given an indication of where a species may be found. No attempt is made of specifying its complete distribution. Since terms used to describe submergence into substrates are not always defined by the author, there may be some overlap in meaning between the different categories shown in the column Mode. Categories used are: dig burrows (DB), sand bury (SB), and sand swim (SS). When a reference to the function of the behavior is given by an author, it is shown in the Function column: spend inactive period (IP), predator avoidance (PA), escape temperature extremes (TE, may include references to maintenance of humidity). ? = indicates reference in article to DB, SB or SS is unclear. The survey does not pretend to be exhaustive but to be illustrative.

Difficulties

An initial difficulty in such a survey is semantic. Norris and Kavanau (1966), for example, use the term "burrowing" when describing the submerging behavior into loose sand of the snake Chionactis occipitalis, Colubridae (which is also referred to as "sand swimmer" by other authors, e.g., Pough, 1970:145). In contrast, Gans (1974) uses "burrowing" when describing the excavation or construction of an open tunnel in firm soils of varying types in Amphisbaenians.

Before going further, it is important to note that burrowing activity has often been described in female lizards that dig a cavity or tunnel to lay their eggs (e.g., Cogger, 1978; Jenkins and Bartell, 1979; Greer, 1989). Although this shows capability for "digging" or "burrowing", references to females digging a nest are not shown in Table 1.

Confusing or interchanging terms is not new in the literature. Mosauer (1932:72) describes some sand reptiles as being able to "travel at extraordinary speed over the surface, and which are also able to burrow. They do not, however, proceed beneath the surface of the sand for any considerable horizontal distance. Some of them sink into the sand in a vertical direction, so that they are found beneath the spot where they left the surface" [underline is mine]. Apparently, the author refers to "sand burying" when using

the terms "burrow" and "sink" into sand. Huey et al. (1974) use the term "fossorial" and "sand-swimming" interchangeably when describing the sand-swimming behavior in two species of skinks of the genus Typhlosaurus.

Although Davey (1970:58) seems to imply "sand-swimming" in the skink Siaphos aqualis, he uses the term "burrowing". He writes, "When alarmed, they burrow into the soil, disappearing in a few seconds.... it is a burrowing, semi-nocturnal lizard which moves in a snake-like manner. Its retarded limbs do not help much in movement and are held beside the body when the lizard is in motion." He also describes Lerista bipes (Scincidae), that when disturbed, will "quickly dig their pointed snout into the sand and tunnel to cover. But on the surface, they are out of their element and do not make such headway. They move with a snake-like motion" (p. 67). Later, Davey (1970:67) adds referring to L. macropisthopus, "Since this lizard is a burrower, it has no need for functional limbs."

Ehmann and Swan (1987) use the term "swim" (pp. 25 and 26) when referring to Anomalopus spp. (Scincidae) moving into loose soil but the title of the article refers to "burrowing skinks". Pough (1970:145) describes Uma notata as a "quiescent burier" but in the title of the article refers to its "burrowing" ecology.

Gans (1974:129) notes that although "sand swimmers" are often called "burrowers", they are specialized for life in a particular medium, dry sand. Because surface layers of dry sands may show little adhesion between grains, "an animal moving through such a medium forms only an instantaneous tunnel and the displaced overburden collapses just as soon as the animal moves on.... The sides of the 'tunnel' are at any instant defined by the sides of the animal."

Another difficulty encountered in the literature, was that it was not always clear whether a lizard actually had dug a burrow or was using another animal's shelter. Ford, for instance, wrote (1965:175) that he collected specimens of the skink Egernia bos "from shallow burrows". Although this author might be giving an indication of burrow digging in this species as was later confirmed by other references (Ford, 1963; Storr, 1960; Table 1), such ambiguous references were discarded. Another example of this type is found in Chapman and Dell (1974:120). These authors write about specimens of the skink Egernia inornata, that were "dug out of burrows in shrublands on sandy loam." Whether these burrows were dug by the skinks or just occupied is not clear.

Many of these natural history notes are valuable descriptions and their "incompleteness" is only relative to the interests of another researcher. However, clarity and consistency in the use of terms can only facilitate a

correct use of the information provided. Stebbins (1944:330) is one of the few authors who is clear and consistent in defining terms. He defines "burrowing" in lizards as soil being "scraped to one side and backward by rapid successive strokes given with one forelimb and then a series executed with the other. The heaped-up sand is pushed backwards with the hind limbs." If the soil is loose, slumping occurs and the lizard gets partially covered in the process of burrowing or digging. As for "burying" in sand lizards of the phrynosomatid genus Uma, Stebbins (1944:313) describes it as "submergence into the loose substratum of the habitat by diving or wriggling into the soil rather than by construction of a burrow or tunnel for retreat. Fossorial activity of this type results in direct contact between the surface of the animal's body and the small fragments which compose the wind-blown deposits."

Pough (1970:145) recognizes three types of subterranean activity in reptiles: the "true burrowers" (Amphisbaenidae) which construct open burrows in firm soil; the "sand swimmers" (e.g., Scincus, Scincidae; Ophiomorus, Scincidae; Chionactis, Colubridae) which "move freely through loose sand and spend much of their time buried but do not construct open burrows" and finally, the "quiescent buriers" which correspond to those reptiles which "bury themselves in loose soil and remain quiescent" (e.g., Uma).

Arnold (1994a, 1995) mainly uses two terms when referring to submergence into loose sand, each one corresponding to a different function. He refers to "sand diving" (sometimes called "rapid burial", 1995:363; or "burying behavior", 1995:366) as a response to predator avoidance in lizards (e.g., in Uma, Phrynocephalus, some Meroles, Scincus, Angolosaurus) and to "burial" or "nocturnal burial" when a lizard seeks cover for the night as it becomes inactive. When alluding to specific methods of "sand diving" as a function of predator avoidance, Arnold (1995) uses the term "sand burial" when describing burying behavior for species of Phrynosoma, and "shimmy burial" in species of Uma (term coined by Axtell, 1956).

Implications and Conclusions

In this study, the terms "sand burying" or "burying behavior" will be used as defined by Stebbins (1944). This term is equivalent to what Pough (1970) terms "quiescent buriers" and what Arnold (1995) describes as "nocturnal burial". The group of lizards that is investigated here belongs mostly to the quiescent burier type and were observed when burying at night upon ceasing diurnal activity.

The main conclusions that can be advanced from the survey shown in Table 1, are that:

- digging burrows, sand burying and/or sand swimming are widespread behaviors in lizard families, and

- some of these behaviors seem to be more characteristic for some lizard families. For instance, digging burrows seems prominent in the families Chamaeleonidae (subfamily Agaminae, with a few exceptions showing sand burying) Gekkonidae, Teiidae and Varanidae. Sand burying seems typical of the Lacertidae and the Phrynosomatidae. Both sand swimming and burrow digging are present in the Scincidae. Sand burying and burrow digging both occur in the Tropiduridae.

Because many references were not clear as to the type of burying behavior used by a lizard, the information provided in Table 1 is only indicative of the potential source of knowledge this behavior could be for furthering our understanding of the evolutionary history of various taxa of lizards. It would certainly help if only we could agree on the different behavioral patterns observed in the different modes of entering loose sand.

CHAPTER 3

NATURAL HISTORY OF THE GENUS LIOLAEMUS

The genus Liolaemus, first diagnosed in 1834 by A. F. A. Wiegmann (in Vanzolini, 1977(I):51), belongs to the iguanian family of Tropiduridae (Frost and Etheridge, 1989) and includes more than 150 species (Etheridge, 1992). Liolaemus ranges from the high cordilleras of Peru and Bolivia in the North, to Tierra del Fuego in the South, from the sandy beaches of the Pacific Ocean in the West, throughout most of Argentina, to the sandy Atlantic beaches of Argentina, Uruguay and southeastern Brazil (Donoso-Barros, 1966; Cei, 1986; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989).

Liolaemus shows an exceptional capacity for adaptive radiation, living in a wide variety of habitats:deserts, ocean beaches, patagonic steppes, austral forests, and the high andean mountains (Donoso-Barros, 1966). Liolaemus huacahuasicus, for example, is found at about 3700 m in the Cumbres Calchaquíes of Northern Argentina (Halloy and Laurent, 1988) and L. andinus is found at about 4500 m, 20 km east of Salar de Maricunga, in Chile (Halloy et al., 1991). Other species live on sand dunes next to the ocean (e.g., L. lutzae, along the coast of Rio de Janeiro

State, Brazil, Rocha and Bergallo, 1992, and Rocha, 1993; and L. multimaculatus, along the coast of the Buenos Aires Province, Argentina, Laura Vega, pers. comm.).

The great majority of species are terrestrial but a few are arboreal (e.g., L. tenuis and L. pictus). Some species occur in different types of habitats (e.g., L. quilmes and L. wiegmannii) but others are restricted to specific terrestrial environments such as rocks (e.g., L. elongatus petrophilus) or sand (e.g., L. multimaculatus and L. scapularis), (Etheridge and de Queiroz, 1988).

Liolaemus are diurnal lizards. Some are insectivorous, some are herbivorous, and some eat both insects and plant parts depending on the season and availability (Donoso-Barros, 1966). Many species are oviparous but some species living at high altitudes or at high latitudes, are viviparous (e.g., L. huacahuasicus, Halloy and Halloy, in press; L. pictus, and L. ruibali, pers. obs.).

Taxonomic Arrangement of the Genus Liolaemus

Even though Liolaemus occupies a large geographic range and contains numerous species exhibiting a lot of diversity, Donoso-Barros (1966) observes a continuity in the group (in morphological characters) that warrants keeping this polymorphic genus as a whole. Nevertheless, different taxonomic groupings of such a large collection of species

have been proposed by Girard (1858, in Vanzolini, 1977(I): 81-82), Laurent (e.g., 1983a, 1983b, 1984, 1985, 1995), Cei (e.g., 1979, 1986, 1993) and Etheridge (1995). The taxonomy specified by Etheridge (1995) and its implied phylogeny is adopted here because it recognizes only monophyletic groups, all of which are defined in terms of synapomorphies.

Liolaemus, together with Phymaturus (10 species) and Ctenoblepharys (1 species), constitute the subfamily Liolaeminae (Frost and Etheridge, 1989). Although no formal cladistic analysis of Liolaeminae has been published, Etheridge (1995) proposed a taxonomy of the subfamily, presented in an indented format of internested groups, without the recognition of formal hierarchical categories other than genera and species. However, because this indented taxonomy consists of internested sets of monophyletic groups, it can be directly translated into a phylogeny.

Etheridge's taxonomy (1995) recognizes two very large groups of Liolaemus, the nitidus and signifer groups, that form an unresolved polytomy with Liolaemus archeforus and L. kingii. Within the signifer group*, the large montanus group that forms an unresolved polytomy with Liolaemus anomalus and L. pseudoanomalus, is recognized.

---

footnote: * This is not the same "signifer group" used by Laurent (1992).

All of the species examined here for both ingroup and outgroup analysis are members of the montanus group, diagnosed by Etheridge (1995) as possessing a large, blade-like process on the posterior distal tibia associated with a greatly hypertrophied tibialis anterior muscle. In order to facilitate recalling the internesting of groups defined at various hierarchical levels, the terms "supergoup", "group", and "subgroup" (going from a more encompassing unit to a less encompassing unit) will be used here. These will be used to refer to the montanus group (supergroup), the boulengeri group (group) and the wiegmannii group (subgroup, see below). In essence they correspond to the different clades diagnosed on the basis of morphological characters. These terms were not used by Etheridge (1995, see indented classification below).

The montanus supergroup includes 61 described species and an undetermined number of undescribed forms. Of the 61 known species, 26 are placed in the boulengeri group, diagnosed by a patch of enlarged, spinose scales on the posterior medial surface of the thigh, bulged out in adult males due to hypertrophy of the underlying puboischiotibialis muscle. This group was earlier referred to as the "patch group" by Etheridge (1992, 1993).

A subset of 9 species of the boulengeri group was further recognized as the wiegmannii subgroup, based on sublabial-mental contact and smaller, more numerous lorilabials. Moreover, species of this subgroup, except for L. wiegmannii, the least specialized (e.g., Laurent, 1983a, 1984), have long claws, depressed bodies, keeled infralabials and are confined to sand dunes. Based on morphological characters, this complex appears to be monophyletic (Etheridge, 1995). Of the 9 species known for this subgroup, one species, L. rabinoi, is believed to be extinct (Cei, 1986), and another, L. cranwelli, is based on the description of one specimen and has possibly been confused with L. wiegmannii (Etheridge, pers. comm.).

All but one of the remaining species of the boulengeri group fall into two subgroups of phenetically similar species, here referred to as the darwinii complex and the fitzingerii complex. The term "complex" is used for these subgroups because their monophyletic status is uncertain (Etheridge, 1993). According to Etheridge (1993), the darwinii complex includes 8 species, not including L. darwinii Nihuil, an undescribed species first located near Lago Nihuil, Mendoza province. In addition to the undescribed species, species that were included in this study were:

L. darwinii
L. darwinii Nihuil
L. koslowskyi
L. laurenti
L. olongasta
L. ornatus
L. quilmes

According to Etheridge (pers. comm.), the fitzingerii complex includes 7 species. Of these, 6 species were included in the study:

L. boulengeri
L. canqueli
L. donosobarrosi
L. fitzingerii
L. melanops
L. xanthoviridis

The remaining species is Liolaemus cuyanus, a taxonomic challenge due to the presence of intermediate characters (e.g., Laurent, 1983a).

The complete list of species used in this study is given following Etheridge's indented classification (1995). The number of known species for each group, as of today, is shown in parentheses. The darwinii complex and fitzingerii complex are not identified in the following indentation since their status is still unclear.

Liolaemus signifer group (63)

montanus group (61)

L. andinus
L. huacahuasicus
L. multicolor
L. ruibali (Fig. 1)

boulengeri group (26)

L. boulengeri (Fig. 2)
L. canqueli (Fig. 3)
L. cuyanus (Fig. 4)
L. darwinii
L. donosobarrosi (Fig. 5)
L. fitzingerii (Fig. 6)
L. koslowskyi
L. laurenti
L. melanops (Fig. 7)
L. olongasta (Fig. 8)
L. ornatus
L. quilmes (Fig. 9)
L. xanthoviridis

wiegmannii group (9)

L. multimaculatus (Fig. 10)
L. riojanus
L. salinicola
L. scapularis (Fig. 11)
L. wiegmannii (Fig. 12)

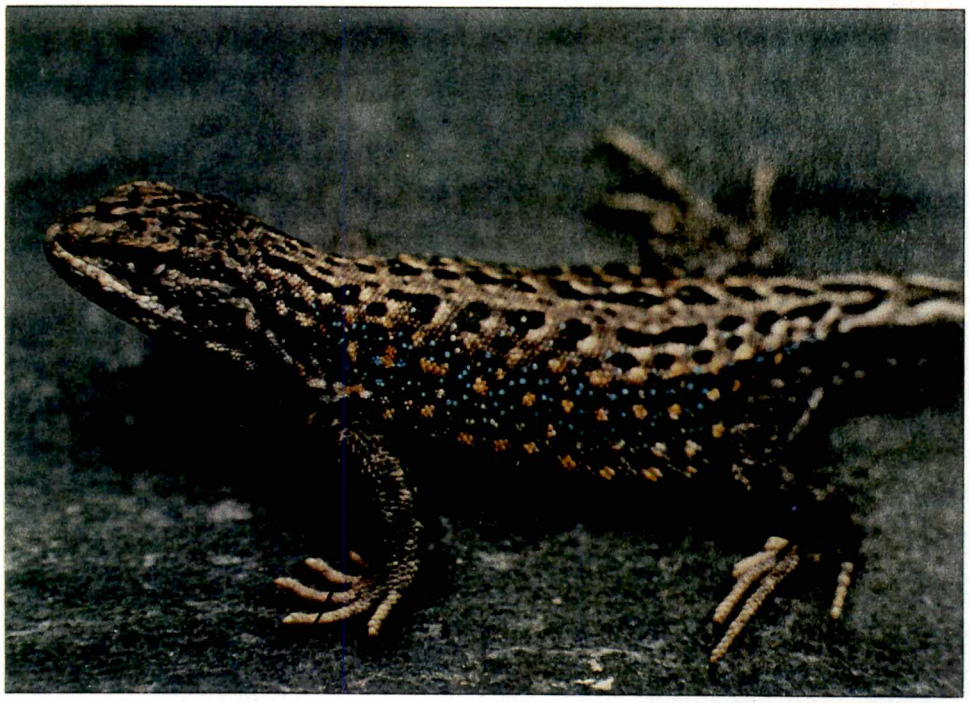
For the purpose of phylogenetic analysis, the ingroup, which is monophyletic, corresponds to the boulengeri group of Etheridge (1995), and no a priori assessment of relationships among its members is made. The outgroup comprises the 4 species not belonging to the boulengeri group but that are included in the montanus supergroup.

Figure 1. Liolaemus ruibali.

a. Male L. ruibali (from location NA, see Appendices A and B).

b. Habitat L. ruibali, 33-36 km east of Paso Aguas Negras, San Juan, Argentina (location NA in Appendix B).

a



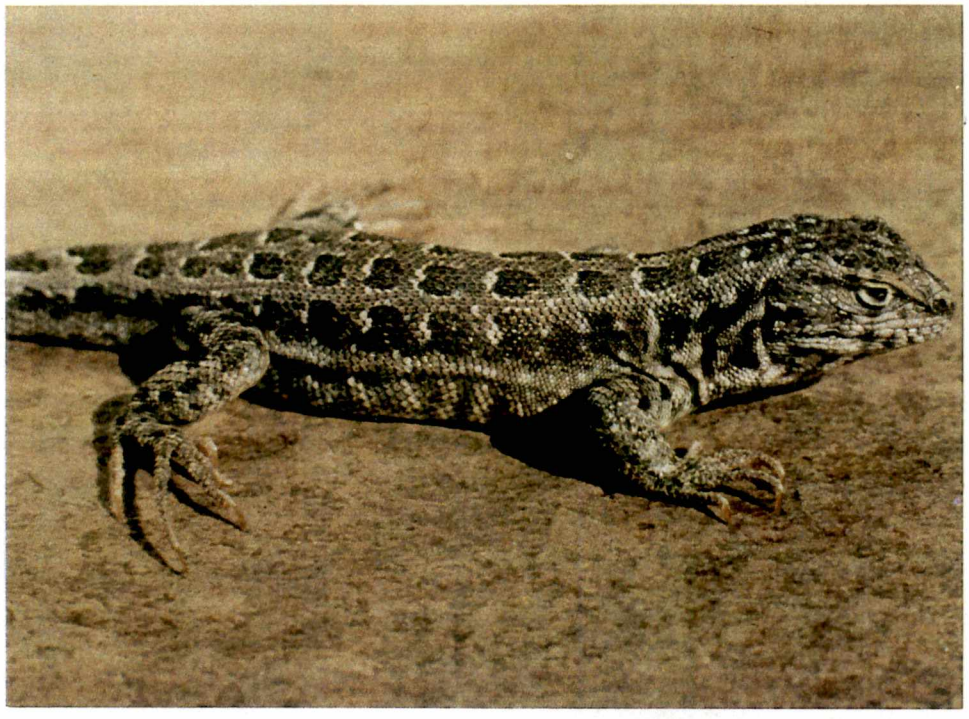
b

Figure 2. Liolaemus boulengeri.

a. Male L. boulengeri (from location CR, see Appendices A and B).

b. Habitat L. boulengeri, 7 km southwest of Cortadera, Mendoza, Argentina (location CR in Appendix B).

a



b

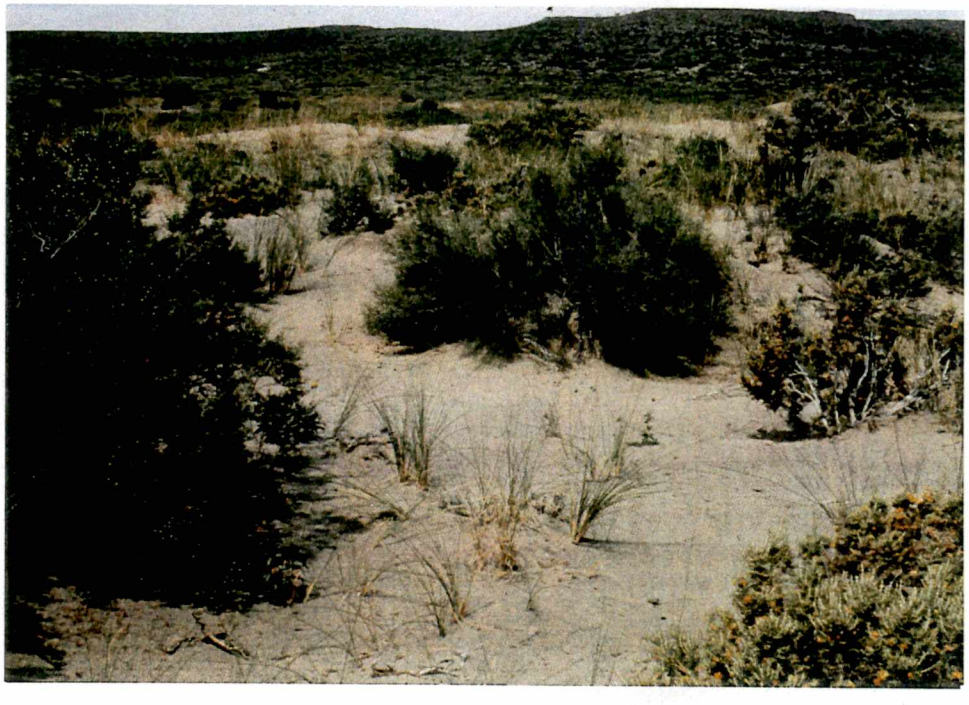


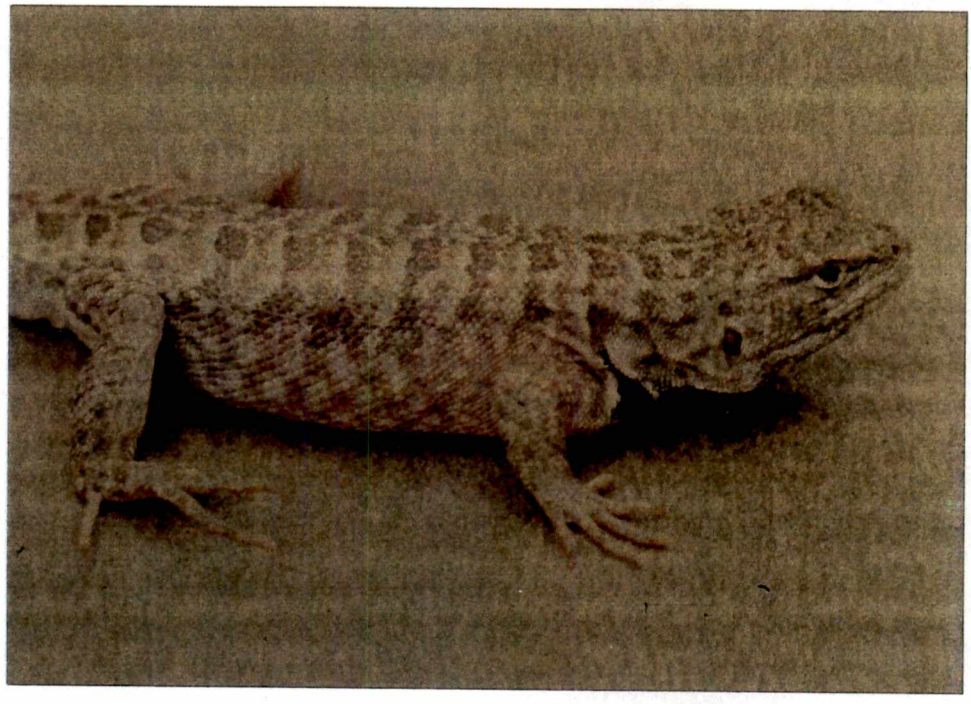
Figure 3. Liolaemus canqueli. Female in habitat, 20 km southeast of Paso de los Indios, towards El Sombrero, Chubut, Argentina (from location IN, see Appendices A and B).

Figure 4. Liolaemus cuyanus.

a. Male L. cuyanus (from location PI, see Appendices A and B).

b. Habitat L. cuyanus, 20 km southeast of Tinogasta (Medanos), Catamarca, Argentina (location TI in Appendix B). Liolaemus laurenti and L. salinicola are also found here.

a



b

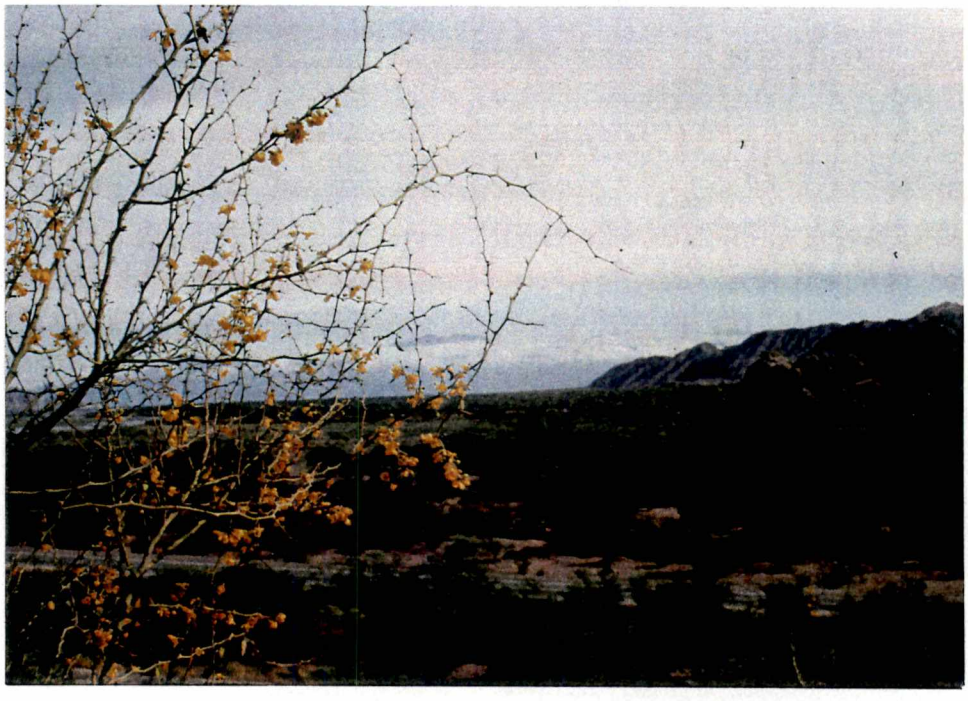


Figure 5. Liolaemus donosobarrosi.

a. Male L. donosobarrosi (from location MA, see Appendices A and B).

b. Habitat L. donosobarrosi, Matancilla, Mendoza, Argentina (location MA in Appendix B).

a

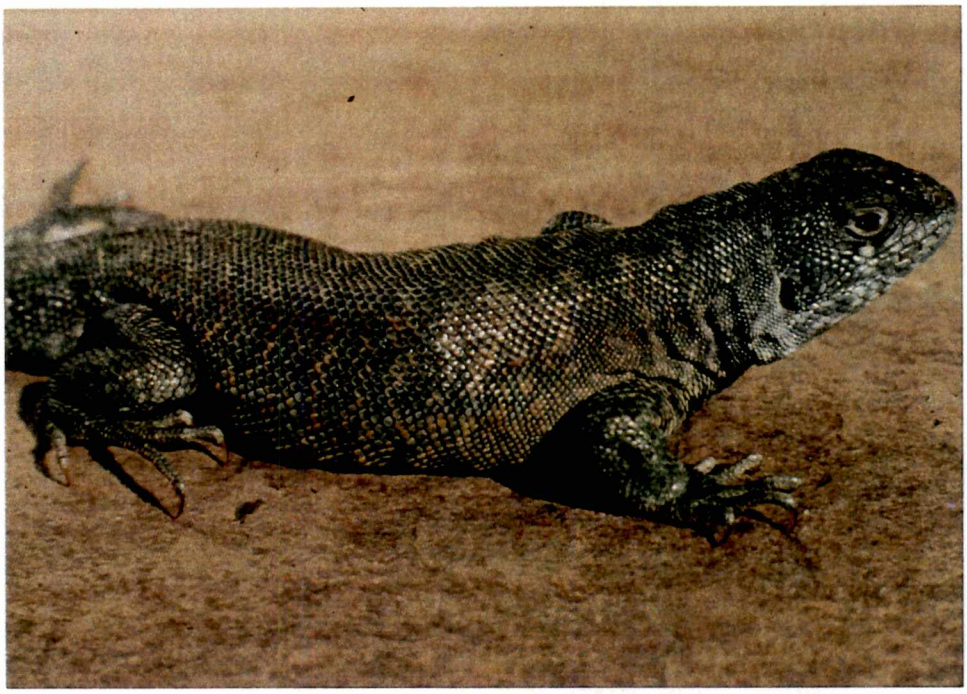
b

Figure 6. Liolaemus fitzingerii.

a. Female L. fitzingerii (from location CH, see Appendices A and B).

b. Habitat L. fitzingerii, ruta 32 near intersection ruta 1, Chubut, Argentina (location CH in Appendix B).

a



b

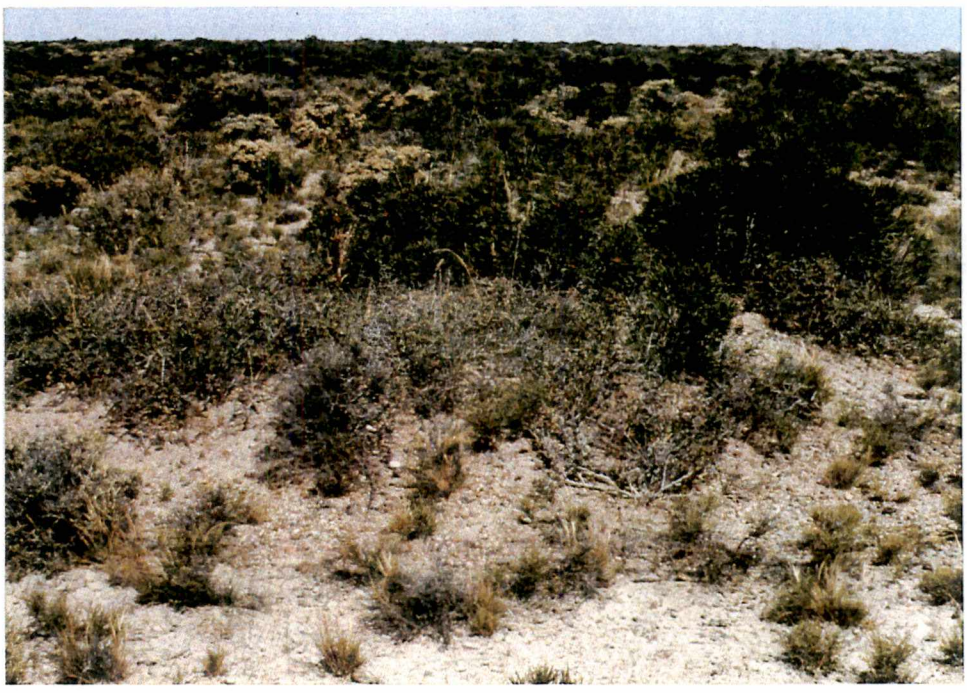
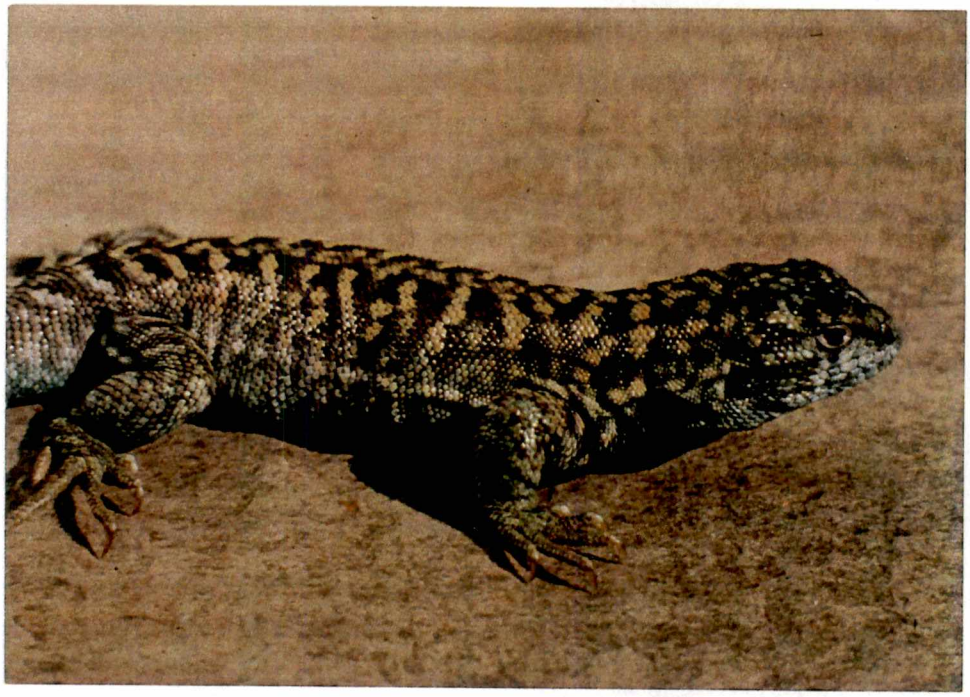


Figure 7. Liolaemus melanops.

a. Male L. melanops (from location PV, see Appendices A and B).

b. Habitat L. melanops shared by penguins which come here every Summer to nest, Caleta Valdés, Peninsula Valdés, Chubut, Argentina (location PV in Appendix B).

a



b

Figure 8. Liolaemus olongasta. Male from location TA (see Appendices A and B).

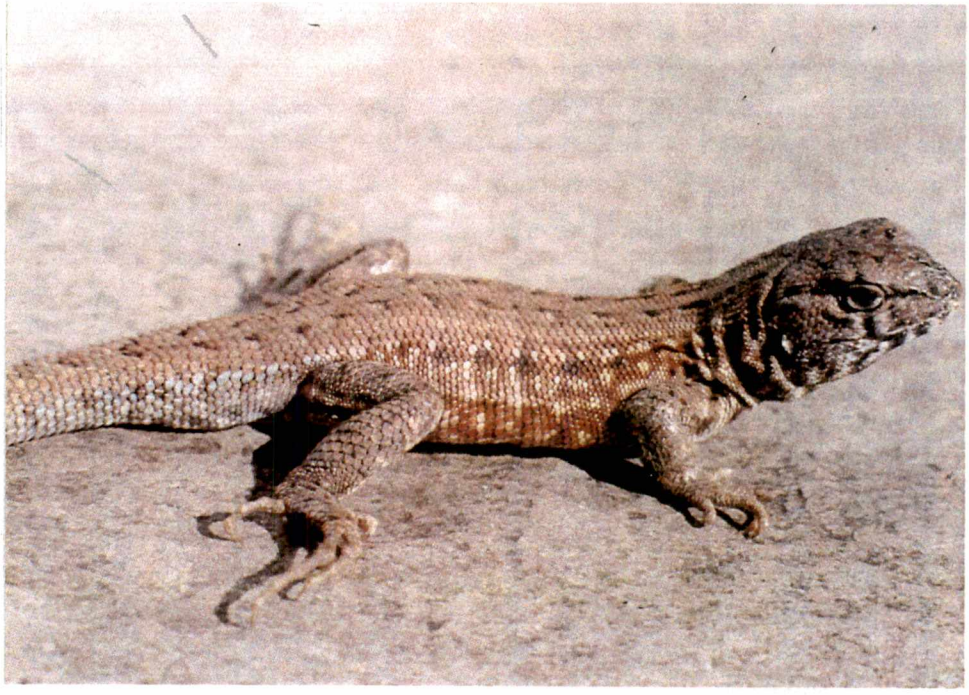


Figure 9. Liolaemus quilmes. Male in its habitat, about 10 km north of Cafayate, Salta, Argentina (from location AN, see Appendices A and B).

Figure 10. Liolaemus multimaculatus. Female from location FQ (see Appendices A and B).

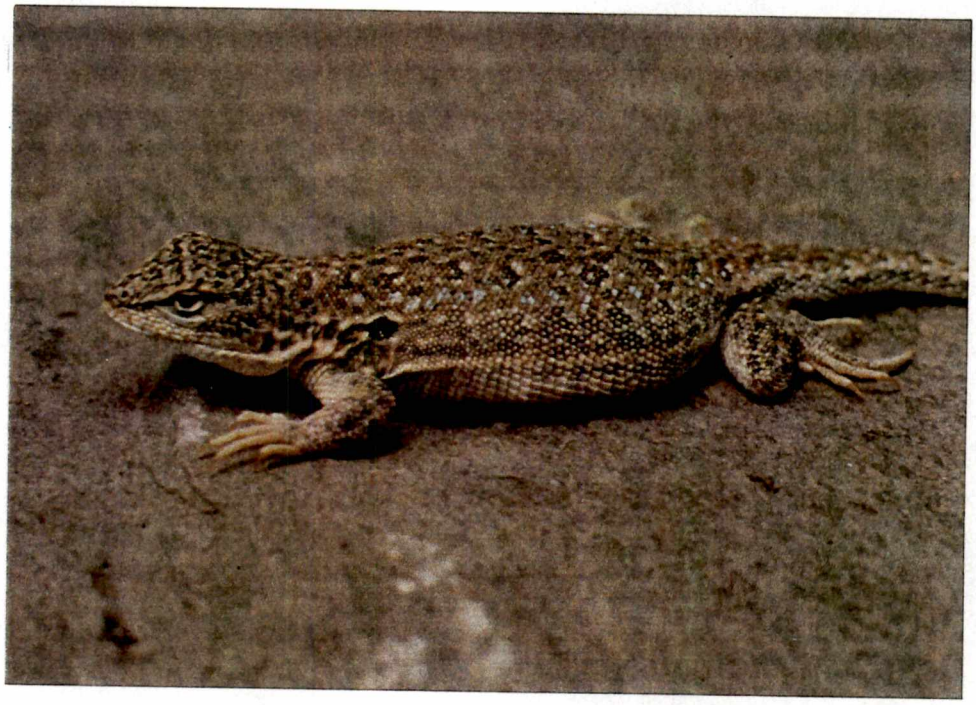


Figure 11. Liolaemus scapularis.

a. Male L. scapularis (from location IT, see Appendices A and B).

b. Habitat L. scapularis, Los Medanos, Cafayate, Salta, Argentina (location CF in Appendix B).

a

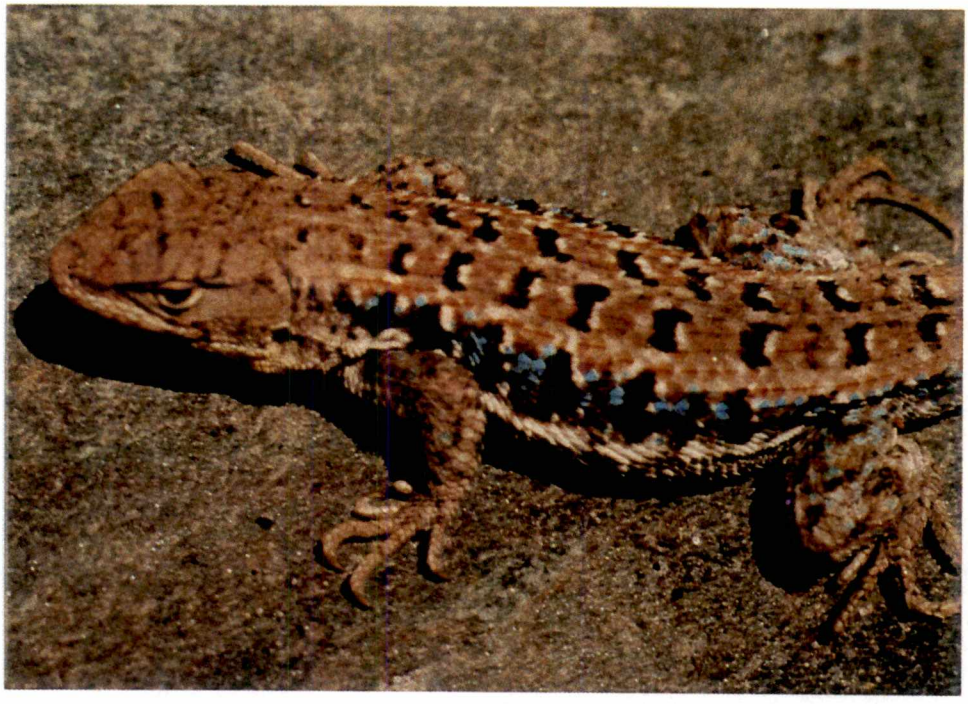
b

Figure 12. Liolaemus wiegmannii.

a. Male L. wiegmannii (from location MD, see Appendices A and B).

b. Habitat L. wiegmannii, Sierra Medina, Tucumán, Argentina (location MD in Appendix B).

a



b

CHAPTER 4

OBJECTIVES OF THE STUDY

Information on sand burying behavior in Liolaemus species belonging to the boulengeri group may prove useful in reconstructing their evolutionary history within a phylogenetic framework based on morphological traits (Etheridge, 1995). Although many species of Liolaemus are known to sand bury (e.g., Cei, 1986, and Gallardo, 1977:117, the latter pointing out that already Darwin had taken note of the sand burying behavior of L. multimaculatus), this behavior has not been described nor has it been used as evidence in the reconstruction of phylogenetic relationships among species.

Arnold (1994a) points out that sand burying behavior has evolved independently at least 9 times in surface-dwelling lizards from 6 different families. Although it is not clear which are the 9 independent occurrences, the 6 families correspond to one subfamily of the family Chamaeleonidae, Agaminae (according to Frost and Etheridge's taxonomic arrangement of lizard families, 1989), and 5 families: Cordylidae, Lacertidae, Phrynosomatidae, Scincidae and Tropiduridae. Examples of burying styles were given for the

first 5 taxa in Part I, Chapter 1). No description is given for tropidurid lizards except for a small reference to sand-diving species of the genus Liolaemus in Arnold (1994b, based on a pers. comm. from Etheridge).

Considering the lack of information on sand burying behavior in tropidurids, and in Liolaemus of the boulengeri group, in particular, the following questions were addressed: Do sand burying species of the genus Liolaemus all bury head first? Do they all follow the same sequence when entering loose sand? Are there differences among species? Are there differences within species? What are the implications of possible intra and inter-specific differences? Are the behavioral patterns used in sand burying species characteristic enough that they can be used to estimate phylogenetic relationships among species? Do the results agree or disagree with existing taxonomic arrangements of these species? How do burying sequences compare to those observed in species belonging to other lizard families? These questions were specifically addressed through the following three objectives:

Description of Sand Burying Behavior

Lizards belonging to different species of the boulengeri group (the ingroup) and to species of the functional outgroup were observed on loose sand in the evening in order to assess whether they buried into sand

and, if they did, how was this accomplished. Specifically, description of the use of head, limbs and tail as well as recording of time taken in entering loose sand were examined. Results were compared to descriptions of sand burying behaviors observed in various taxa of Old World lizards (Arnold, 1994a, 1995).

Variability in Burying Behavior within a Species

To use behavior patterns as characters in a phylogenetic reconstruction it is important to investigate how much variability these show within a species. The more a behavior pattern is homogeneous among individuals of a species, the more stereotyped the performance, the more it can be used in a hypothesis of its evolutionary history. This is something that Arnold (1994a, 1995) has assumed when describing burying behavior in various taxa of the Old World but has not established. If behaviors are highly variable, they may not be useful for a cladistic analysis. For instance, Stamps and Barlow (1972) found variations in the display behavior within a population of Anolis aeneus. If, however, the range of this variation does not overlap that displayed by another population or species, then it is potentially useful in a phylogenetic context (e.g., McLennan et al., 1988). To address this point, the following comparisons were investigated:

1. Intraindividual variability: Do lizards of a species use the same burying patterns (described in Chapter 2, Part II) when tested a second time, within 24 hours (short term variation) and when tested several weeks or months later (long term variation)?

2. Variability with respect to context: Do lizards of a given species bury in the same manner when tested on a different type of sand? Pough (1970), for example, found differences in the response of the sand lizard, Uma notata, when confronted with sands of different grain sizes.

3. Variability between males and females within a species: Are males and females different or similar in the way they use their head, limbs or tail in sand burying or in the time they take to sand bury?

4. Variability among populations of a species: Do lizards of the same species but from different populations use the same or a different behavioral pattern in sand burying? Do they take the same amount of time? Ferguson (1971), for example, found geographical variation in the display rituals of the side-blotched lizard, Uta stansburiana (Phrynosomatidae).

5. Variability between adults and neonates of a species: Do adults differ from neonates in their sand burying

behavior? Similarities as well as differences may have a genetic component, differences reflecting ontogenetic or developmental changes. Carpenter (1967b) has suggested that stereotyped behavioral characters in lizards are inherited.

Formulation of a Phylogenetic Hypothesis

Based on information obtained from observations of burying sequences in species of the boulengeri group, and on results from the variability tests, behavioral characters were defined and used to formulate an hypothesis of historical relationships. This hypothesis was then used to explain the distribution of character states among the species (e.g., McLennan, 1993). This has been criticized as "circular reasoning" (e.g., Coddington, 1988) but Arnold (1994a:134) considers that this rationale is inappropriate and argues that, "The reconstruction of relationships should take account of all possible evidence and exclusion of characters [in order to avoid circularity] may well alter the final result or prevent a result being obtained at all". De Queiroz (1989:455-456) observes that "although caution is in order when drawing conclusions about character evolution from phylogenies based wholly or partly on the characters under investigation, the generalization that all such analyses are circular is false." Later, he writes (p. 458), "if it were logically indefensible to analyze character

evolution in the context of phylogenies based at least partly on those same characters, the following paradox would exist: the best analysis of the evolution of particular characters would require the best estimate of phylogenetic relationships, but the best estimate of phylogenetic relationships is based on all available evidence, including the characters being studied, and consequently could not be used." And further (p. 459), "The mistaken notion that it is necessarily fallacious to reach conclusions about the evolution of characters in the context of phylogenies based on those same characters is an incorrect generalization that seems to result from a superficial understanding of the relationship between premises and conclusions. Although it may seem circular to propose that a hypothesis about phylogeny based on characters serves as a context (assumption) in which conclusions about the phylogeny of these characters are reached, 'phylogeny' here has different meanings. The first phylogeny, that is, phylogenetic relationships among taxa, does not necessarily presuppose or bias conclusions about the second phylogeny, that is, patterns and processes of character evolution."

The resulting cladogram of boulengeri species based on behavioral characters was then compared to Etheridge's indented classification of this group based on morphological traits (1995, listed in Chapter 3, Part I). In this

classification, the boulengeri group was proposed as monophyletic within the montanus supergroup and the wiegmannii subgroup was also considered monophyletic within the boulengeri group.

Some studies have used only behavioral characters to reconstruct a phylogeny, which is the case here (also in McLennan et al., 1988). Others have interpreted the evolution of behavioral characters by mapping these onto a cladogram constructed with different characters. For instance, Lauder (1986) mapped characters corresponding to feeding behavior, morphology, and physiology of sunfishes (Centrarchidae) onto a preexisting phylogeny based on other characters. In other examples, Prum (1990) superimposed display behavioral characters of neotropical manakins (Aves: Pipridae) on a phylogenetic tree based on morphological characters (syringeal characters). He finds that this analysis "yields the most behaviorally independent hypotheses of behavioral homology", (p.202). Packer (1991) mapped behavioral characters of sweat bees, Evylaeus (Hymenoptera: Halictidae), onto a cladogram based on electrophoretic information. This author suggests that behavioral characters exhibit more homoplasy than electrophoretic characters although "Phylogenetic analysis of electrophoretic data is highly controversial ..." citing Swofford and Berlocher (1987) among others (p. 155).

Other studies have combined different sets of characters to reconstruct phylogenies. In this case, there is some controversy whether it is more appropriate to combine the resulting analyses (cladograms) of each type of data set (the consensus approach, de Queiroz, 1993) or to combine all the information into one large data set (the combined approach, proposed by Miyamato, 1985; Brooks and McLennan, 1991) to obtain a phylogenetic estimate of two or more data sets (both approaches reviewed in de Queiroz, 1993). Kluge (1989) used the latter approach and conducted a combined analysis of two types of data: biochemical and morphological. The author found that both sets of data were "highly consistent with a phylogenetic hypothesis of Epicrates species relationships" (p.18). Another example is given by Prum (1990). This author combined a behavioral and a syringeal data set available for manakins and found that the analysis was highly congruent with a phylogenetic hypothesis which used only the syringeal data set suggesting that the behavioral characters were phylogenetically highly informative.

The consensus approach tends to give equal weight to each data set and thus reduces the potential for large data sets swamping smaller data sets (Kluge, 1983). However, giving equal weight to different data sets is arbitrary and may be a problem. This approach is considered to give a more

conservative estimate of phylogeny than the combined approach (de Queiroz, 1993). Furthermore, de Queiroz (1993) points out that the consensus approach will be more appropriate than the combined approach if some of the data sets used contain nonindependent characters and if different data sets give conflicting trees that are strongly supported.

The combined approach to data analysis, on the other hand, may be more resolved than the consensus approach because it combines the original data from different data sets and thus uses the total evidence including information that may be only in some of the data sets. Therefore, combined trees can diminish the effects of homoplasy by increasing the number of characters in the combined data sets. Miyamato (1985) considers the combined approach to be a better choice because less information is lost than in the consensus approach and it maximizes parsimony and stability. De Queiroz (1993), however, is more for a pluralistic approach depending on the data sets involved.

Therefore, whether the consensus or combined approach is preferred will depend on the type of data sets, the size of the samples, the independence among characters used, and how well the data support the conflicting trees. In the end, the goal is to obtain a hypothesis that best explains all the available data, and not just part of it.

PART II

MATERIALS AND METHODS

CHAPTER 1

SUBJECTS AND GENERAL TESTING PROCEDURE

Subjects and Housing

Most of the lizards were collected during the months of January and February of 1991 and 1992 (summer months in the Southern Hemisphere). A total of 455 lizards were collected belonging to 23 different species of Liolaemus, 4 species from the outgroup (n=77) and 19 species from the ingroup (n=378, Appendix A). Each lizard was weighed and measured (snout-vent and total lengths, see Appendix A for averages). Individuals were identified either by a particular trait (such as a missing toe or body scar) or color pattern or by marking them with white nail polish (one to three small spots on neck or back). During field trips, characteristics of the local habitats were recorded, samples of vegetation and soil were gathered when possible (Appendices B and C) and pictures of lizards and corresponding habitats were taken (e.g., Figs. 1 through 12).

The lizards were kept 6 to 8 in outdoor terraria (some measured 80x40x25 cm, others 100x40x30 cm, Fig. 13) that received direct sunlight and were covered with metal sheets (that let air and light pass) when it rained. The terraria contained a 4-5 cm layer of sand, stones, pieces of wood,

Figure 13. Home terrarium set up (100x40x30 cm). Substrate of sand, stones, pieces of wood and leaf litter. A lizard, Liolaemus zapallarensis from Chile, can be seen in the front right section of the terrarium. This species was not used in the study but it is of the approximate weight and size of the larger Liolaemus used here (e. g., L. canqueli and L. cuyanus) and it provides an indication of proportions.

and leaf litter. The lizards were provided with water and fed tenebrionid larvae, crickets (when available), fruit flies, and other insects that were attracted to fruits left in the cages. These were the "home" cages of the lizards where they remained when not tested.

Testing Procedure and Statistical Analyses

The lizards were tested in the evening when they naturally seek cover whether by burying into sand or by finding shelter under a rock or some other element. Lizards were tested individually and out of sight of other lizards. Room temperatures were held constant between 20-25°C. A lizard was placed on loose sand (5 cm layer) in a testing aquarium (24x13x25 cm) and its activity was recorded with a Minolta compact color video camera K-500S (with zoom lens) and a VHS general Electric Model 9-7100 videocassette recorder. On a monitor in an adjacent room, I checked the lizard's activity. Once the lizard was completely covered by sand or partly covered but had stopped moving (usually within 5 to 10 minutes at most), I left it for another 30 to 40 minutes after which I took it out for a second trial. Once buried a second time, it was left alone all night. If the lizard did not bury, it was left in the aquarium all night.

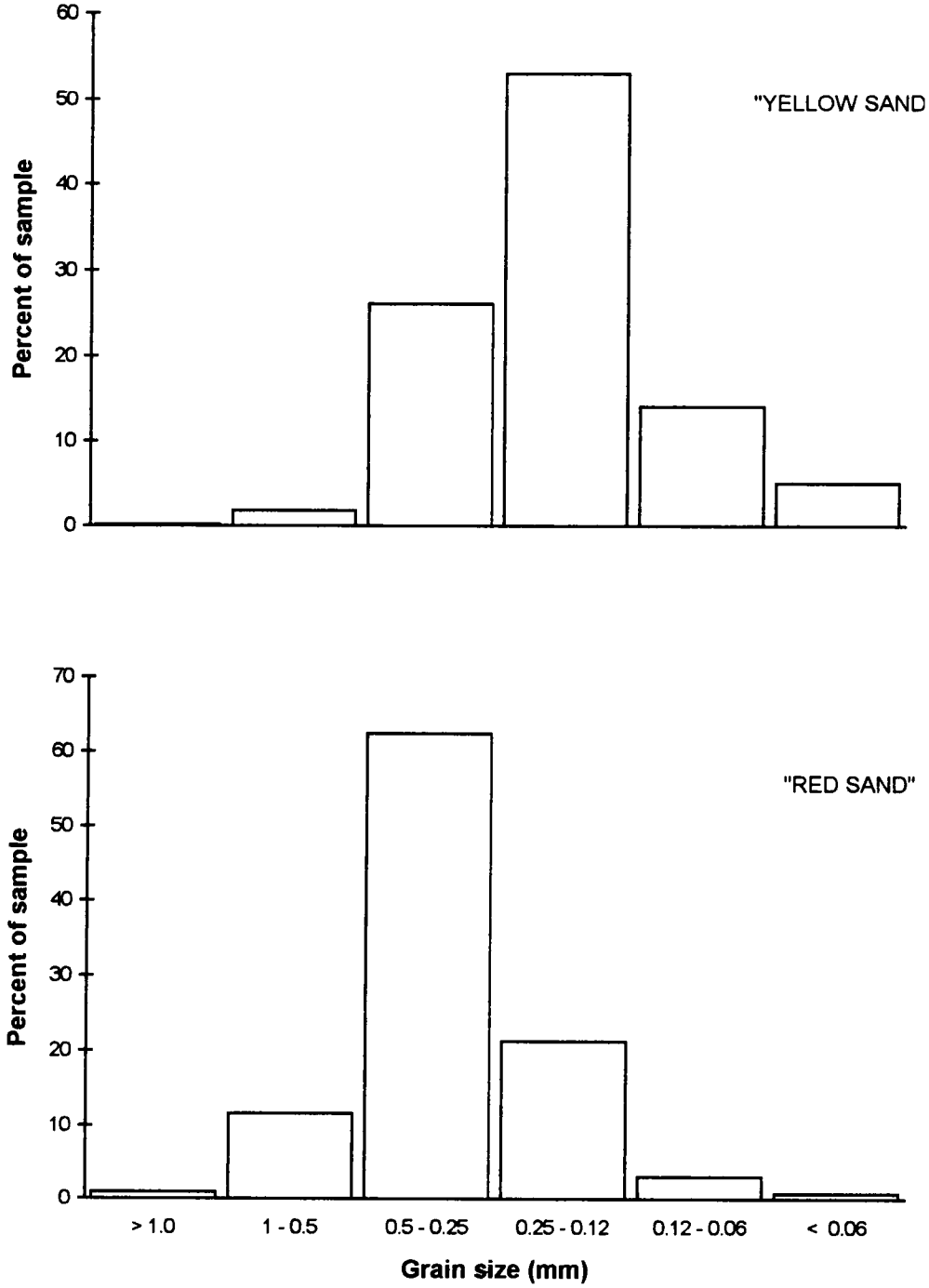
The lizards were tested on two types of sand: a fine loose yellowish sand from Cafayate, Salta, called "yellow sand", and a loose reddish sand from Sierra Medina, Tucumán,

a little coarser than the first type and called the "red sand" (the color is due to presence of clay). The lizards were tested twice on each type of sand in random order with 1-2 days interval between tests.

Figure 14 shows the results of a mechanical analysis of soil texture. Soil texture refers "to the relative proportion of the various size-groups in a given soil" (Buckman and Brady, 1969:41). The mechanical analysis corresponds to the procedure by which the particles are separated into groups or "separates" according to size. The analysis was performed on a 1 kg sample taken from the upper 5 cm layer from each of the two locations. According to the classification of the United States Department of Agriculture System (Buckman and Brady (1969:43), the "yellow sand" is about 50% "fine sand", about 25% "medium sand" and most of the rest "very fine sand" (Fig. 14). The "red sand", on the other hand, is mostly made of "medium sand" sized particles (62.5%, Fig. 14), less than 25% of "fine sand" particles and about 12% formed by "coarse sand" particles.

The information collected on video tapes was transcribed to a notebook. A description of the movements involved in sand burying (use of head, limbs and tail) and the amount of time it took a lizard to get buried (partially or totally) were recorded. This information was used to address the presence of different burying modes among species.

Figure 14. Results of a mechanical analysis of soil texture for the two types of sand used in the study: "YELLOW SAND" from Cafayate, Salta, Argentina, and "RED SAND" from Sierra Medina, Tucumán, Argentina.


"YELLOW SAND
Percent of sample
60
50
40
30
20
10
0
"RED SAND"
Percent of sample
70
60
50
40
30
20
10
0
> 1.0
1 - 0.5
0.5 - 0.25
0.25 - 0.12
0.12 - 0.06
< 0.06
Grain size (mm)

Specific Procedures Related to Behavioral Variability

To respond to the different points addressing the issue of behavioral variability, lizards were tested twice on the same type of sand and on a different type of sand depending on the question. For each type of variation, 5 subsets of behavioral characters were compared, each subset corresponding to various behavioral categories. The 5 subsets dealt with:

1. Type of movement of the head as the lizard entered loose sand.
2. Type of movement of the tail as the lizard became completely covered.
3. Section of the body reached at lizard's first stop (many lizards did not get covered in one movement but sometimes stopped several times before settling for the night).
4. Number of stops a lizard made before settling for the night.
5. The time in seconds taken by a lizard to its first stop.

These subsets of behavioral characters are explained in more detail in the next Chapter on Phylogenetic Analysis. They are also discussed in Chapter 2, Part III.

Intraindividual variability. To determine whether the burying behavior was constant within individuals, lizards

were tested twice on the same type of sand ("yellow" sand) within 24 hours (short term variation) and several weeks or months later (long term variation).

Context variability. To address variability with respect to context a comparison was made of the 5 character subsets in lizards on their first test in "yellow" sand and their first test in "red" sand.

Variability between males and females within species. Males and females were tested in the same conditions and the burying behavior in their first test on yellow sand was compared. Yellow sand was chosen over red sand because it was a more typical sand dune type of sand and it was the type more commonly found in habitat substrates from which most of the species came from.

Variability among populations within a species. Different populations for three of the species were compared (L. cuyanus, L. riojanus, and L. scapularis). The first test on yellow sand was used.

Variability between adult and neonate Liolaemus melanops. The first test on yellow sand of 5 neonate and 8 adult L. melanops was compared. Although juveniles and subadults were collected, it was difficult to establish age groups without knowing more about the life history of each species. Because

of the difficulty of assigning lizards to age categories, a comparison separating juveniles and subadults was not attempted. Neonates, on the other hand, presented no difficulty in identification. However, neonates were hard to find in the field and difficult to keep in captivity, which explains the small sample size. Nevertheless, neonates from other species, L. canqueli (1), L. xanthoviridis (1), and from 3 species belonging to the outgroup L. andinus (9), L. huacahuasicus (15), and L. ruibali (3), were also observed and tested. Statistical analyses were not done with these species, either because numbers were too low or lizards from some of the species did not bury.

CHAPTER 2

PHYLOGENETIC ANALYSIS

With the information obtained in the previous Chapter, a phylogenetic analysis was undertaken. To avoid pooling data, only one record per individual was kept: the first record that had complete information or almost all the information. Of these records, only those obtained in similar testing conditions were used, i.e., records when lizards buried into the same type of sand ("yellow").

In addition, not all individuals of species belonging to the darwinii complex (sensu Etheridge, 1993) entered into sand. Therefore, only lizards that got partially or totally covered were used. In the case of L. quilmes, for example, about a third of individuals entered sand. Of 161 trials on both types of sand for 35 L. quilmes, lizards became covered only 56 times (34.78%). This includes 90 trials on yellow sand, in which lizards covered themselves 33 times (36.67%) and 71 trials on red sand, in which lizards covered themselves 23 times (32.39%).

All these considerations reduced the sample size significantly (see Appendix A for total number of lizards tested) but still most species were represented by 5 or more individuals (15 out of 19 species of the boulengeri group) and 7 species had more than 10 individuals.

For the phylogenetic analysis, Hennig86 (version 1.5, J. S. Farris, 1988) was used. Cladograms were generated using the "ie*" command which finds all trees of minimal length. The "xs h" command was used to list the possible states of each hypothetical ancestor of each tree for each character. Finally, the "nelsen" command was used to generate a Nelson consensus tree which Forey et al. (1994:155) describe as an "appropriate device for determining the intersecting information in different cladograms".

Character State Transformations

For purposes of polarizing character state transformations, the outgroup method was used (Watrous and Wheeler, 1981; Maddison et al., 1984). The ingroup comprises 19 species belonging to the boulengeri group, which is included in the montanus supergroup. The functional outgroup contains 4 species of the montanus supergroup not belonging to the boulengeri group (see list of species in Chapter 3 of Part I). Although the first and second outgroups of the boulengeri group are unknown, they are both assumed to be among the remaining members of the montanus supergroup. Therefore, if a character exhibits two or more states in the boulengeri group (the ingroup), and only one of these occurs in the remaining species of the montanus supergroup

(functional outgroup), then the latter state is considered plesiomorphic.

The following premises were applied:

- plesiomorphic states are indicated by (0) and apomorphic states by (1);
- all characters are binary at the level of the individual; frequency coding is employed at the species level at which time characters are treated as polymorphic (explained at the end of this Chapter);
- sequences of mechanical actions in different taxa are considered to be homologous if they are identical or very similar;
- and except for the character "di" (digging), none of the actions described for the ingroup are present in the outgroup.

Character Descriptions and Character States

Characters were organized into 7 subsets of behavioral characters, each subset corresponding to an ensemble of related behaviors. The behavioral categories described in the first 3 subsets are defined in terms of a sequence of mechanical actions and they correspond to movements of head, limbs and tail. The next 3 subsets refer to number of stops and location of stops on lizard's body, and the final subset corresponds to time recordings of the submerging lizard.

Lizard Movements prior to Entering Sand

1. **di (digging)**: (0) digging; (1) no digging. The lizard removes sand using both front and hind limbs alternately. One front limb is first extended forward and then flexed backward along the flank bringing back some sand which is then picked up by the hind limb which is extended forward and then back pushing the sand further back. This is repeated with the opposite limbs. After some time, these movements create a depression in the sand. While digging, the head is flexed downward with the snout in contact with the sand. It is often done in a corner of the aquarium. Digging is equivalent to burrowing as defined by Stebbins (1944, see Chapter 2, Part I).

2. **sc (scratching)**: (0) no scratching; (1) scratching. The lizard scratches the surface with a quick back and forth movement of one forelimb often alternating with the other forelimb. Hind legs are rarely used. Very little sand is thrown back. Head is up and it is often done away from the sides and corners of the aquarium.

3. **bm (back movement)**: (0) no back movement; (1) back movement. Just prior to putting the head in the sand, the entire body moves slightly posterior without a change in position of the limbs.

4. **bs (back steps)**: (0) no back steps; (1) back steps. The lizard makes one or more steps back and then quickly advances to bury into the sand.

Head Movement as Lizard Enters Sand

1. **in** (**introducing head**): (0) not introducing head; (1) introducing head. Head pushes forward into sand. It is mostly maintained in a straight position.

2. **lm** (**lateral movement of head**): (0) no lateral movement of head; (1) lateral movement of head. Head is flexed laterally in a back and forth movement as it enters the sand.

3. **pl** (**plunging**): (0) no plunging; (1) plunging. There is a forward thrust of the head and body into the sand. The head enters the sand in a straight position. This behavior is usually accompanied by a previous "back movement" or "back stepping" as described in the above section.

Tail Positions and Movements as Lizard Enters Sand

1. **ct** (**tail in contact with substrate**): (0) not in contact with substrate; (1) in contact with substrate. While entering the sand, the lizard maintains hind legs low and tail is partly or totally in contact with the surface of the sand.

2. **fo** (**tail follows**): (0) tail does not follow; (1) tail follows. While burying, the tail is kept straight and does not participate with any type of movement. It just follows the body. A portion of it often remains uncovered.

3. **rt** (**tail retrieved**, pulled in): (0) tail not pulled in; (1) tail is pulled in. After reaching the base of the tail

and in a final movement, the tail is pulled in towards the body in a curving motion. The tail usually gets completely covered.

4. **lr** (**tail lashed left and right**): (0) tail is not lashed; (1) tail is lashed. The tail is covered by lashing it laterally from the base of the tail in broad whip-like sweeps.

Location on Lizard's Body at First Stop. When burying, many lizards stopped for a few seconds, then resumed burying, stopped and so on. They might stop only once or several times (see subset on number of stops). Here is noted the area on the lizard's body at which it stopped the first time.

1. **mb** (**midbody**): (0) lizard did not reach midbody section at first stop; (1) midbody section is reached at first stop. If zero is scored it only implies that the lizard did not reach that section but might have reached further or less.

2. **bt** (**basetail**): (0) lizard did not reach basetail section at first stop; (1) basetail section is reached at first stop.

3. **mt** (**midtail**): (0) lizard did not reach midtail section at first stop; (1) midtail section is reached at first stop.

4. **c1** (**covered in one stop**): (0) lizard did not get covered in one stop; (1) covered in one stop.

Lizard's Final Stop

1. **pc (partly covered)**: (0) lizard is not partly covered at final stop; (1) lizard is partly covered at final stop.
2. **cc (completely covered)**: (0) lizard is not completely covered at final stop; (1) lizard is completely covered at final stop.

Total Number of Stops Made by Lizard

1. **s5 (five stops)**: (0) lizard did not stop 5 or more times before settling for the night; (1) lizard made 5 or more stops.
2. **s4 (four stops)**: (0) lizard did not stop 4 times before settling for the night; (1) lizard made 4 stops.
3. **s3 (three stops)**: (0) lizard did not stop 3 times before settling for the night; (1) lizard made 3 stops.
4. **s2 (two stops)**: (0) lizard did not stop 2 times before settling for the night; (1) lizard made 2 stops.
5. **s1 (one stop)**: (0) lizard did not bury in one movement before settling for the night; (1) lizard buried in only one movement.

Time recordings. Because a lizard made one to several stops before remaining still for the night, 3 different times were recorded (taken with a Micronta chronometer LCD Quartz stopwatch).

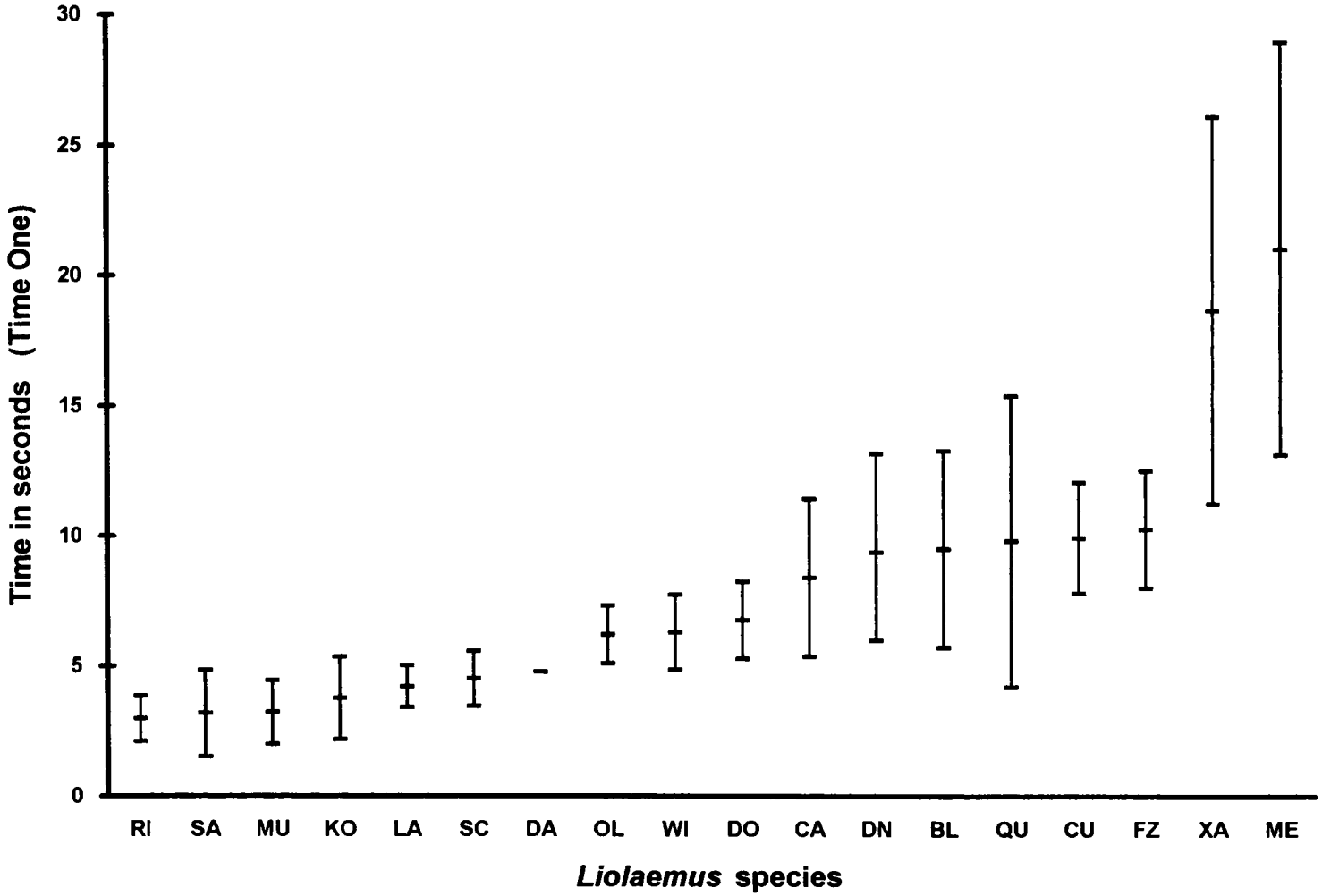
- TIME ONE: the time to the hundredth of a second that it took a lizard from first entering the sand (which was always

with the head) to the first stop. To find out if any groupings of species and/or gaps among species could be visualized with respect to this variable, averages and standard deviations were calculated and graphed for each species (Fig. 15, L. ornatus is not included in this figure because it did not bury). Based on discontinuities in the data, character states were established. Stevens (1991) extensively reviewed the problems of character state delimitations when treating continuous variables. He recommends that character states be defined by carefully analyzing discontinuities in the variation (these need not be in the form of absolute gaps) and by explicit justification. Moreover, Thiele (1993) shows that in some cases, cladistic analysis of overlapping morphometric data may help in inferring a reasonable hypothesis of relationship, which would have been less resolved had these data not been used.

As can be seen in Fig. 15, there seems to be a slow increase in the average speed at which the different species enter the sand to their first stop. The exception in this progression is given by L. xanthoviridis and L. melanops which show an abrupt increase in the time taken during the first entrance into the sand with standard deviations that do not overlap with the highest average speed shown by L. fitzingerii. However, L. xanthoviridis and L. melanops are

Figure 15. Average ± a standard deviation of TIME ONE, time taken to first stop for 18 species of *Liolaemus* belonging to the *boulengeri* group. Codes are, following the order shown on the figure, going from quickest to slowest species (more details in Methods):

RI - *L. riojanus*	DO - *L. donosobarrosi*
SA - *L. salinicola*	CA - *L. canqueli*
MU - *L. multimaculatus*	DN - *L. darwinii* Nihuil
KO - *L. koslowskyi*	BL - *L. boulengeri*
LA - *L. laurenti*	QU - *L. quilmes*
SC - *L. scapularis*	CU - *L. cuyanus*
DA - *L. darwinii*	FZ - *L. fitzingerii*
OL - *L. olongasta*	XA - *L. xanthoviridis*
WI - *L. wiegmannii*	ME - *L. melanops*


30
25
20
15
10
5
0
Time in seconds (Time One)
RI
SA
MU
KO
LA
SC
DA
OL
WI
DO
CA
DN
BL
QU
CU
FZ
XA
ME
Liolaemus species

relatively heavy Liolaemus species (14.25±3.57 g and 9.98±2.25 g respectively for males, Appendix A). Could speed be correlated to body mass? Examining Fig. 15 and average weights for species of the boulengeri group (Appendix A), it would seem not. Liolaemus canqueli, L. cuyanus, and L. fitzingerii are heavier species than the former two species (18.7±4.54 g, 20.59±3.47 g for location PI, and 23.74±0.42 g respectively for males, Appendix A) and yet are quicker at entering the sand (Fig. 15). Liolaemus salinicola and L. scapularis have about the same average weights than L. xanthoviridis and L. melanops (12.45±1.82 g for location MN, and 8.66±1.63 g for location CF, respectively for males, Appendix A) and they are also much quicker at entering the sand (Fig. 15).

To make sure that TIME ONE was not correlated with body mass, a Spearman rank-order correlation coefficient (Siegel and Castellan, 1988) was calculated for 14 of the 19 species of the boulengeri group (4 species that had less than 5 individuals per species and L. ornatus which did not bury were not used in this calculation) to determine whether speed at which a lizard entered the sand might be significantly correlated to its body mass (i. e., heavier lizards might be slower than lighter individuals or heavier lizards might be stronger and therefore quicker than lighter ones). In almost all cases, the results showed no

correlation between speed at which a lizard entered the sand and its body mass. Nevertheless, there was a significant negative correlation in L. quilmes (Spearman r_s = -.77, n=8) and significant positive correlations in L. xanthoviridis (r_s =.82, n=9) and in L. salinicola (r_s = .54, n=14). The alpha level used was $p < .05$.

Because speed of entry into sand did not seem to be correlated with weight of lizards (aside from the exceptions cited above) and because of the abrupt increase in time taken to enter sand shown by L. melanops and L. xanthoviridis, thus creating a gap between these two species and the rest (Stevens, 1991), two characters for time taken to first stop were recognized:

1. **r1 (reached first stop between 1 and 12.99 seconds)**: (0) lizard did not reach first stop in 1 to 12.99 seconds; (1) lizard reached first stop in 1 to 12.99 seconds.

2. **r2 (reached first stop between 13 and 32 seconds)**: (0) lizard did not reach first stop in 13 to 32 seconds; (1) lizard reached first stop in 13 to 32 seconds.

- TOTAL TIME: The time in hundredth of seconds from the time the lizard started introducing itself into the sand to when it stopped completely and did not move any further, be it completely covered or not. TOTAL TIME was not considered in the phylogenetic analysis due to its high variability.

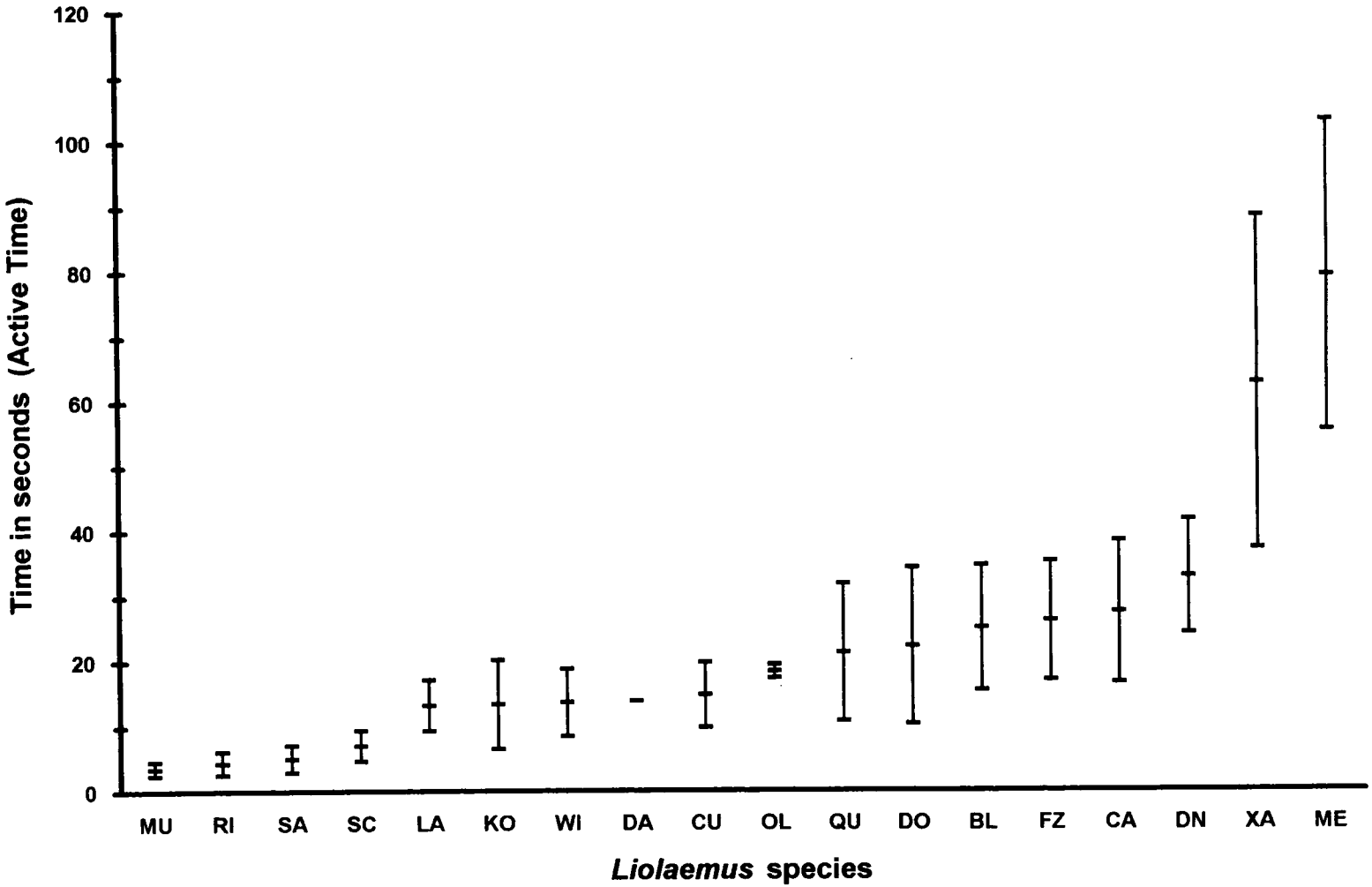
- ACTIVE TIME: The time in hundredth of seconds that the lizard has been moving and burying into sand, that is, TOTAL TIME less the time taken during stops. Here also, averages and standard deviations of ACTIVE TIME were calculated and graphed for each species (Fig. 16, L. ornatus is not included in this analysis because it did not bury; species with N<5 are excluded as well). A similar increase in average time that the lizard is actively burying is observed here for the first 16 species although the order of species is not the same as in Fig. 15. Liolaemus xanthoviridis and L. melanops show an abrupt increase in the ACTIVE TIME taken to bury as they did in TIME ONE.

The Spearman rank-order correlation coefficient was calculated for the same 14 species as in the section on TIME ONE but this time between weight and ACTIVE TIME. Significant positive correlations were obtained only in L. melanops (r_s = .76, n=8) and in L. salinicola (r_s = .71, n=14).

Because ACTIVE TIME taken to bury into sand did not seem to correlate with weight of lizards (aside from the exceptions noted above), and because of the abrupt increase in ACTIVE TIME shown by L. melanops and L. xanthoviridis, which thus forms a gap between these two species and the rest (Stevens, 1991), two characters for this variable were recognized:

Figure 16. Average ± a standard deviation of ACTIVE TIME, total active time taken to bury, for 18 species of *Liolaemus* belonging to the *boulengeri* group. Codes are, following the order shown on the figure, going from quickest to slowest species (more details in Methods):

MU - *L. multimaculatus*
RI - *L. riojanus*
SA - *L. salinicola*
SC - *L. scapularis*
LA - *L. laurenti*
KO - *L. koslowskyi*
WI - *L. wiegmannii*
DA - *L. darwinii*
CU - *L. cuyanus*
OL - *L. olongasta*
QU - *L. quilmes*
DO - *L. donosobarrosi*
BL - *L. boulengeri*
FZ - *L. fitzingerii*
CA - *L. canqueli*
DN - *L. darwinii* Nihuil
XA - *L. xanthoviridis*
ME - *L. melanops*


120
100
80
60
40
20
0
Time in seconds (Active Time)
MU
RI
SA
SC
LA
KO
WI
DA
CU
OL
QU
DO
BL
FZ
CA
DN
XA
ME
Liolaemus species

1. **a1 (active between 1 to 39 seconds)**: (0) lizard was not active during 1 to 39 seconds; (1) lizard was active during 1 to 39 seconds.

2. **a2 (active between 40 to 118 seconds)**: (0) lizard was not active during 40 to 118 seconds; (1) lizard was active during 40 to 118 seconds.

Species Character State Determination from Individuals

Based on the definitions given in the above section, individual lizards were scored either 1 or 0 for each character. Since in many cases not all individuals would perform a behavior, a system based on scoring percentage evaluations was devised to characterize species. This method seemed to best represent the state of a character for a species as well as allow for finer discrimination among species. Since this method was not found described in the literature and yet seemed appropriate for this type of data set, an example showing the steps used to determine character states for a species from individuals is explained in detail. A logical consequence of this analysis is that the characters are treated as additive or ordered. In this example, the species L. cuyanus and the first 11 of 26 characters are used. Table 2 describes the procedure used (this table is partly reproduced from a section of Table 8).

Table 2 - Example illustrating steps used to determine character states for a species from individuals.

No.	ID	di	sc	bm	bs	in	lm	pl	ct	fo	rt	lr
205	CUTIF1	1	0	0	0	0	1	0	0	0	0	1
210	CUTIM1	1	0	0	0	0	1	0	0	0	0	1
211	CUTIM2	1	0	0	0	0	1	0	0	0	0	1
642	CUPIM2	1	0	0	0	0	1	0	0	0	0	1
643	CUPIM1	1	0	0	0	1	0	0	0	0	0	1
728	CUPRM4	1	1	1	0	0	1	0	0	0	0	1
729	CUPRM5	1	0	0	0	0	1	0	0	0	0	1
732	CUPRF1	1	0	0	0	0	1	0	0	?	?	?
736	CUPRM2	1	1	0	0	0	1	0	0	0	0	1
737	CUPRM3	1	1	0	0	?	?	?	0	0	0	1
756	CUPRM1	1	1	0	0	0	1	0	0	0	0	1
757	CUPRF2	1	0	0	0	0	1	0	0	0	0	1
846	CUBAF1	1	0	0	0	0	1	0	0	0	0	1
frequency		13	4	1	0	1	11	0	0	0	0	12
---		--	--	--	--	--	--	--	--	--	--	--
total		13	13	13	13	12	12	12	13	12	12	12
percent		100	31	8	0	8	92	0	0	0	0	100
character state		9	3	0	0	0	9	0	0	0	0	9

Step 1: Determine character state for each behavioral character for each individual of a species. For this example, the species Liolaemus cuyanus and 11 behavioral characters (defined in the above section) are used.

Step 2: Count the number of times a behavioral character is present and divide by the total possible frequency. Question marks are not counted and so totals may change.

Step 3: Calculate the percentage for each character.

Table 2 (continued)

Step 4: Determine which state corresponds to each percentage based on the following list:

If 1 to 9 % of individuals do the behavior then it is assigned state 0 for the species.

If 10 to 19 % " " " " " " " " 1 " " "

20 to 29 % " " " " " " " " 2 " " "

30 to 39 % " " " " " " " " 3 " " "

40 to 49 % " " " " " " " " 4 " " "

50 to 59 % " " " " " " " " 5 " " "

60 to 69 % " " " " " " " " 6 " " "

70 to 79 % " " " " " " " " 7 " " "

80 to 89 % " " " " " " " " 8 " " "

90 to 100 % " " " " " " " " 9 " " "

CHAPTER 3

OBSERVER RELIABILITY

All the data were collected, transcribed and analyzed by the same person to favor recording of consistent data. At the time of transcribing, all times were checked twice to ensure accuracy. Nevertheless, intra and interobserver reliability checks were made to make sure that in fact the data were consistent over time and consistent with another observer.

Intraobserver Reliability

1. Intraobserver reliability over 5 months. To examine intraobserver reliability with respect to recording of temporal measures, 30 records were pulled out that spanned over five months of observations (July to December 1992) and included 5 species (15 males, 9 females and 6 neonates). The first and second annotation for TIME ONE and for TOTAL TIME were considered (see subset on Time recordings in previous Chapter for definitions). The Spearman rank-order correlation coefficient was used (Siegel and Castellan, 1988). Spearman r was .9982 for TIME ONE (n=30) and .9996 for TOTAL TIME (n=30). The values z were 5.3755 and 5.3830, respectively, $p < .0001$, two-tailed. Therefore,

intraobserver agreement over a short period of time was very high.

2. Intraobserver reliability after several years. To assess intraobserver reliability over longer durations, another thirty records were pulled out from the months of October 1990, January, October and December 1991, and January to March 1992. They were reviewed in March 1995 after an interval of 3 to 4 years and 5 months (depending on when the original record was taken). TIME ONE and location on lizard's body at first stop (see corresponding subsets in previous Chapter for definitions) were recorded for these 30 records without looking at what I had obtained the first time. The 30 records represented 10 species (17 males and 13 females).

For TIME ONE the Spearman rank-order correlation coefficient was again used (Siegel and Castellan, 1988). Spearman r was .9911, $z = 5.3372$, and $p < .0001$, two-tailed. This result also shows a very high agreement for scoring TIME ONE after an interval of more than 3 years.

To assess agreement of intraobserver coding of location at first stop, before and after the interval of more than 3 years, Cohen's kappa (Bakeman and Gottman, 1989) was used (kappa = .83, $z = 8.4711$, $p < .0001$, two-tailed). This result is also highly significant and shows that the

intraobserver agreement over time with respect to coding location at first stop is significantly better than chance.

Interobserver Reliability

An observer was trained to record the time of TIME ONE and recognize the location on the body of the lizard where it first stopped. The same 30 records as in the above section, were used. The results of the second observer were compared to the original results of the first observer. For TIME ONE, Spearman r was .9907, $z = 5.3351$, $p < .0001$, two-tailed. For location on lizard's body at first stop, the results obtained were the same as in the above section (Cohen's kappa = .83, $z = 8.4711$, $p < .0001$, two-tailed).

These results show that data recording was consistent over time and consistent with another observer. Due to the high agreement obtained for the variables considered here, no further reliability tests were made.

PART III

RESULTS

CHAPTER 1

THREE BURYING MODES IN THE BOULENGERI GROUP

Although belonging to the boulengeri group (sensu Etheridge, 1995), L. ornatus was the only species that did not bury into sand. Members of this species dug the same way as members of species belonging to the functional outgroup (L. andinus, L. huacahuasicus, L. multicolor, L. ruibali). As the outgroup species, they did not attempt to get covered by sand.

As for the remaining 18 species that did bury into sand, results suggest three different styles of burying within the boulengeri group. Figures 17 to 19 show the general sequence in sand burying in three species of the boulengeri group: L. boulengeri (Fig. 17), L. canqueli (Fig. 18) and L. riojanus (Fig. 19). These picture sequences do not show enough detail to discriminate among species (see further for differences) but they do show the general pattern observed in all the ingroup species, except L. ornatus, of entering head first into loose sand, placing front limbs alongside the body and pushing on the substrate with the hind limbs.

Figure 17. Liolaemus boulengeri submerging into sand.

a. L. boulengeri on sand before entering it.

b. L. boulengeri has reached the neck area. Front limbs are placed along body.

c. L. boulengeri has just passed the mid body area and is reaching the hind limbs.

d. L. boulengeri has just passed the base of the tail area.

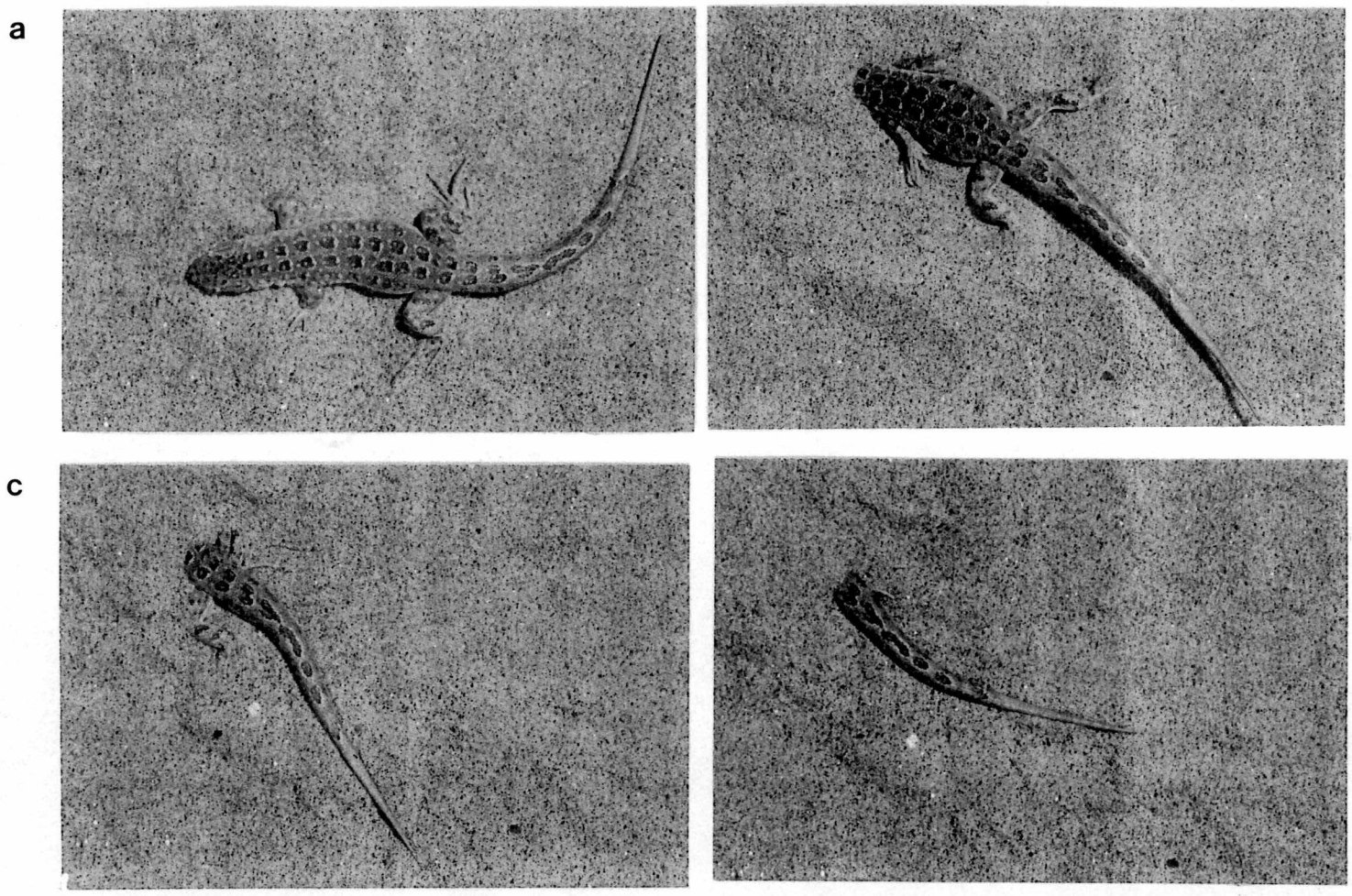

a
b
c
d

Figure 18. Liolaemus canqueli submerging into sand.

a. L. canqueli on sand before entering it.

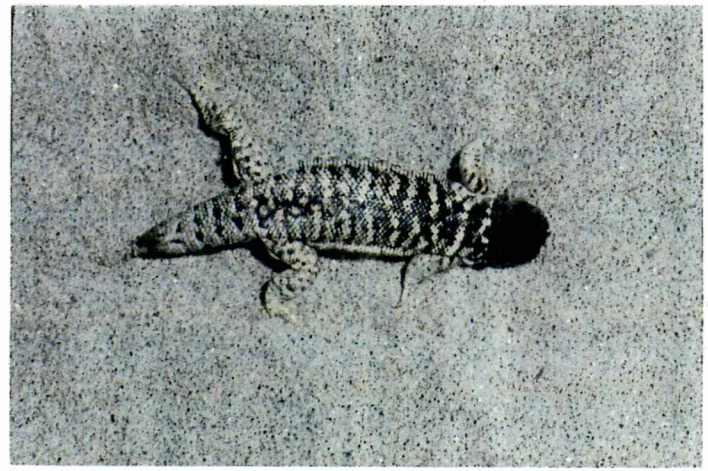
b. L. canqueli initiating entrance into sand (not the same individual as in 18a).

c. L. canqueli has reached neck area. Front limbs are placed along body.

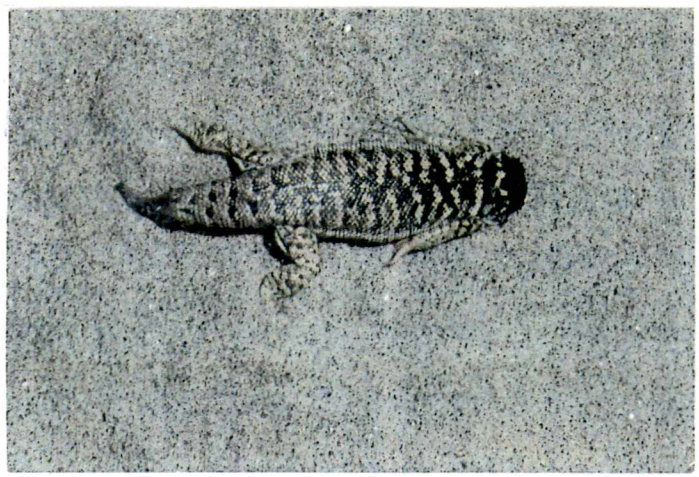
d. L. canqueli has reached the base of the tail area. A section of the right hind limb and the tail stub are still visible.

a

b



c



d

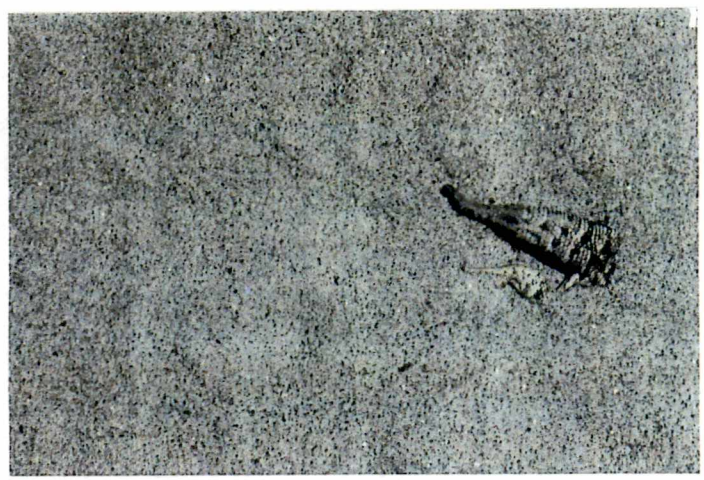


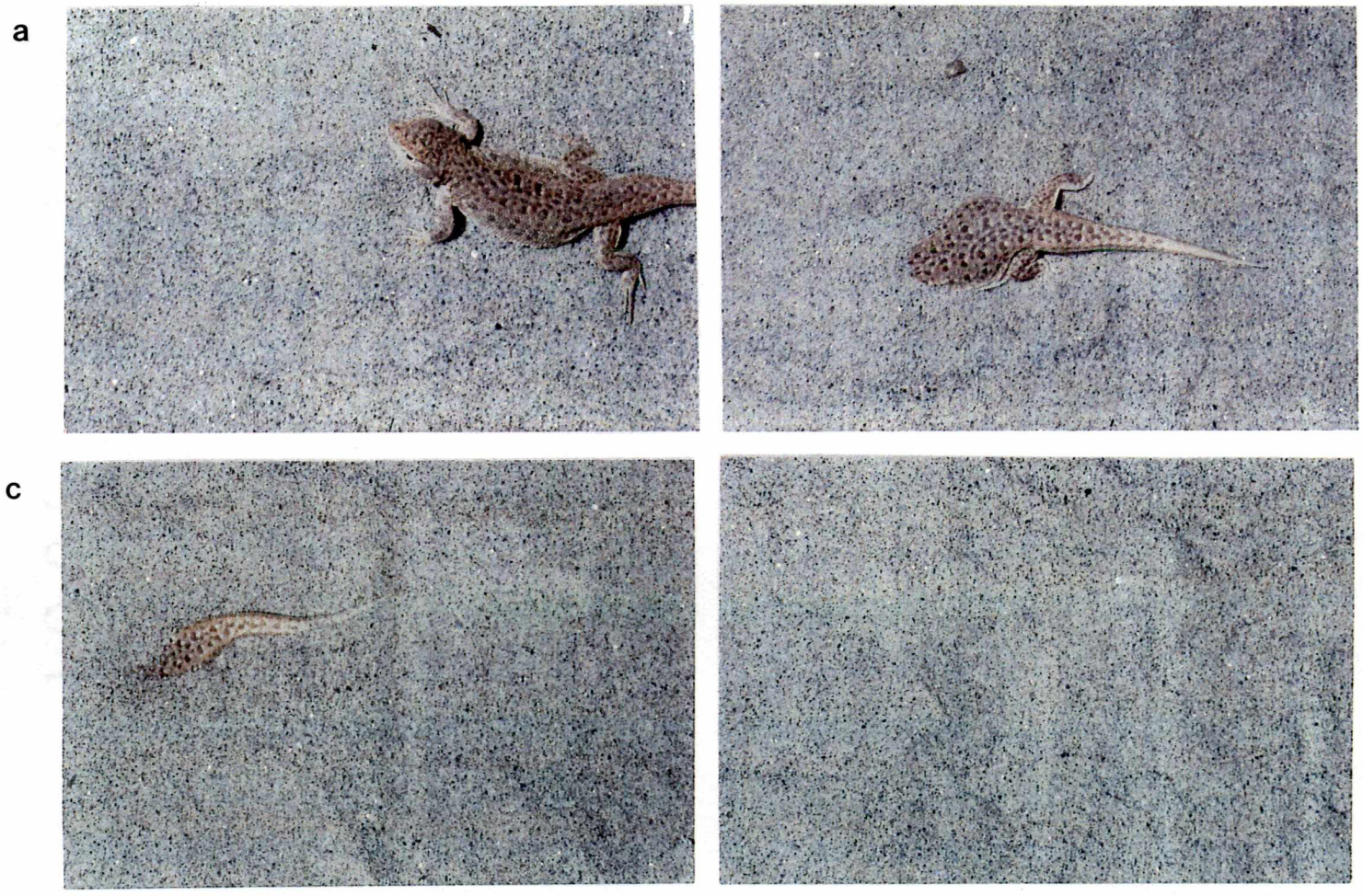
Figure 19. Liolaemus riojanus submerging into sand.

a. L. riojanus on sand before entering it.

b. L. riojanus has just passed the front limbs and is reaching the mid body area.

c. L. riojanus has reached the base of the tail and is starting to lash the tail (see description in text).

d. Only sand, no trace of submerged lizard can be seen.


a
b
c
d

Lizards that Dig/Burrow their Way into Sand

An example of a digging species (as defined by Stebbins, 1944, see Chapter 2, Part I) is L. quilmes. Digging in this species is similar to what Werner (1977) describes for gekkos, and Norris (1953) for Dipsosaurus dorsalis (Iguanidae). Lizards that dig go to a corner or along a wall of the terrarium, lower their head, snout in contact with surface, and start removing sand using first one front limb then the corresponding hind limb alternately then the front and hind limbs of the opposite side. In this manner, the lizard pushes sand back and creates a depression in the loose sand. Digging was interspersed with rest periods, until the lizard either settled down in the cavity that it had formed or it introduced its head into the side of the cavity and pushed with its hind legs, the sand collapsing on it as it moved along. As the lizard entered the sand, the head was kept straight following the body axis (Fig. 20a).

While burying, species belonging to this burying type stopped more often than species from the other two burying styles (see cladistic analysis Chapter 3, Part III), the first stop usually being close to the midbody or just behind the front legs. The tail followed and stayed in contact with the surface (Fig. 21a). Lizards from this burying mode usually did not get completely covered. They often stopped

Figure 20. Drawing of three different types of head movements observed in species of Liolaemus belonging to the boulengeri group. Arrows indicate direction of movement (drawing by P. Vince).

a. Head movement in L. quilmes is straight forward into the sand.

b. Head movement in L. canqueli is lateral as it enters the sand.

c. Head movement in L. riojanus is a forward thrust into the sand with a prior back movement of the body and/or back stepping to obtain the forward impulse.

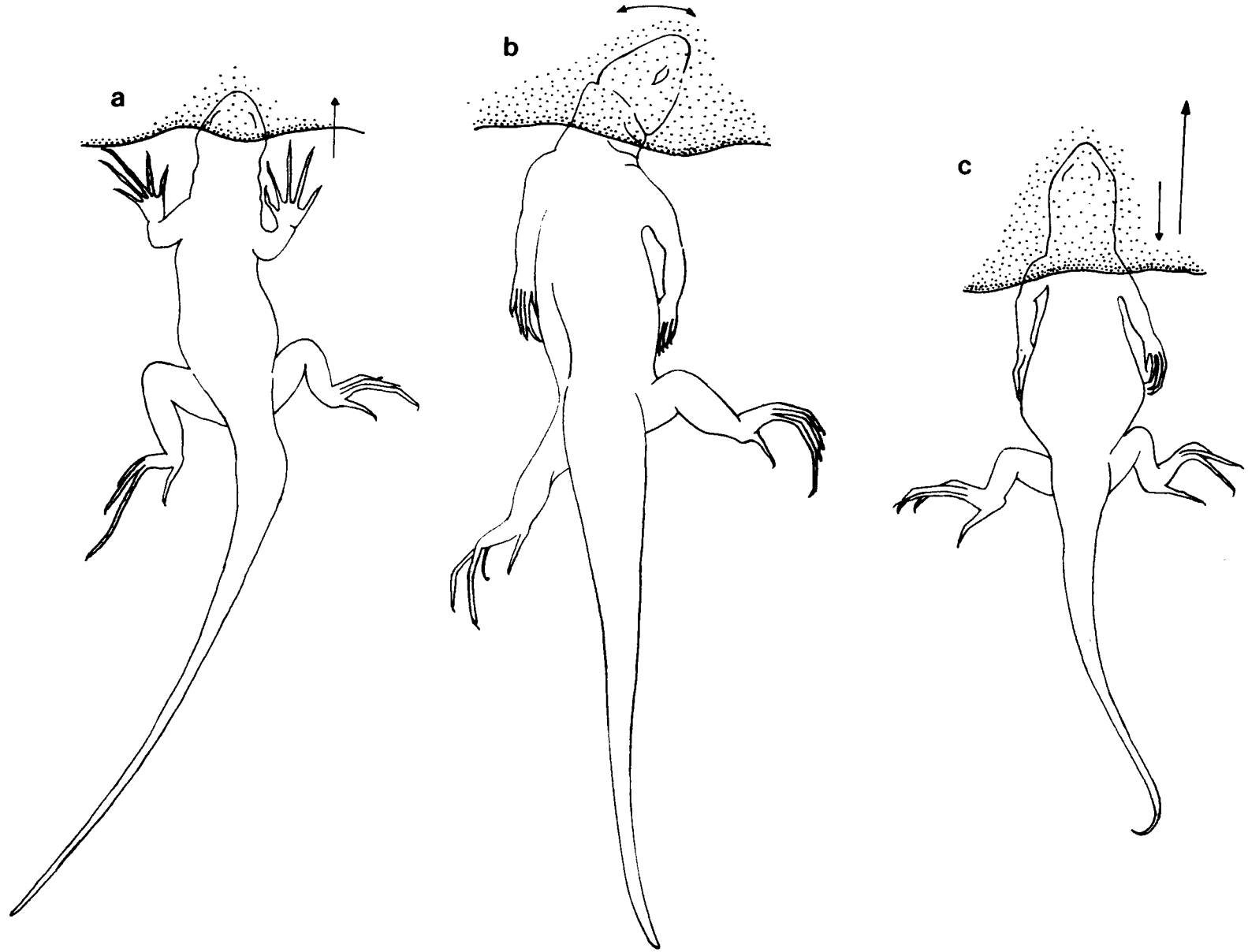
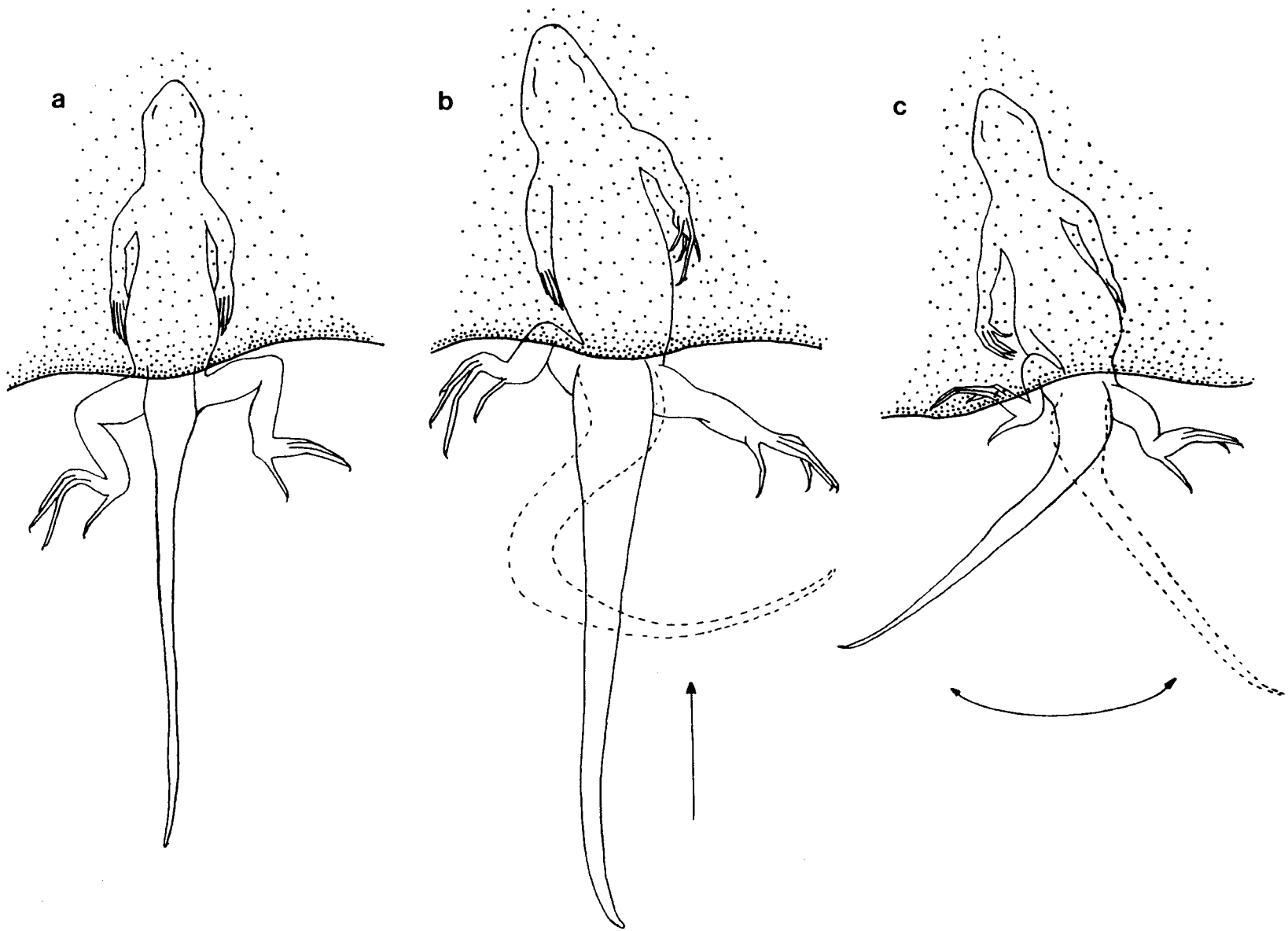

a
b
c

Figure 21. Drawing of three different types of tail movements observed in species of *Liolaemus* belonging to the *boulengeri* group. Arrows indicate direction of movement. Dashed lines indicate the movement of the tail as it is being covered (drawing by P. Vince).

a. Tail in *L. quilmes* is maintained straight as it goes into the sand and does very little movement. The whole tail or parts of it may stay uncovered.

b. Tail in *L. canqueli* is "retrieved" or pulled in by which it gets completely covered.

c. Tail in *L. riojanus* is "lashed" left and right in a whip-like manner getting it thus completely covered.


a
b
c

at the base of the tail, the tail remaining uncovered for the rest of the night.

In their home terraria, lizards belonging to the digging-style type of burying usually spent the night in cavities that they had dug under stones, and sometimes under pieces of wood or leaf litter. In some cases they had dug tunnels in sections of the terrarium where the sand had compacted. In the field, when the lizards had not yet emerged, they could be found under rocks or in small tunnels at least 15 cm long, with a 3 cm wide oval shaped opening.

Lizards that Bury their Way into Sand

An example of this burying style is given by L. canqueli (Fig. 18). Before going into sand, these lizards occasionally scratched the surface of the sand. This was also observed in species of the third type of burying. Its function is not clear. It is suggested that by scratching the surface of the substrate, a lizard may be "testing" the type of substrate it is on. If the lizard finds it "adequate" for burying, it will then proceed.

A lizard belonging to this burying mode entered the sand with a lateral motion of the head (Fig. 20b). Hind limbs were slightly lifted as it walked and pushed its way in. Soon the lizard laid its front limbs along the body (Fig. 18c). While burying the lizard kept its tail straight

sometimes lifting it in a position diagonal to the substrate's surface. When the lizard reached the base of the tail, the tail was lowered and was then "retrieved", that is, it was pulled in towards the body by which it became completely covered (Fig. 21b).

When given a choice in their home terrarium between spending the night under stones, wood, leaves or sand, lizards of this burying mode usually spent the night under sand, occasionally under an object. Once under sand no trace of their body could be seen. This is unlike the sand-swimming Neoseps reynoldsi which leave "characteristic sinusoidal tracks" documenting in this manner their whereabouts just below the sand surface (Andrews, 1994:92). Another example of tracks left by a subsurface moving lizard is in Lerista bipes (Greer, 1989:165) which leaves an undulating continuous track on the surface showing the path it is following beneath the surface.

Lizards that Dive into Sand

An example of this burying mode is given by L. riojanus (Fig. 19). These lizards "plunged" or "dived" (forward thrust of the head) into the sand (Fig. 20c). Before diving, they often scratched the surface followed by a back movement of the body or by taking a few steps backwards as if taking impulse. They entered the sand quickly (also placing their front limbs along side their body), and gave the impression

of doing so effortlessly (compared to species of the second burying mode which seemed to labor at it).

While burying, the tail was kept close to the surface and when the lizard reached the midbody to basetail section of the body, it was lashed several times horizontally in a wide half circle in a whip-like manner (Fig. 21c). With this last tail movement, the lizard became totally covered and no trace of its location could be discerned by just looking at the sand's surface (Fig. 19d).

When given a choice in their home terrarium between spending the night under a rock, piece of wood, leaves or sand, lizards belonging to this burying mode always spent the night under sand.

CHAPTER 2

VARIABILITY IN SAND BURYING LIZARDS

Although behavioral patterns observed in each of the three burying modes seemed consistent within species, this had to be established before attempting a phylogenetic analysis. That a species showed some variability in a trait is not a problem. This may even be characteristic of that species. However, when the variability of a trait in one species overlaps the variability shown by other species, the trait ceases to be informative because it cannot be established as diagnostic for that species (unless levels of variability are species specific). McLennan (1993:324) best summarizes it in the following paragraph: "Many authors have voiced concern over the structural and temporal plasticity of behavior, arguing that it is far more environmentally sensitive than morphology and, thus, difficult to characterize.... On the surface, this concern seems valid. Verbs are intuitively more labile than nouns. These perceptions, however, are based upon an assumption that variability within a species automatically disqualifies a character from examination of relationships among species. Consider the following example: male three-spine sticklebacks court females with an elegant, horizontal

zigzag dance. The form, sequence, and duration of the dance components are highly variable both within and among individuals. However, no male G. [Gasterosteus] aculeatus ever executes the staccato, vertical zigzag courtship dance typical of P. [Pungitius] pungitius, and no other members of the Gasterosteidae dance like G. aculeatus. The character is diagnostic for the species and is, therefore, potentially a useful systematic tool at that level."

In order to address the question of within-individual variability, context variability, differences between males and females, differences among populations within a species, and differences between adults and neonates of a species, 5 subsets of behavioral characters were compared (of the 7 subsets described in Chapter 2, Part II). These subsets are summarized here (the two-letter codes correspond to those shown in the next 5 tables, see below):

1. MH: Types of movements of the head when entering sand. These included:
    a. IN: Introducing head straight into the sand.
    b. LM: Lateral movement of the head as lizard entered the sand.
    c. PL: Plunging/diving with a forward thrust into the sand.

2. MT: Types of movements of the tail. These included:
    a. FO: Tail followed straight as lizard entered sand.
    b. RT: Tail is "retrieved" or pulled in to get covered.
    c. LR: Tailed is lashed left and right in a whip-like motion.
3. LO: Location on lizard's body at first stop. These were:
    a. MB: Lizard reached midbody section at first stop.
    b. BT: Lizard reached base of tail at first stop.
    c. MT: lizard reached midtail section at first stop.
    d. C1: lizard was completely covered at first stop.
4. #S: Number of stops taken by the lizard.
5. T1: Time One, time taken in seconds to first stop.

Other information regarding the following 5 tables are: Column N shows the total number of individuals used per species whereas (n) gives the actual number for a particular cell if this value is different from N. The N-value might be lower in some of the cells, due to missing data in some categories or, in the case of the Wilcoxon signed ranks test, pairs that matched were eliminated thus lowering the N-value for that cell (referred to as n). Species for which information on 5 or more individuals was available were used (see next 5 tables for listing of species). Individuals used were adults or sub-adults except when specified otherwise. Tests used are indicated in the tables (from Siegel and

Castellan, 1988). A test was not applied if more than 90% of individuals showed the behavior. When this occurred, the behavior code is indicated in the corresponding table following the definitions given above.

Intraindividual Variability

A summary of the results obtained for variation within individuals in burying into the same type of sand (yellow) within 24 hours (short term variation) and after several weeks or several months (long term variation) is shown in Table 3. With respect to the section on "long term variation", there is a three-week separation time between the first and second test for 3 L. wiegmannii and 3 L. scapularis. For the other 3 L. scapularis, the second test took place 5 months later. Age of neonate L. melanops for test 1 and 2 (not necessarily their first and second tests but used here for the purpose of comparing two burying behavior sessions separated by several months) was 4, 3, 3, 1, and 3 months old and 11, 6, 11, 11, an 11 months old, respectively. The two tests for the neonates were therefore, on average, 7.2 ± 2.6 months apart. Tests used are shown in Table 3.

Two significant differences were found at p-level $\leq .05$ in short term variation (Table 3). These were in L. fitzingerii which made significantly fewer stops on the

Table 3 - Summary results for intraindividual variability in sand burying into the same type of sand (yellow) with respect to short term variation (within 24 hours) and with respect to long term variation (several weeks or several months later) in species of the boulengeri group. See notes below.

SHORT TERM VARIATION

		Behavioral Character Subsets				
	N	MH	MT	LO (n)	#S (n)	T1 (n)
				Test Statistics		
Species				k	T/z	T/z
L. boulengeri	6	IN	-	-	16 (6)	12 (6)
L. cangueli	10	IN	RT	1 (5)	38 (9)	28(10)
L. cuyanus	13	LM	LR	1 (4)	27 (8)	48(12)
L. donosobarrosi	9	IN	-	-	19 (7)	38 (9)
L. fitzingerii	10	IN	-	1 (4)	28*(7)	38(10)
L. melanops	7	IN	RT	-	15 (7)	14 (7)
L. melanops (neonates)	5	IN	-	2 (4)	8 (5)	12 (5)
L. riojanus	17	PL	LR	3(10)	36.5(10)	1.3(17)
L. salinicola	14	PL	LR	3 (8)	4 (3)	53(14)
L. scapularis	39	PL	LR	2 (7)	1.49(17)	.01(38)
L. wiegmannii	16	-	-	-	23 (7)	.4(16)
L. xanthoviridis	9	IN	RT	-	11.5(6)	44**(9)

Table 3 (continued)

LONG TERM VARIATION

		Behavioral Character Subsets				
	N	MH	MT	LO (n)	#S (n)	T1 (n)
		Test Statistics				
Species				k	T/z	T/z
L. melanops (neonates)	5	IN	-	-	6 (4)	8.5(5)
L. scapularis	6	PL	LR	-	-	12 (6)
L. wiegmannii	3	-	-	-	6 (3)	5 (3)

Notes: Tests used were the Binomial test for character subset LO (test statistic k), and the Wilcoxon matched pairs-signed ranks test for character subsets #S and T1. Test statistics for this test were T when $n \leq 15$ and z when $n \geq 15$ (Siegel and Castellan, 1988). If $(n) < 4$ in the Binomial test or $(n) < 3$ in the Wilcoxon matched pairs-signed ranks test, then these tests were not applicable. This is indicated by a dash. * $p \leq .05$, ** $p \leq .01$ (both two-tailed). Details on character subsets, behavioral codes, and on columns N and (n) are given in the general section at the beginning of this chapter.

first test than on the second (for #S, p=.02) and L. xanthoviridis is significantly slower in the first test than in the second (for T1, p=.008). The two differences might have occurred just by chance (see discussion Chapter 1, Part IV). No other significant differences were found. In many instances (especially in Movement of the Head, MH, and Movement of the Tail, MT), more than 90% of individuals showed specific behavioral patterns (indicated in Table 3) and thus a statistical test was not appropriate. In addition, in some cases, the resulting (n)-values were very low, preventing the use of a statistical test (Table 3).

A similar situation occurred in long term variation (Table 3). No significant differences were found even for neonate L. melanops with several months between the two tests and with an average weight increase of 3 to 4 times their weight at the first test.

Context Variability

Burying behavior in yellow and in red sand was compared for the same individuals (Table 4). Tests used are shown in Table 4. Two significant differences were found. Liolaemus salinicola was significantly faster when burying into yellow sand than when burying into red sand (for T1, p=.001), and L. scapularis significantly changed from stopping at the base of the tail at its first stop when burying in yellow sand to being covered at its first stop when burying in red

sand (for LO, p=.02). Again, these might be due to chance alone (see Chapter 1, Part IV). No other significant differences were found. In many cases, more than 90% of individuals showed the same behavioral patterns (character subsets MH and MT, Table 4) whether burying in yellow or in red sand and thus a statistical test was not appropriate. In addition, the low (n)-values obtained for some cells prevented the use of a statistical test.

Variability between Males and Females

A summary of the results on variation in sand burying behavior between males and females within species, comparing the first test on yellow sand of each lizard, is given in Table 5. Number of males and females used are shown under columns M, for males, and F, for females, with N being the total number of individuals used. Tests used are shown in Table 5. No significant differences were found in the behavioral patterns observed in males and females of the same species.

Variability among Populations within a Species

The first test on yellow sand for each lizard was used for the comparison on variation among populations within a species with respect to their sand burying behavior (Table 6). Different populations per species were available for 3

Table 4 - Summary results for context variability in sand burying into two different types of sand (yellow and red) for the same individuals, in species of the boulengeri group. See notes below.

		Behavioral Character Subsets				
	N	MH	MT	LO (n)	#S (n)	T1 (n)
		Test Statistics				
Species				k	T/z	T/z
L. boulengeri	5	IN	-	2 (4)	7.5(4)	13 (5)
L. canqueli	10	IN	RT	-	27.5(10)	44(10)
L. cuyanus	13	LM	LR	2 (4)	22 (7)	68(13)
L. donosobarrosi	8	IN	-	BT	-	19 (8)
L. fitzingerii	10	IN	-	0 (4)	33 (9)	44(10)
L. laurenti	5	IN	FO	-	8.5(4)	8 (5)
L. melanops	8	IN	-	-	11 (6)	23 (8)
L. melanops (neonates)	5	IN	-	-	4.5(3)	9 (5)
L. riojanus	17	PL	LR	2 (8)	40.5(12)	1.06(17)
L. salinicola	14	PL	LR	4 (8)	11 (5)	105**(14)
L. scapularis	36	PL	LR	3*(16)	.59(18)	.03(35)
L. wiegmannii	13	-	-	-	22 (8)	47(13)
L. xanthoviridis	9	IN	-	2 (4)	20 (7)	35 (9)

Notes: Tests used were the Binomial test for character subset LO (test statistic k), and the Wilcoxon matched pairs-signed ranks test for character subsets #S and T1. Test statistics for this test were T when $n \leq 15$ and z when $n \geq 15$ (Siegel and Castellan, 1988). If (n)<4 in the Binomial test or (n)<3 in the Wilcoxon matched pairs-signed ranks test, then these tests were not applicable. This is indicated by a dash. * $p \leq .05$, ** $p \leq .01$ (both two-tailed). Details on character subsets, behavioral codes, and on columns N and (n) are given in the general section at the beginning of this chapter.

Table 5 - Summary results for variability in sand burying between males and females within species of the *boulengeri* group, comparing the first test on yellow sand of each lizard. See notes below.

				Behavioral Character Subsets				
	M	F	N	MH	MT	LO	#S	T1
				Test Statistics				
Species				p	p	p/X^2	W/z	W/z
L. canqueli	3	7	10	IN	RT	1.00	14	14
L. cuyanus	9	4	13	LM	LR	1.00	24	21
L. donosobarrosi	3	6	9	IN	FO	.50	17.5	15
L. fitzingerii	4	6	10	IN	1.00	1.00	21	21
L. riojanus	9	8	17	PL	LR	.35	59.5	57
L. salinicola	5	9	14	PL	LR	1.00	34	45
L. scapularis	28	12	40	PL	LR	4.1(df=1)	0.65	0.61
L. wiegmannii	4	13	17	.38	.30	.27	1.08	0.79
L. xanthoviridis	3	6	9	IN	1.00	1.00	13	21

Notes: The Fisher exact test (test statistic was the p-value) was used for character subsets MH, MT and LO except in *L. scapularis* with N = 40. In this case, the Chi-square test (test statistic was X^2, degrees of freedom specified in parentheses) was used. For character subsets #S and T1, the Wilcoxon-Mann-Whitney test was used (test statistics were W when $m \leq 10$ and $n \leq 10$, and z when these parameters were greater than 10). No significant differences were found at $p \leq .05$. Details on character subsets, behavioral codes, and on column N are given in the general section at the beginning of this chapter.

Table 6 - Summary results for variability in sand burying among populations within species of the boulengeri group comparing the first test on yellow sand of each lizard.

		Behavioral Character Subsets				
	N	MH	MT	LO	#S	T1
		Test Statistics				
Species				p	W/KW	W/KW
L. cuyanus PI=7, TI=3	10	LM	LR	.20	22.5	16
L. riojanus BA=10, VU=7	17	PL	LR	.27	48	43
L. scapularis CF=17, PM=10, PZ=8	35	PL	LR	-	3.31(df=2)	7.66*(df=2)

Notes: The Fisher exact test was used for character subset LO (test statistic was the p-value). In the case of L. scapularis, a Chi-square test was considered for this character subset since there were 3 populations to be compared. However, 2 of the expected frequencies were lower than 5. Therefore the test was not applicable. The Wilcoxon-Mann-Whitney test (test statistic W) was used for character subsets #S and T1 for L. cuyanus and L. riojanus. The Kruskal-Wallis one-way analysis of variance (test statistic KW) was used for L. scapularis (degrees of freedom specified in parentheses). * $p \leq .05$, ** $p \leq .01$ (both two-tailed). Details on character subsets, behavioral codes, and on column N are given in the general section at the beginning of this chapter.

species. Number of lizards coming from each population is specified below the species name. Populations were all within Argentina (see Appendix B for more details). These were:

BA - Baldecitos, La Rioja

CF - Cafayate, Salta

PI - Pituil, La Rioja

PM - Pie de Medanos, Catamarca

PZ - Pozuelos, Catamarca

TI - Tinogasta, Catamarca

VU - Villa Unión, La Rioja

Tests used are specified in Table 6. There was one significant difference among two populations of L. scapularis (for T1, p=.04, Table 6). There was a significant difference between the population coming from Cafayate (CF) and the population from Pozuelos (PZ) (z=11.33, critical value = 10.52, p=.05, Multiple Comparisons Between Treatments for the Kruskal-Wallis one-way analysis of variance, Siegel and Castellan, 1988) with respect to the time taken in burying to first stop on their first test in yellow sand. Lizards from Cafayate were significantly slower in entering sand to their first stop (average speed = 5.08 ± 1.14 seconds) than those from Pozuelos (average speed = 3.90 ± 0.62 seconds). The other population from Pie de Medanos

(PM) was not significantly different from either CF or PZ. There were no other significant differences in the behavior patterns compared among different populations of three species.

Variability between Adult and Neonate Liolaemus melanops

A summary of the results on variation in sand burying behavior between adults and neonates is shown in Table 7. The first test on yellow sand for each lizard was used for the comparison. Sufficient numbers of adults and neonates were available for one species. Tests used are specified in the table.

There was one significant difference between adult and neonate L. melanops with respect to Time One (for T1, $p=.006$, Table 7). The neonates were quicker to reach their first stop than the adults (average speed for neonates = 8.18 ± 2.11 seconds and for adults = 20.01 ± 7.04 seconds). Size might be an important factor here since adults may weight about 12 to 20 times more than a neonate. Nevertheless, when the weights of different species were compared to average time taken to bury to first stop, overall, no correlations were found (see section on Time Recordings, Chapter 2, Part II) but differences in weights were also not as large as between neonate and adult L. melanops. Adults and neonates did not differ with respect to the other behavior patterns considered.

Table 7 - Summary results for variability in sand burying between adult and neonate Liolaemus melanops.

		Behavioral Character Subsets				
	N	MH	MT	LO	#S	T1
				Test Statistics		
Species				p	W	W
L. melanops (8 adults, 5 neonates)	13	IN	-	.51	25.5	17**

Notes: The Fisher exact test (test statistic was the p-value) was used for character subset LO, and the Wilcoxon-Mann-Whitney test (test statistic W) for character subsets #S and T1. The Fisher exact test was not applied for character subset MT because, although adults showed a majority of the RT behavioral character (7 out of 8), the neonates had 2 RT, 2LR, and 1 FO. * $p \leq .05$, ** $p \leq .01$ (both two-tailed). Details on character subsets, behavioral codes, and on column N are given in the general section at the beginning of this chapter.

CHAPTER 3

PHYLOGENETIC ANALYSIS OF SAND BURYING IN THE BOULENGERI GROUP

The matrix showing the character states for 26 behavioral characters corresponding to sand burying for 4 species belonging to the montanus supergroup (the functional outgroup) and for individuals of 19 species belonging to the boulengeri group (the ingroup) is given in Table 8. Behavioral characters and character states were defined in Chapter 2, Part II. Based on this matrix, character states for all the species were determined following a procedure outlined in Table 2 (Chapter 2, Part II). The results are shown in Table 9. This is the matrix that was used for the construction of cladograms generated with Hennig86. Four trees and one consensus tree were obtained. The consistency index was 48, the retention index 72, and tree length 424.

The four trees (Fig. 22) obtained with the matrix in Table 9 differ slightly from one another and from the Nelsen consensus tree. The 4 trees form 2 major branches with one branch subdividing into two other branches. The differences are:

- In tree 0 (Fig. 22a), node 36 splits in two and there is another splitting at node 35. Stem 33 contains all the

Table 8 - Character states for 26 behavioral characters for 4 species of *Liolaemus* that belong to the *montanus* supergroup, the functional outgroup, and for individual lizards from 19 species of *Liolaemus* belonging to the *boulengeri* group, the ingroup. See Chapter 2, Part II, for definition of characters and character states, and Chapter 3, Part I, for taxonomic arrangement of the genus *Liolaemus*.

Species\Characters	di	sc	bm	bs	in	lm	pl	ct	fo	rt	lr	mb	bt	mt	c1	pc	cc	s5	s4	s3	s2	s1	r1	r2	a1	a2
functional outgroup																										
L. andinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. huacahuasicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. multicolor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. ruibali	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ingroup (=*boulengeri* group, monophyletic group within the *montanus* supergroup)																										
L. boulengeri (7)																										
856 BLBPF2	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	1
857 BLMTF2	1	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0
860 BLCRM1	1	1	0	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
862 BLBPF1	1	1	0	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
863 BLCTF1	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0
867 BLMTM1	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0
896 BLLNF6	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0
L. canqueli (10)																										
1035 CAINF1	1	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
1036 CAINF4	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0
1037 CAINF3	1	1	1	0	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0
1042 CAINM3	1	1	0	0	0	1	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1
1048 CAINF6	1	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0
1050 CAINM4	1	1	0	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0
1051 CAINM1	1	0	1	0	1	0	0	1	0	1	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0
1054 CAINF7	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1
1055 CAINF5	1	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0
1058 CAINF2	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0

Table 8 (continued)

Species\Characters	di	sc	bm	bs	in	lm	pl	ct	fo	rt	lr	mb	bt	mt	c1	pc	cc	s5	s4	s3	s2	s1	r1	r2	a1	a2
L. cuyanus (13)																										
205 CUTIF1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
210 CUTIM1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
211 CUTIM2	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
642 CUPIM2	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
643 CUPIM1	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
728 CUPRM4	1	1	1	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
729 CUPRM5	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
732 CUPRF1	1	0	0	0	0	1	0	0	?	?	?	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
736 CUPRM2	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0
737 CUPRM3	1	1	0	0	?	?	?	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
756 CUPRM1	1	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
757 CUPRF2	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
846 CUBAF1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
L. darwinii (1)																										
459 DAMZF1	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0
L. darwinii Nihuil (2; undescribed species, see Appendix A)																										
898 DNLNM3	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0
899 DNLNFT	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0
L. donosobarrosi (9)																										
901 DOMAF6	1	1	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0
902 DOMAM2	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0
904 DOMAF5	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0
909 DOMAM3	1	1	0	0	1	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1
913 DOMAF2	1	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0
914 DOMAF4	0	0	0	0	1	0	0	1	?	?	?	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1
916 DOMAM4	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0
918 DOMAF3	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
919 DOMAF1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
L. fitzingerii (10)																										
1008 FZCHM2	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0
1009 FZCHF4	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0
1010 FZCHM4	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1
1015 FZCHF2	1	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0
1016 FZCHF1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0
1018 FZCHF5	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
1022 FZCHM3	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
1023 FZCHF7	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
1024 FZCHM1	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
1033 FZCHF6	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0

Table 8 (continued)

Species\Characters	di	sc	bm	bs	in	lm	pl	ct	fo	rt	lr	mb	bt	mt	c1	pc	cc	s5	s4	s3	s2	s1	r1	r2	a1	a2
L. koslowskyi (5)																										
214 KOTIM1	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0
215 KOTIF1	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0
216 KOTIF2	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0
310 KONTM1	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0
311 KONTM2	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0
L. laurenti (6)																										
312 LATIM1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	1	0
959 LAPRM4	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0
961 LAPRM11	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0
964 LAPRF6	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0
965 LAPRM8	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0
966 LAPRF12	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0
L. melanops (8)																										
1171 MEPVF8	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1
1174 MEPVM8	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1
1175 MEPVM5	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1
1178 MEPVM1	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1
1179 MEPVF2	1	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1
1180 MEPVM9	1	0	1	0	1	0	0	1	?	?	?	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1
1186 MEPVM2	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1
1187 MEPVM10	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1
L. olongasta (3)																										
969 OLTAF2	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0
970 OLTAM5	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0
971 OLTAM3	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0
L. ornatus (8)																										
386 (4 males)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
387 (4 fem.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. quilmes (8)																										
106 QUSMM3	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0
164 QUQUM3	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	1	0
307 QUPZF1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	1	0
323 QUPBF3	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0
324 QUPBF1	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0
326 QUPBM1	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0
327 QUPBM2	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
329 QUPBM4	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0

Table 8 (continued)

Species\Characters	di	sc	bm	bs	in	lm	pl	ct	fo	rt	lr	mb	bt	mt	c1	pc	cc	s5	s4	s3	s2	s1	r1	r2	a1	a2
L. xanthoviridis (9)																										
1112 XALIM6	1	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1
1114 XALIF2	1	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	1
1118 XALIM3	1	0	0	0	0	1	0	1	?	?	?	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1
1121 XALIF7	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1
1122 XALIM1	1	1	0	0	0	1	0	1	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	1
1123 XALIF3	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1
1127 XALIF1	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1
1128 XALIF4	1	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1
1130 XALIF5	1	0	1	0	1	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0
wiegmannii subgroup (monophyletic group within the *boulengeri* group)																										
L. multimaculatus (3)																										
1168 MUALM1	1	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
1476 MUFQF2	1	0	0	1	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
1489 MUFQF1	1	0	1	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
L. riojanus (17)																										
370 RIVUM3	1	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
372 RIVUM2	1	1	1	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
375 RIVUM1	1	1	0	1	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
378 RIVUF3	1	0	1	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
379 RIVUF4	1	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
380 RIVUF2	1	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
383 RIVUF1	1	0	0	1	0	0	1	1	?	?	?	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0
644 RIBAM5	1	1	1	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
649 RIBAM3	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
650 RIBAM2	1	0	1	1	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0
652 RIBAM4	1	0	1	1	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0
653 RIBAF1	1	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	1	0
656 RIBAF2	1	0	1	1	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
657 RIBAM1	1	0	1	1	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
833 RIBAF10	1	1	0	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
839 RIBAF13	1	0	1	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0
842 RIBAM10	1	0	1	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
L. salinicola (14)																										
206 SATIF1	1	1	1	1	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
208 SATIM1	1	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
704 SAMNM2	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0

Table 8 (continued)

Species\Characters	di	sc	bm	bs	in	lm	pl	ct	fo	rt	lr	mb	bt	mt	c1	pc	cc	s5	s4	s3	s2	s1	r1	r2	a1	a2
L. salinicola (continued)																										
706 SAMNF7	1	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
707 SAMNM1	1	1	1	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
709 SAMNM3	1	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
712 SAMNF5	1	1	1	1	0	0	1	1	?	?	?	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
713 SAMNF8	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
715 SAMNF2	1	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0
717 SAMNF3	1	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
718 SAMNF4	1	1	1	1	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
719 SAMNF1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
723 SAMNF6	1	0	0	0	0	0	1	0	?	?	?	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
727 SAMNM4	1	1	1	1	0	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0
L. scapularis (40)																										
98 SCCFM2	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
100 SCCFM3	0	1	1	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
107 SCSMM1	1	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
108 SCSMM2	1	1	1	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
113 SCSMM3	1	1	1	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
116 SCCFM1	0	1	1	0	0	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0
286 SCPEM3	1	1	1	0	0	0	1	?	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
290 SCPEM2	1	1	0	0	0	0	1	?	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
293 SCPEM5	1	1	0	0	0	0	1	?	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
296 SCPEM1	1	1	1	0	0	0	1	?	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
297 SCPEM4	1	1	1	0	0	0	1	?	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
299 SCPZF1	1	1	1	0	0	0	1	?	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
302 SCPZM1	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
303 SCPZM2	1	1	0	1	0	0	1	?	?	?	?	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
306 SCPZF2	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
313 SCPMF2	1	1	0	1	0	0	1	?	?	?	?	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
316 SCPMF1	1	0	1	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
318 SCPMF3	1	0	1	0	0	0	1	?	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
319 SCPMF4	1	1	0	1	0	0	1	?	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
322 SCPMM1	1	1	1	0	0	0	1	?	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
531 SCITF1	1	1	1	0	0	0	1	?	?	?	?	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
533 SCITF2	1	1	0	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
557 SCCFM4	1	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
559 SCCFF2	1	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
562 SCCFF1	1	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
565 SCCFM8	1	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
567 SCCFM12	1	0	0	1	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
569 SCCFM9	1	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0

Table 8 (continued)

Species\Characters	di	sc	bm	bs	in	lm	pl	ct	fo	rt	lr	mb	bt	mt	c1	pc	cc	s5	s4	s3	s2	s1	r1	r2	a1	a2
L. scapularis (continued)																										
571 SCCFM14	1	0	0	1	0	0	1	?	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
573 SCCFM13	1	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
575 SCCFM10	1	1	1	0	0	0	1	?	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
577 SCCFM5	1	0	0	1	0	0	1	?	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
579 SCCFM6	1	1	0	1	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
581 SCCFM11	1	0	0	1	0	0	1	?	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
583 SCCFF3	1	1	1	0	0	0	1	?	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0
585 SCCFM7	1	1	0	1	0	0	1	?	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
834 SCPZF3	1	1	1	1	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0
835 SCPZM6	1	1	1	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
841 SCPZM7	1	1	0	0	0	0	1	0	?	?	?	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
845 SCPZM5	1	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
L. wiegmannii (17)																										
103 WIMDM3	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
104 WIMDFG	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
123 WIMDF2	1	1	0	0	0	0	1	0	?	?	?	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0
124 WIMDM1	1	1	1	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
764 WIMDF15	1	1	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
765 WIMDF17	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0
768 WIMDF20	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	1	0
770 WIMDF23	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
773 WIMDF25	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
774 WIMDF22	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0
777 WIMDF24	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
779 WIMDF26	1	1	0	0	1	0	0	?	?	?	?	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
780 WIMDM11	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0
782 WIMDM12	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0
784 WIMDF21	1	1	0	0	1	0	0	0	?	?	?	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0
786 WIMDF19	1	0	0	0	0	0	1	0	?	?	?	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0
789 WIMDF16	1	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0

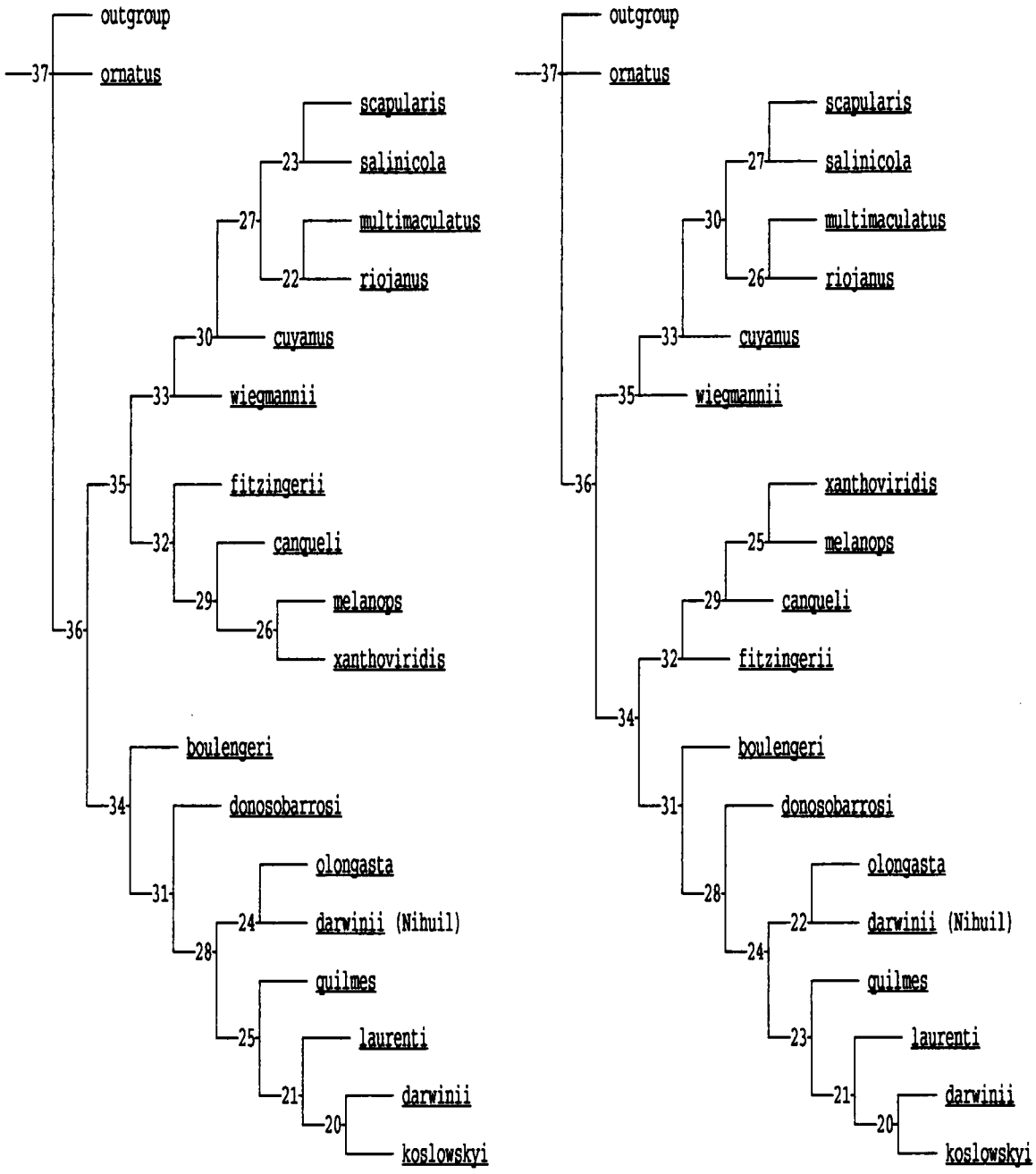
Notes: *Liolaemus darwinii* Nihuil corresponds to an undescribed species from southern Mendoza, Argentina, and belongs to the *darwinii* complex (Etheridge, 1993). Under each species name of the ingroup is given a record number and an identification number of the lizards used for the matrix. Question marks indicate information that was not obtained (either because it was unclear on the tape, or section of tape had been erased, or in the case of movements of the tail, tail was autotomized and movement could not be determined). At the end of each species name is given the number of lizards used for that species.

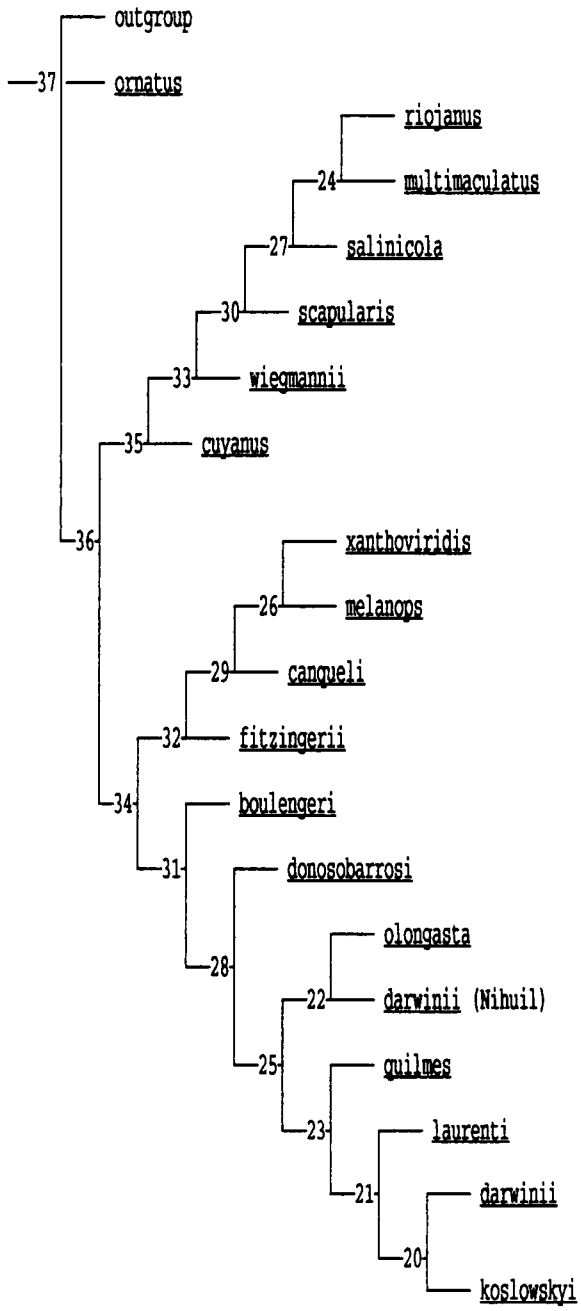
Table 9 - Matrix used in constructing cladograms (Figs. 22 and 23) for 19 species of Liolaemus belonging to the boulengeri group, the ingroup, and a functional outgroup comprising 4 species of Liolaemus belonging to the montanus supergroup which includes the former group. See Chapter 2, Part II, for definition of the 26 behavioral characters and character states, and Chapter 3, Part I, for taxonomic arrangement of the genus Liolaemus.

	di	sc	bm	bs	in	lm	pl	ct	fo	rt	lr	mb	bt	mt	c1	pc	cc	s5	s4	s3	s2	s1	r1	r2	a1	a2
outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. boulengeri	4	2	1	0	8	0	1	8	5	2	1	5	4	0	0	2	7	1	2	5	0	0	8	1	8	1
L. canqueli	9	6	5	0	6	4	0	4	0	9	0	7	3	0	0	0	9	7	1	1	1	0	9	1	8	2
L. cuyanus	9	3	0	0	0	9	0	0	0	0	9	0	4	2	2	0	9	0	0	5	2	2	9	0	9	0
L. darwinii	0	0	0	0	9	0	0	9	9	0	0	9	0	0	0	9	0	0	9	0	0	0	9	0	9	0
L. darwinii Nihuil	0	0	0	0	9	0	0	9	9	0	0	9	0	0	0	5	5	9	0	0	0	0	9	0	9	0
L. donosobarrosi	3	2	0	0	9	0	0	9	6	2	0	7	2	0	0	2	7	2	2	5	0	0	9	0	7	2
L. fitzingerii	7	4	2	0	7	3	0	0	2	8	0	5	5	0	0	0	9	2	2	4	2	0	9	1	9	1
L. koslowskyi	0	0	0	0	9	0	0	9	9	0	0	8	2	0	0	8	2	0	6	0	4	0	9	0	9	0
L. laurenti	0	0	0	0	9	0	0	9	9	0	0	6	3	0	0	9	0	3	1	3	1	0	9	0	9	0
L. melanops	8	2	1	0	7	2	0	2	0	9	0	7	2	0	0	0	9	6	0	3	0	0	2	7	0	9
L. olongasta	0	0	0	0	9	0	0	9	9	0	0	6	3	0	0	3	6	6	3	0	0	0	9	0	9	0
L. ornatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. quilmes	0	0	0	0	9	0	0	9	9	0	0	5	5	0	0	6	3	2	2	2	2	0	7	2	9	0
L. xanthoviridis	9	1	4	0	3	6	0	6	0	9	0	4	5	0	0	0	9	4	4	1	0	0	1	8	1	8
L. multimaculatus	9	0	3	6	0	0	9	9	0	0	9	0	3	0	6	0	9	0	0	0	3	6	9	0	9	0
L. riojanus	9	4	5	4	0	0	9	9	0	0	9	0	2	5	2	0	9	0	0	2	4	2	9	0	9	0
L. salinicola	9	7	3	5	0	0	9	7	0	0	9	0	4	4	0	0	9	0	0	3	5	0	9	0	9	0
L. scapularis	9	8	4	3	0	0	9	5	0	0	9	0	6	2	1	0	9	0	0	2	6	1	9	0	9	0
L. wiegmannii	9	8	0	0	8	0	1	1	0	0	9	1	7	0	0	0	9	0	2	4	2	0	9	0	9	0

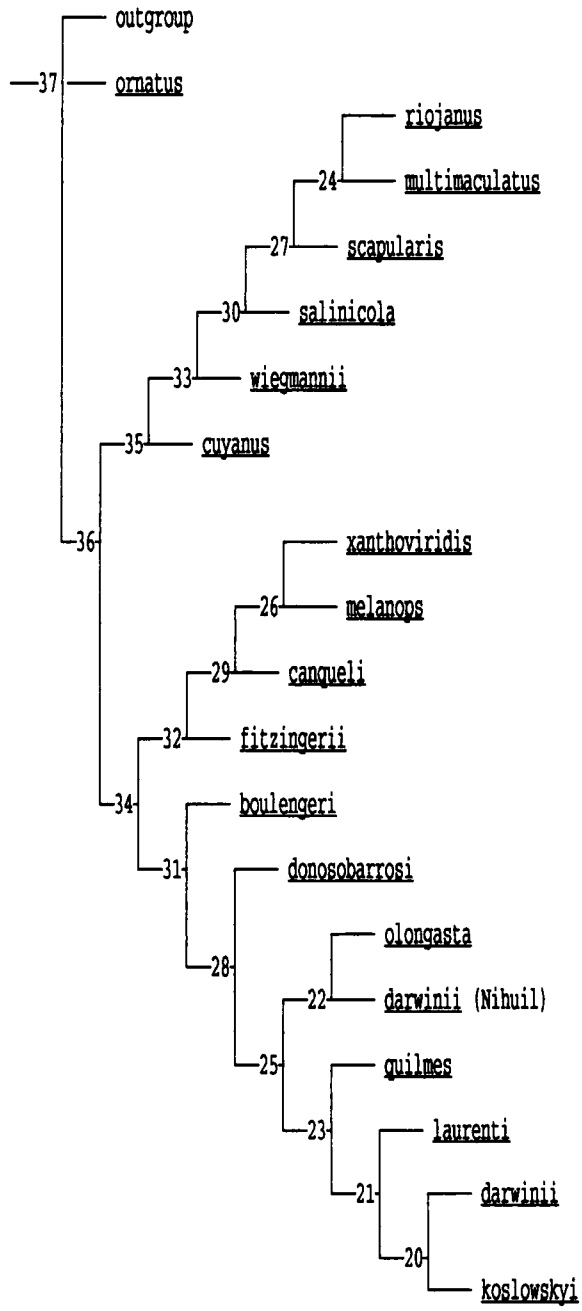
Notes: Liolaemus darwinii Nihuil corresponds to an undescribed species from southern Mendoza, Argentina, belonging to the darwinii complex (Etheridge, 1993). Character states for individual lizards are given in Table 8.

Figure 22. Four possible cladograms showing the distribution of 19 species belonging to the boulengeri group, Liolaemus. The trees were obtained from the matrix in Table 9: Trees # 0 (a), 1 (b), 2 (c) and 3 (d).


outgroup
ornatus
scapularis
salinicola
multimaculatus
riojanus
cuyanus
wiegmannii
fitzingerii
canqueli
melanops
xanthoviridis
boulengeri
donosobarrosi
olongasta
darwinii (Nihuil)
quilmes
laurenti
darwinii
koslowskyi
37
23
27
22
30
33
35
32
29
26
36
34
31
24
28
25
21
20
a.
b.


outgroup
37
ornatus
riojanus
24
multimaculatus
27
salinicola
30
scapularis
33
wiegmannii
35
cuyanus
36
xanthoviridis
26
melanops
29
canqueli
32
fitzingerii
34
boulengeri
31
donosobarrosi
olongasta
28
22
darwinii (Nihuil)
25
quilmes
23
laurenti
21
darwinii
20
koslowskyi

c.


outgroup
37
ornatus
riojanus
24
multimaculatus
27
scapularis
30
salinicola
33
wiegmannii
35
cuyanus
36
xanthoviridis
26
melanops
29
canqueli
32
fitzingerii
34
boulengeri
31
donosobarrosi
olongasta
28
22
darwinii (Nihuil)
25
quilmes
23
laurenti
21
darwinii
20
koslowskyi

d.

species of the wiegmannii group specified in Etheridge's indentation (1995) plus L. cuyanus. Stem 32 contains L. fitzingerii, L. canqueli, L. melanops and L. xanthoviridis. Stem 34 contains species belonging to the darwinii complex (Etheridge, 1993) plus L. boulengeri and L. donosobarrosi.

- In tree 1 (Fig. 22b), node 36 also splits in two but now the other branching off occurs at node 34. In this tree, at node 34, L. fitzingerii, L. canqueli, L. melanops and L. xanthoviridis are linked to the darwinii complex (Etheridge, 1993) plus L. boulengeri and L. donosobarrosi. Stem 35 contains species of the wiegmannii complex (Etheridge, 1995) plus L. cuyanus.

- Tree 2 (Fig. 22c) is very similar to tree 1. The only difference is in the position of 4 species within a branch (stem 35). In tree 2, L. cuyanus branches off first at node 35 followed by L. wiegmannii at node 33. In tree 1, the reverse occurs. The other difference is between L. scapularis and L. salinicola. In tree 2, the former species branches off at node 30 followed by the latter at node 27. In tree 1, these species are not discriminated.

- Tree 3 (Fig. 22d) is very similar to tree 2 except for a switching of places between L. salinicola and L. scapularis.

It is important to note that the disposition of species from the darwinii complex (sensu Etheridge, 1993) plus L. boulengeri and L. donosobarrosi as well as that of L.

fitzingerii, L. canqueli, L. melanops and L. xanthoviridis stay the same in all 4 trees and in the consensus tree (see below).

Analysis of the CONSENSUS TREE

The Nelson consensus tree is shown in Fig. 23a-g. To help make its interpretation clearer, the tree is shown in 7 separate figures. The branching sequences are the same in each of the 7 figures but each figure shows a different set of behavioral characters and character states corresponding to one of the 7 subsets of behavioral characters that were described in Chapter 2 of Part II. Branch lengths are arbitrary.

Analysis of characters **di, sc, bm** and **bs** (Fig. 23a)

di: digging is the only character that occurs in the outgroup and in L. ornatus. In order to interpret this trait it is important to remember (contrary to the other characters) that the **lower** the character state the **more** frequent its occurrence in a species due to the character coding of "digging" as "0". Because this behavior was present in the outgroup it was considered to be plesiomorphic and as such was coded "0". "No digging" was therefore coded as "1".

In the ingroup digging is practically lost in stem 31, it does not occur at all in stem 32, but it is maintained more than 50% in stem 30 and it is present 100% in stem 24

Figure 23. Consensus tree showing the distribution for 7 behavioral character subsets in 19 species belonging to the boulengeri group, Liolaemus. Determination of character states for species is explained in Table 2.

a. Consensus tree for the behavioral characters **di**, **sc**, **bm**, and **bs** (details in Methods).

di: (0) digging, (9) no digging

sc: (0) no scratching, (9) scratching

bm: (0) no back movement, (9) back movement

bs: (0) no back steps, (9) back steps

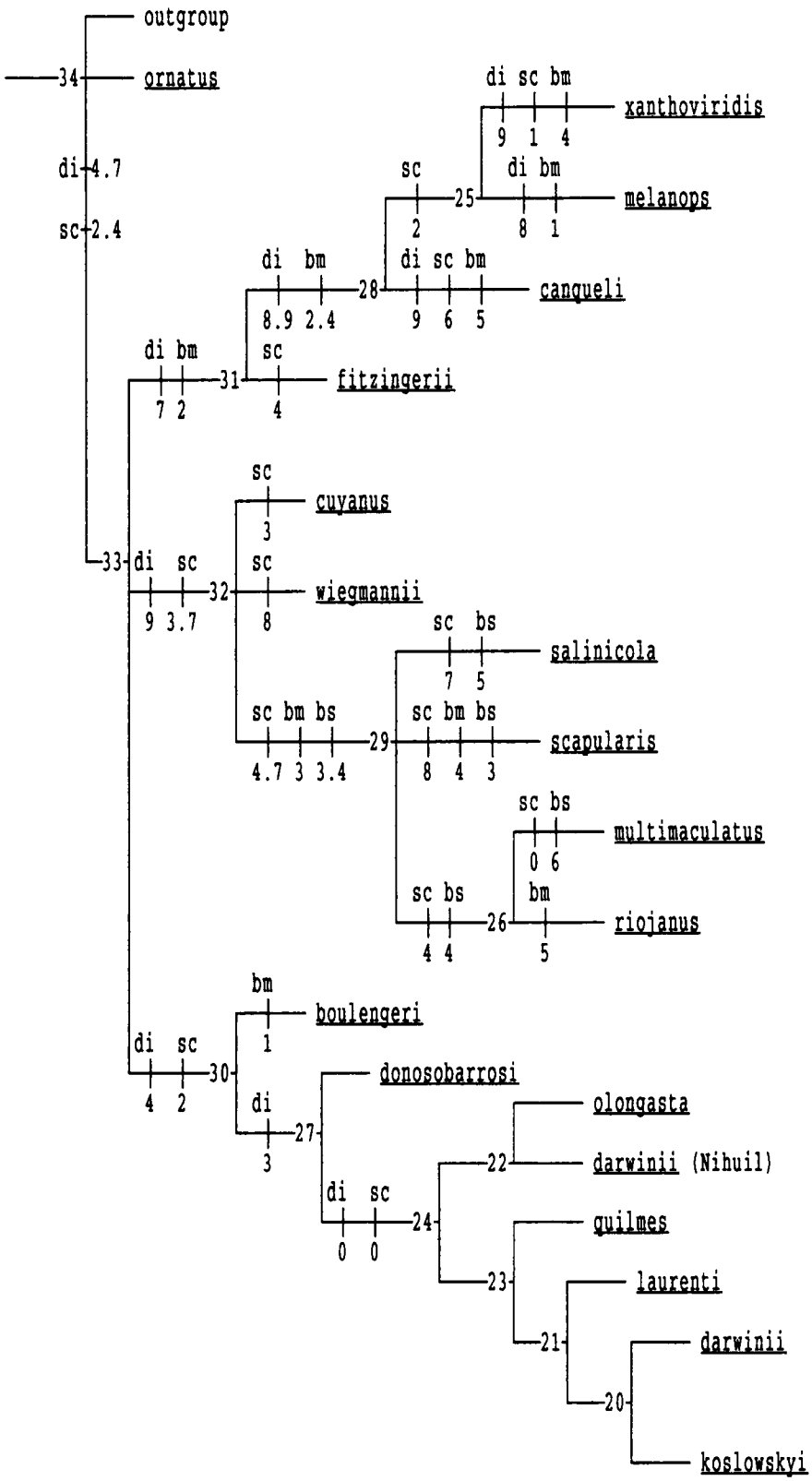

outgroup
ornatus
34
di 4.7
sc 2.4
di sc bm
xanthoviridis
9 1 4
sc
di bm
melanops
25
2
8 1
di bm
di sc bm
canqueli
28
8.9 2.4
9 6 5
di bm
sc
fitzingerii
31
7 2
4
sc
cuyanus
3
33
di sc
sc
wiegmannii
32
9 3.7
8
sc bs
salinicola
7 5
sc bm bs
sc bm bs
scapularis
29
4.7 3 3.4
8 4 3
sc bs
multimaculatus
0 6
sc bs
bm
riojanus
26
4 4
5
bm
boulengeri
1
di sc
donosobarrosi
30
4 2
di
olongasta
27
3
darwinii (Nihuil)
22
di sc
quilmes
24
0 0
laurenti
23
darwinii
21
20
koslowskyi

Figure 23. b. Consensus tree for the behavioral characters **in**, **lm**, and **pl**, (details in Methods).

in: (0) not introducing head,

(9) introducing head

lm: (0) no lateral movement of head,

(9) lateral movement of head

pl: (0) no plunging, (9) plunging

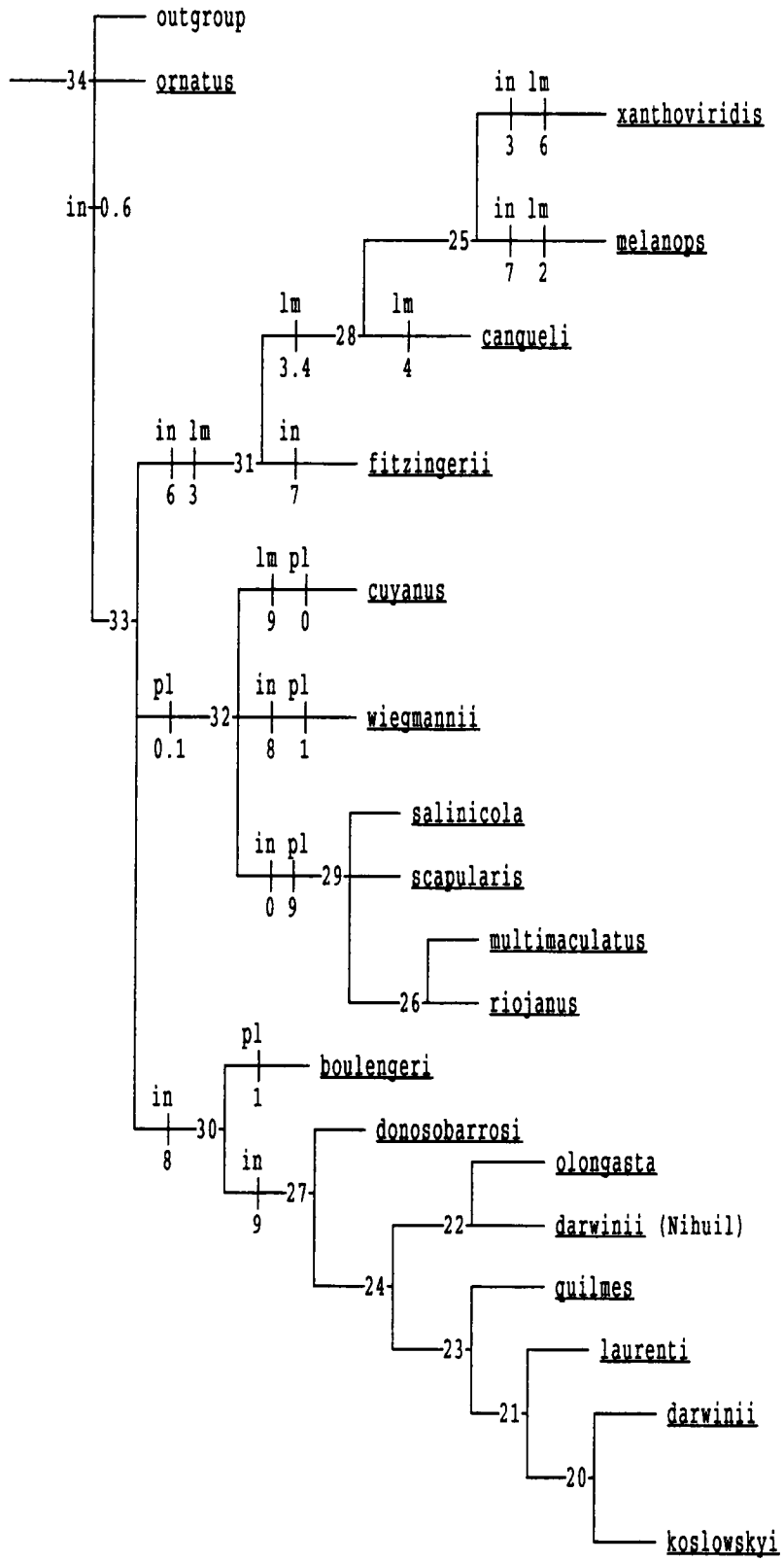

outgroup
34
ornatus
in 0.6
in lm
3 6
xanthoviridis
in lm
7 2
melanops
25
lm
3.4
lm
4
28
canqueli
in lm
6 3
in
7
31
fitzingerii
lm pl
9 0
cuyanus
33
pl
0.1
in pl
8 1
32
wiegmannii
salinicola
in pl
0 9
29
scapularis
multimaculatus
26
riojanus
pl
1
boulengeri
in
8
30
donosobarrosi
in
9
27
olongasta
22
darwinii (Nihuil)
24
quilmes
23
laurenti
21
darwinii
20
koslowskyi

Figure 23. c. Consensus tree for the behavioral characters **ct**, **fo**, **rt**, and **lr** (details in Methods).

ct: (0) tail not in contact with substrate

(9) tail in contact with substrate

fo: (0) tail does not follow, (9) tail follows

rt: (0) tail is not retrieved

(9) tail is retrieved

lr: (0) tail is not lashed, (9) tail is lashed

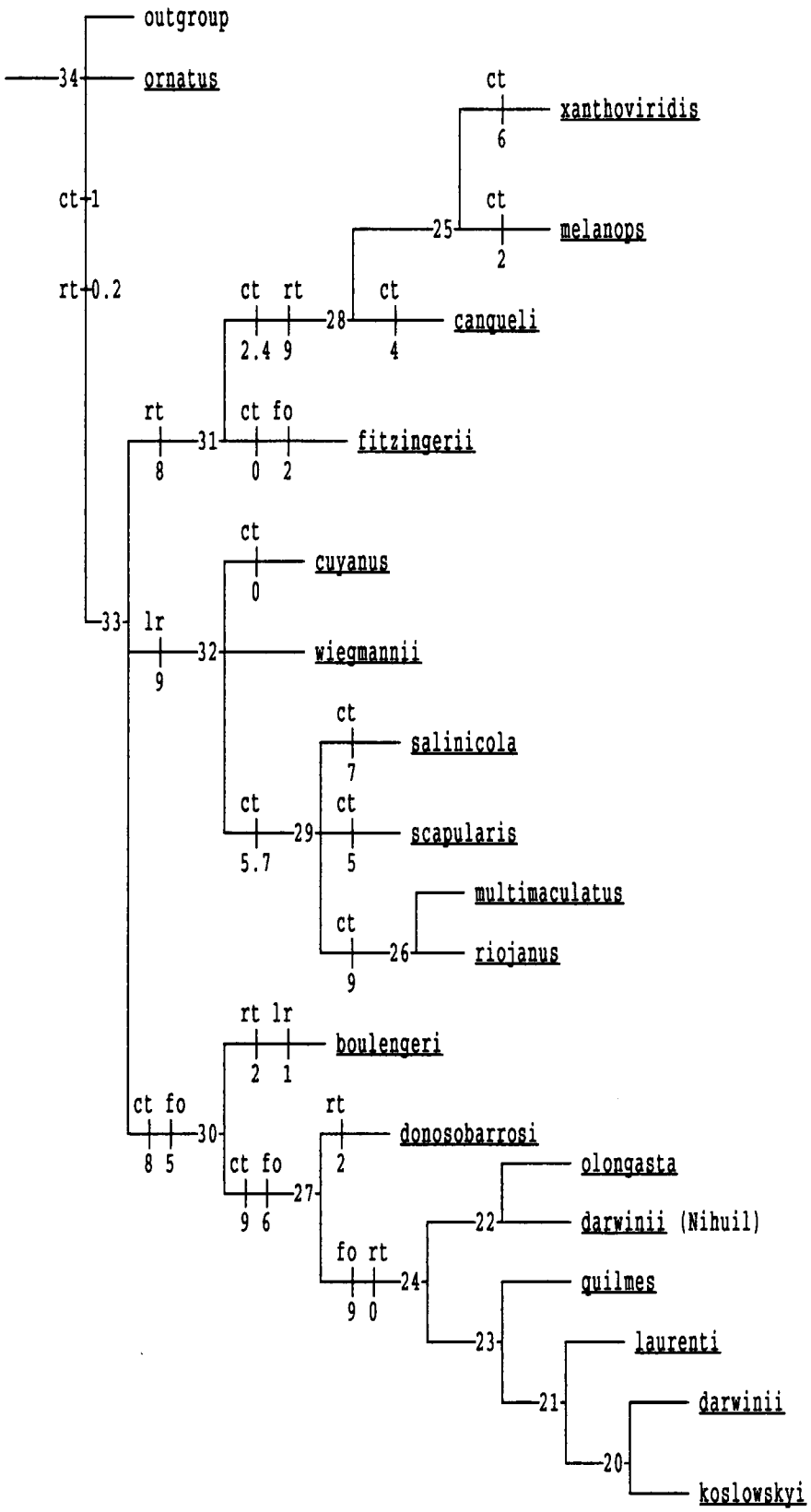

outgroup
34
ornatus
ct
1
rt
0.2
ct
6
xanthoviridis
ct
25
ct
2
melanops
ct rt
2.4 9
28
ct
4
canqueli
rt
8
31
ct fo
0 2
fitzingerii
ct
0
cuyanus
33
1r
9
32
wiegmannii
ct
7
salinicola
ct
5.7
29
ct
5
scapularis
multimaculatus
ct
9
26
riojanus
rt 1r
2 1
boulengeri
ct fo
8 5
30
rt
2
donosobarrosi
ct fo
9 6
27
olongasta
22
darwinii (Nihuil)
fo rt
9 0
24
quilmes
23
laurenti
21
darwinii
20
koslowskyi

Figure 23. d. Consensus tree for the behavioral characters **mb**, **bt**, **mt**, and **c1** (details in Methods).

mb: (0) did not reach midbody section at first stop, (9) reached midbody at first stop

bt: (0) did not reach the base of the tail at first stop

(9) reached base of tail at first stop

mt: (0) did not reach midtail section at first stop, (9) reached midtail at first stop

c1: (0) not covered in one stop

(9) covered in one stop

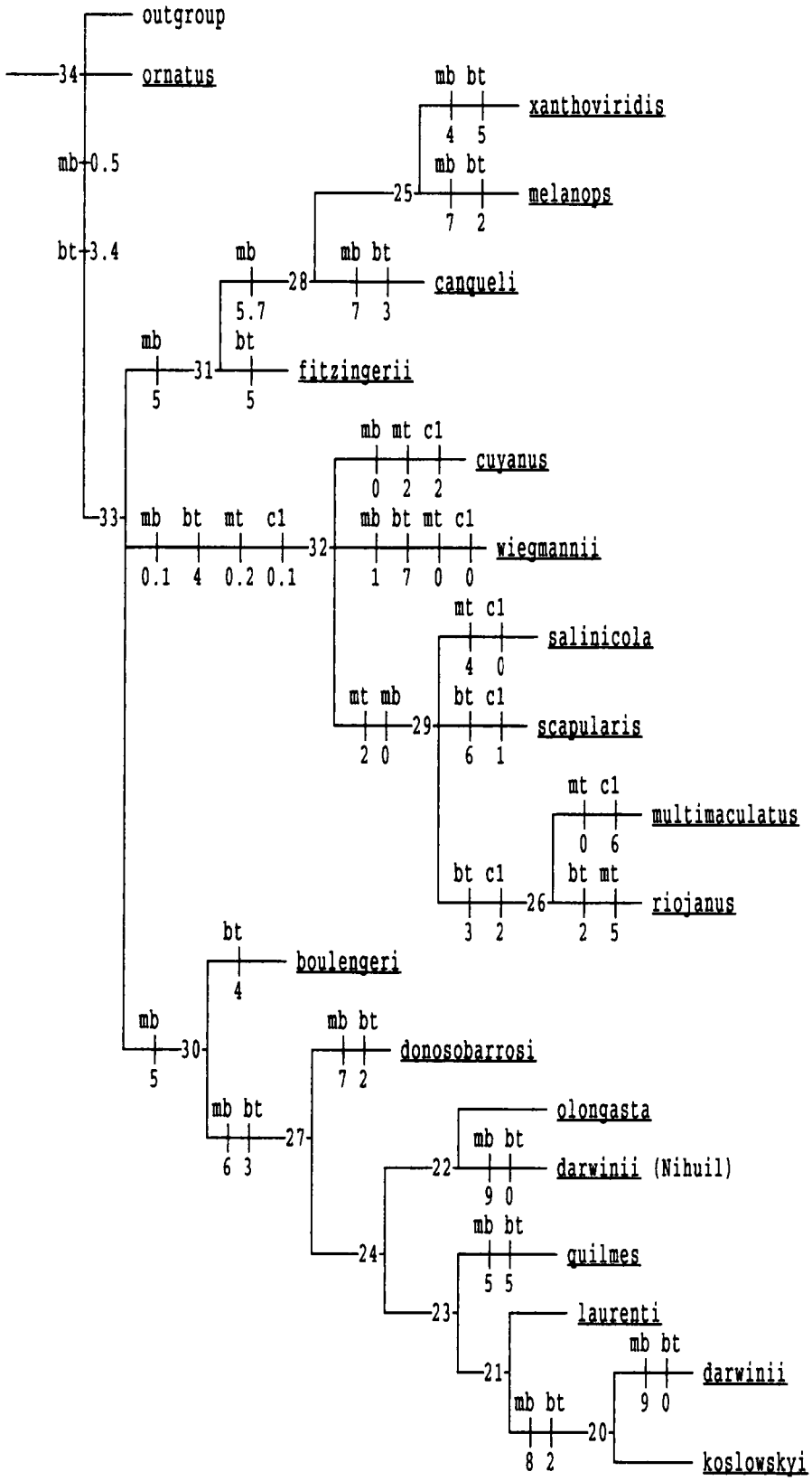

outgroup
ornatus
xanthoviridis
melanops
canqueli
fitzingerii
cuyanus
wiegmannii
salinicola
scapularis
multimaculatus
riojanus
boulengeri
donosobarrosi
olongasta
darwinii (Nihuil)
quilmes
laurenti
darwinii
koslowskyi
mb
bt
mt
c1

Figure 23. e. Consensus tree for the behavioral characters **pc** and **cc** (details in Methods).

pc: (0) not partly covered at final stop

(9) partly covered at final stop

cc: (0) not completely covered at final stop

(9) completely covered at final stop

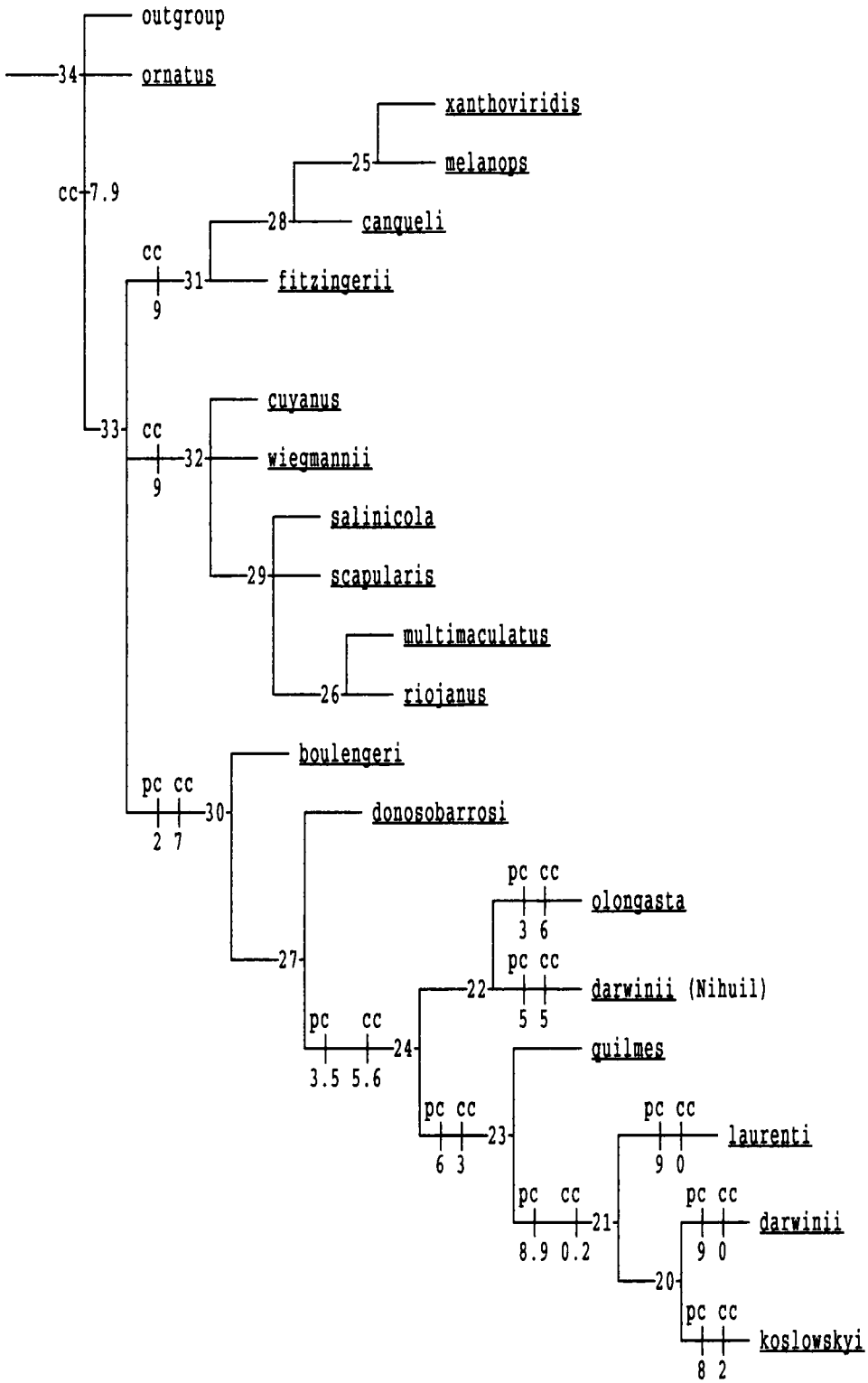

outgroup
34
ornatus
xanthoviridis
25
melanops
cc 7.9
28
canqueli
cc
31
9
fitzingerii
cuyanus
33
cc
32
9
wiegmannii
salinicola
29
scapularis
multimaculatus
26
riojanus
boulengeri
pc cc
30
2 7
donosobarrosi
pc cc
olongasta
3 6
27
pc cc
22
darwinii (Nihuil)
5 5
pc cc
24
quilmes
3.5 5.6
pc cc
23
6 3
pc cc
laurenti
9 0
pc cc
21
darwinii
8.9 0.2
9 0
20
pc cc
koslowskyi
8 2

Figure 23. f. Consensus tree for the behavioral characters **s5**, **s4**, **s3**, **s2**, and **s1** (details in Methods).

s5: (0) did not make 5 stops, (9) made 5 stops

s4: (0) did not make 4 stops, (9) made 4 stops

s3: (0) did not make 3 stops, (9) made 3 stops

s2: (0) did not make 2 stops, (9) made 2 stops

s1: (0) did not make 1 stop, (9) made 1 stop

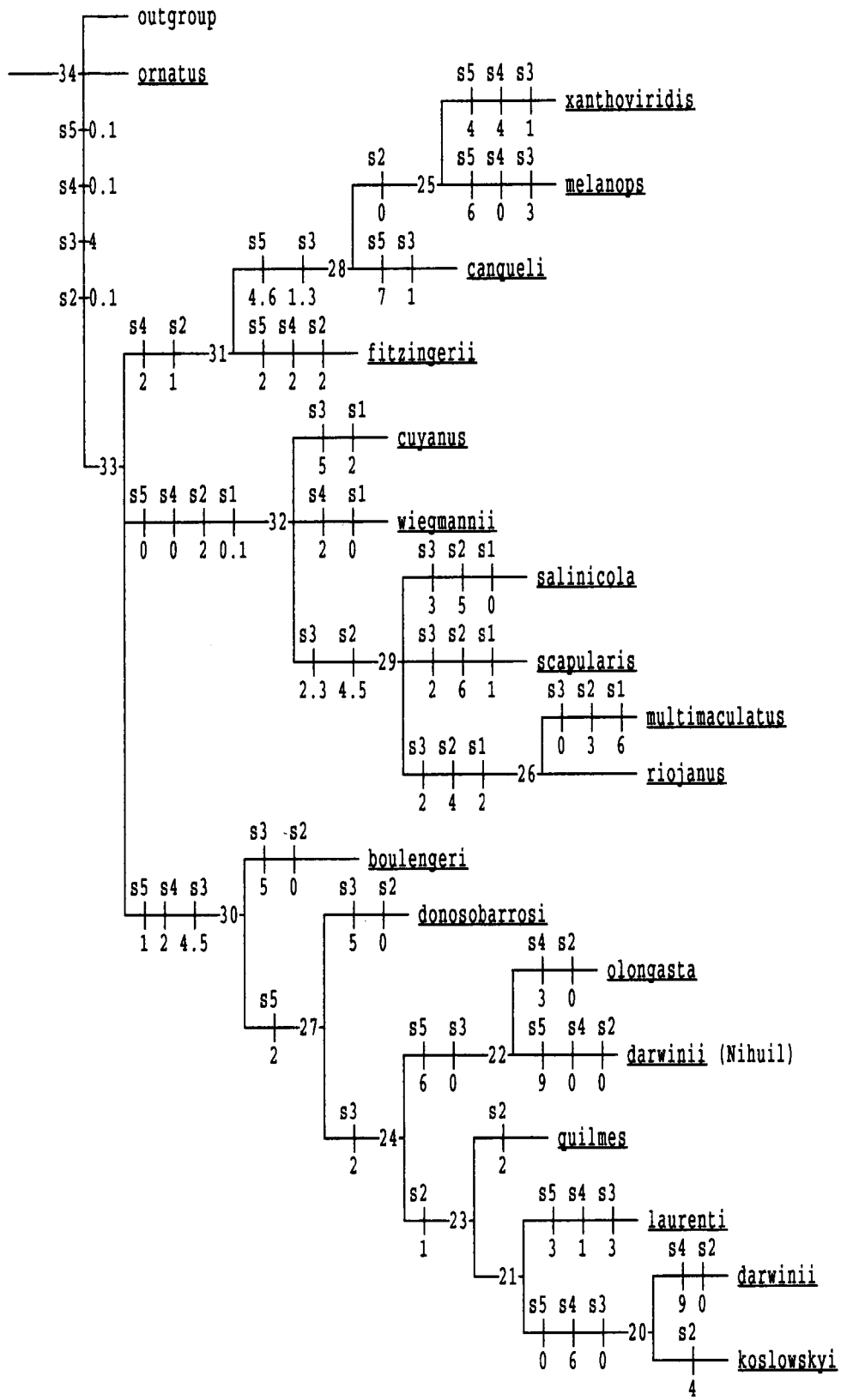

outgroup
ornatus
xanthoviridis
melanops
canqueli
fitzingerii
cuyanus
wiegmannii
salinicola
scapularis
multimaculatus
riojanus
boulengeri
donosobarrosi
olongasta
darwinii (Nihuil)
quilmes
laurenti
darwinii
koslowskyi

Figure 23. g. Consensus tree for the behavioral characters **r1**, **r2**, **a1**, and **a2** (details in Methods).

r1: (0) did not reach first stop in < 13 s

(9) reached first stop in < 13 s

r2: (0) did not reach first stop in 13-32 s

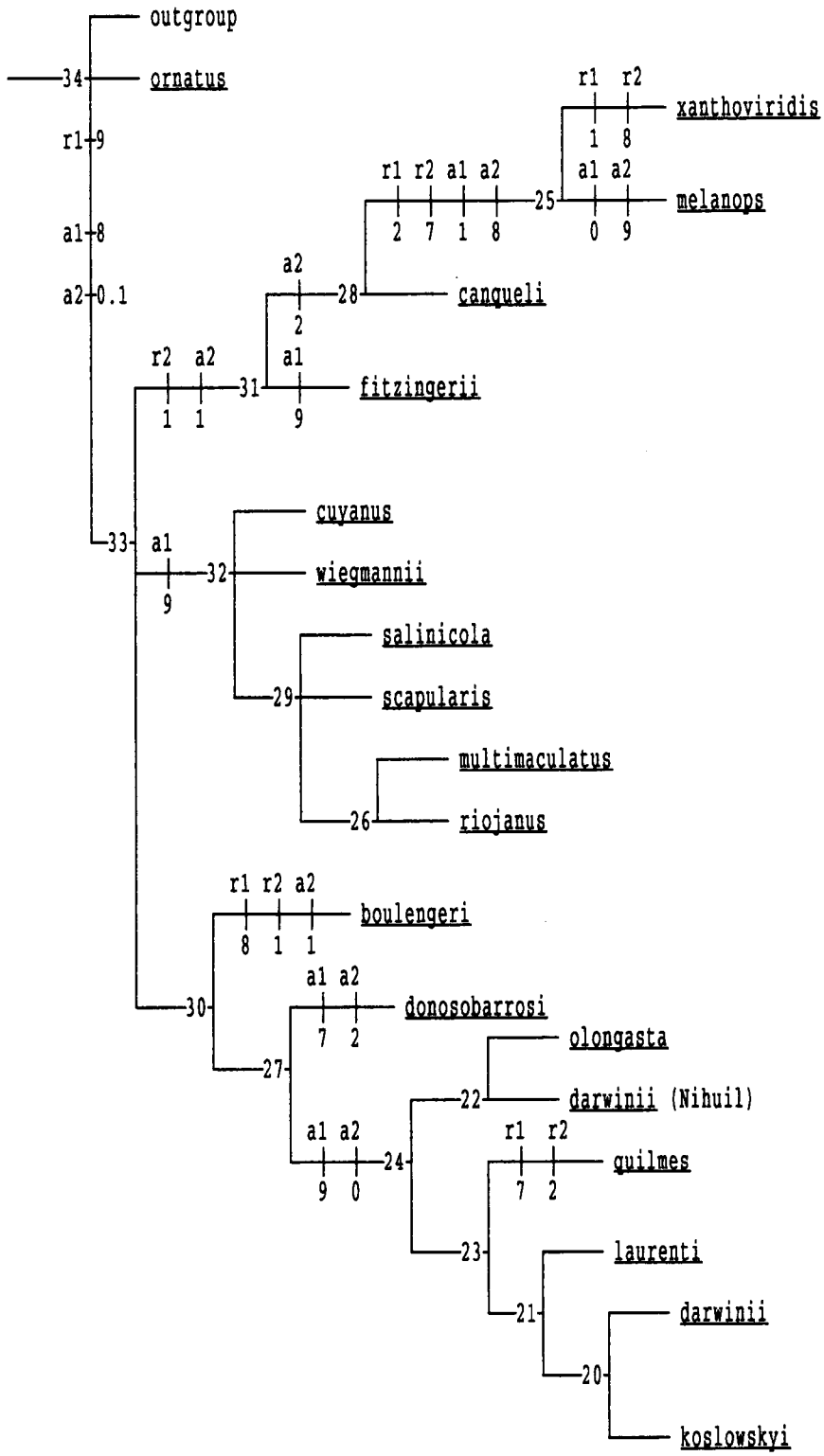
(9) reached first stop in 13-32 s

a1: (0) was not active during < 40 s

(9) was active during < 40 s

a2: (0) was not active between 40-118 s

(9) was active between 40-118 s


outgroup
ornatus
xanthoviridis
melanops
canqueli
fitzingerii
cuyanus
wiegmannii
salinicola
scapularis
multimaculatus
riojanus
boulengeri
donosobarrosi
olongasta
darwinii (Nihuil)
quilmes
laurenti
darwinii
koslowskyi
34
r1
9
a1
8
a2
0.1
33
a1
9
32
29
26
30
27
22
24
23
21
20
25
28
2
31
r1 r2
1 8
a1 a2
0 9
r1 r2 a1 a2
2 7 1 8
a2
2
r2 a2
1 1
a1
9
r1 r2 a2
8 1 1
a1 a2
7 2
a1 a2
9 0
r1 r2
7 2

which corresponds to the darwinii complex, sensu Etheridge (1993, i. e., L. darwinii, L. darwinii Nihuil, L. koslowskyi, L. laurenti, L. olongasta, L. quilmes). The increase in frequency of the digging behavior to 100% constitutes a synapomorphy for this complex.

sc: scratching before entering the sand is most typical in stem 32 and occurs at different frequencies (up to 80% of the time in L. wiegmannii and L. scapularis) except in L. multimaculatus. Scratching occurs only about 20% of the time or less in two species of stem 31, L. xanthoviridis and L. melanops. It is also observed in L. boulengeri and L. donosobarrosi (stem 30, 20%) but it is lost in the darwinii complex (stem 24).

bm: back movement before entering the sand seems to have arisen independently 3 times, in stem 31, in stem 29 (where it could constitute a potential synapomorphy for species in those 2 stems), and in L. boulengeri (where it might be a potential autapomorphy, although the frequency is low, 10%). All species of stem 31 show this behavior at different frequencies going from 10% in L. melanops to 50% L. canqueli. This behavior also occurs in stem 32 (30% in L. salinicola and L. multimaculatus, to 50% in L. riojanus).

bs: back stepping before entering the sand is characteristic of species of stem 29 forming a second synapomorphy. It

occurs between 30% (L. scapularis) and 60% (L. multimaculatus) of individuals of a species. Back stepping does not occur in the other two branches.

Analysis of characters in, lm and pl (Fig. 23b)

in: introducing the head straight in the sand is typical of species of stem 30 and constitutes a synapomorphy for species in this stem. It does not occur in stem 32 and it occurs at different frequencies in stem 31 (from 30% in L. xanthoviridis to 70% in L. melanops and L. fitzingerii). This character seems to have arisen twice, once in stem 31 and another time in stem 30. It forms a synapomorphy for species in stem 30 and appears to be one for species in stem 31 ("appears" since species in this stem show different frequencies for this behavioral pattern).

Since stems 30, 31 and 32 form an unresolved tritomy in the consensus tree, "in" could also be a potential synapomorphy for a clade consisting of stems 30 and 31. In fact, stems 30 and 31 are joined in 3 of the 4 trees found in the cladistic analysis (trees 1, 2, and 3, shown in Figs. 22b, 22c, and 22d, respectively).

lm: lateral movement of the head when entering the sand does not occur in species of stem 30 nor in stem 32 except in L. cuyanus where it constitutes an autapomorphy. This seems to be a case of parallelism since this behavior is also present

in species of stem 31 (from 20% in L. melanops to 60% in L. xanthoviridis).

pl: plunging into the sand appears in L. wiegmannii (10%) in stem 32 and then increases to 90% in the 4 derived species on this branch (stem 29) constituting a synapomorphy for species on stem 29. The only other case where plunging was observed is in L. boulengeri. It occurs in 10% of the cases.

Analysis of characters ct, fo, rt and lr (Fig. 23c)

ct: tail in contact with surface when burying, first appears in stem 33 (the ingroup less L. ornatus). Its frequency then increases or is lost in the 3 major stems (31, 30, and 32). For example, in stem 31, it is lost in L. fitzingerii but it reappears in L. canqueli (40%), increases in L. xanthoviridis (60%) and decreases in L. melanops (20%).

In stem 32, this character is present mostly in the 4 more derived species (stem 29, from 50% in L. scapularis to 90% in L. multimaculatus and L. riojanus), only 10% in L. wiegmannii and not at all in L. cuyanus.

Finally, in stem 30, "ct" increases to 80% then to 90% (stem 27) forming a potential synapomorphy for all the species on stem 30.

fo: the tail following straight the body as it enters the sand is typical of species of stem 30 starting with 50% in

L. boulengeri, increasing to 60% in L. donosobarrosi, and to 90% in the 5 species of the darwinii complex (stem 24) forming thus another synapomorphy for this group. Tail following does not occur in stem 32 and it occurs in 20% of the cases in stem 31. This behavioral character might have arisen independently in stems 31 and 30 but it may also be another potential synapomorphy for a clade containing both stems as observed in trees 1 to 3 (Figs. 22b-d).

rt: retrieval or pulling in of the tail is characteristic of species of stem 31 but it also seems to have arisen independently in L. boulengeri and L. donosobarrosi of stem 30 (only 20%), a possible case of parallelism or it might give further support for a clade consisting of stems 31 and 30 as obtained in trees 1-3 (Fig. 22b-d). The behavioral character "rt" does not occur in stem 32.

lr: lashing left-right movement of tail when lizard buries is a major synapomorphy for the species of stem 32. It does not occur in the other two branches except for a few cases (10%) in L. boulengeri.

Analysis of characters for first stop at **mb**, **bt**, **mt** and **cl** (Fig. 23d)

mb: first stop at midbody, is most characteristic of species of stem 30 going from 50% in L. boulengeri and L. quilmes to 90% in L. darwinii Nihuil and L. darwinii. In stem 31, the

situation is intermediate, going from 40% in L. xanthoviridis to 70% in L. melanops and L. canqueli. It occurs only in 10% of L. wiegmannii and not at all in the other species of stem 32. This is another character that could link species from stems 31 and 30.

bt: first stop at the base of the tail occurs in the three branches to varying degrees although it seems more frequent in species of stem 32 (from 20% in L. riojanus to 70% in L. wiegmannii). In stem 31 it occurs from 20% in L. melanops to 50% in L. fitzingerii and L. xanthoviridis. In stem 30, "bt" is lost in L. darwinii Nihuil and in L. darwinii but goes up to 50% in L. quilmes.

mt: first stop at midtail, occurs only in stem 32 from 20% in L. cuyanus and L. scapularis to 50% in L. riojanus. It is lost in L. wiegmannii and L. multimaculatus.

c1: completely covered at the first stop also occurs only in stem 32 from 10% in L. scapularis to 60% in L. multimaculatus. It does not occur in L. wiegmannii and L. salinicola of this branch nor in the other two branches.

Analysis of characters for final stop at **pc** and **cc**

(Fig. 23e)

pc: partly covered at final stop, is characteristic of species in stem 30 going from 20% in L. boulengeri and L.

donosobarrosi to 90% in L. laurenti and L. darwinii. It does not occur in the other two branches.

cc: completely covered at final stop constitutes a synapomorphy of the ingroup minus L. ornatus (stem 33). It may constitute a synapomorphy for species of stem 31 and for those of stem 32 or it may constitute a synapomorphy for a clade containing both these stems (see Fig. 22a).

This character diminishes in frequency in species of stem 30 going from 70% in L. boulengeri and L. donosobarrosi to 0% in L. laurenti and L. darwinii. Its frequency first decreases then increases in L. olongasta (60%) and decreases in the rest of species on this stem.

Analysis of characters for number of stops: s5, s4, s3, s2, and s1 (Fig. 23f)

s5: a total of 5 stops does not occur in stem 32 but it does occur in the other 2 branches. In stem 31 it occurs from 20% in L. fitzingerii to 70% in L. canqueli. In stem 30 it appears with a frequency of 10% in L. boulengeri and increases to 90% in L. darwinii Nihuil but then is lost in L. darwinii and L. koslowskyi. This character may have arisen independently but it may also form a potential synapomorphy for stems 31 and 30 (see trees 1 to 3, Figs. 22b-d).

s4: except for L. wiegmannii (20%), a total of 4 stops does not appear in stem 32. In species of stem 31, it occurs in 20% of the cases except in the 2 end species. In L. melanops, the frequency of this behavioral character is lost (0%) whereas as in L. xanthoviridis the frequency increases to 40%.

In stem 30, there is a tendency of increasing frequency (20% in L. boulengeri and L. donosobarrosi to 90% in L. darwinii), the exception being L. darwinii Nihuil (0%) and L. laurenti (10%).

s3: a total of 3 stops, is synapomorphic to the ingroup less L. ornatus (stem 33, 40%). It tends to decrease in stem 31 (30% in L. melanops to 10% in L. xanthoviridis and L. canqueli) and in stem 30 (50% in L. boulengeri and L. donosobarrosi to 0% in L. darwinii, L. koslowskyi, L. olongasta, and L. darwinii Nihuil). However, in species of stem 32 it occurs between 20% in L. scapularis and L. riojanus, and 50% in L. cuyanus, the only exception being L. multimaculatus (0%).

s2: a total of 2 stops occurs mostly in species of stem 32 (20% in L. cuyanus and L. wiegmannii to 60% in L. scapularis). It practically does not occur in the other two branches. In stem 31, it occurs 20% in L. fitzingerii, it

decreases to 10% in L. canqueli and it is lost in L. xanthoviridis and in L. melanops. In stem 30, the frequency changes back and forth between 20% in L. quilmes, 10% in L. laurenti, and 40% in L. koslowskyi, all the other species being 0%.

s1: burying in only one stop, occurs only in species of stem 32 and only in L. scapularis (10%), L. cuyanus and L. riojanus (20%), and in L. multimaculatus (60%).

Analysis of characters related to time recordings:

r1, r2, a1, a2 (Fig. 23g)

r1: lizards reaching the first stop in less than 13 seconds, is a synapomorphy for the ingroup minus L. ornatus (stem 33) except in species of stem 31 where it is almost completely lost in L. xanthoviridis and L. melanops where most lizards do not reach the first stop in less than 13 seconds.

r2: lizards reaching the first stop in 13 seconds or more, is a synapomorphy of two species in stem 31, i. e. L. xanthoviridis and L. melanops. Otherwise it generally does not occur except at low frequencies such as in L. fitzingerii (10%).

a1: lizards being active less than 40 seconds, is another synapomorphy of the ingroup minus L. ornatus, the exception being once more L. xanthoviridis and L. melanops of stem 31

which take more than 40 seconds to bury. There are slight variations in frequency in species of stem 30 but the general pattern is the same, i. e. most lizards are actively burying in less than 40 seconds.

a2: lizards being active more than 40 seconds, is a synapomorphy of the same two species of stem 31 as for character "r2", i. e. L. xanthoviridis and L. melanops. Otherwise it generally does not occur except at low frequencies such as in L. canqueli and in L. donosobarrosi (20%).

PART IV

DISCUSSION

CHAPTER 1

VARIABILITY IN SAND BURYING LIZARDS

Three different modes of entering sand were identified. The corresponding behavioral patterns of each burying style were very consistent and stereotyped within species indicating that they could be used as diagnostic characters in a phylogenetic analysis.

The only behavioral character subset that showed variability on some occasions, and that was not due to chance alone (see next section), was the one related to Time Recordings (see Chapter 2, Part II, for definitions). Variability occurred between two populations of one species, L. scapularis, and between adult and neonate L. melanops, with respect to the behavioral category Time One, time taken in seconds to first stop. These results suggest that Time One might not be as reliable a character as the other behavioral characters if it were used in a phylogenetic analysis. However, because this trait was consistent in other species and in other conditions it was considered adequate for this type of analysis pending the fact that any interpretation based on this trait remain somewhat uncertain (see next Chapter).

Intraindividual Variability

Behavioral patterns were very consistent within individuals (short and long term variation, Table 3). Even when tested several months later, lizards (adults and more importantly neonates) used the same behavioral patterns. The two significant differences observed in L. fitzingerii and L. xanthoviridis (Table 3) occurred in two behavioral characters (#S and T1) that may be susceptible to a lizard's general condition or to an environmental factor (such as small temperature fluctuations) or a combination of both.

However, these differences might also have occurred just by chance. Sixty comparisons were made in this condition (Table 3). Two significant differences were found. If a p-level of .05 is accepted, as was the case, this indicates that one significant difference could be obtained just by chance for every 20 comparisons. The two significant differences found here in 60 comparisons are well within chance level. Furthermore, the two significant results go in opposite direction giving more support to the idea of chance as a factor. Liolaemus fitzingerii made significantly fewer stops in the first test whereas L. xanthoviridis was slower in the first test.

Context Variability

The burying behavior was very consistent and stereotyped whether the lizard buried in "yellow" or in

"red" sand. Two significant differences were found, one in L. salinicola with respect to character T1 and the other in L. scapularis with respect to character LO (Table 4). However, the trend is not clear. Because "red" sand is a little coarser than "yellow" sand (Fig. 14), it could be expected that lizards would be relatively slower in the "red" sand. This seems to be the case for L. salinicola which was significantly faster in "yellow" sand than in "red" sand. But the difference is not clear in L. scapularis since the difference is in character LO, which is location on body at first stop. Liolaemus scapularis stopped significantly more often at the base of the tail in yellow sand and was significantly more often completely covered in red sand. Again, these results might be due to chance alone (see previous section). Three significant differences could be found just by chance when doing 60 comparisons and there were 65 comparisons in this condition (Table 4).

Consistency in the behavioral patterns used whether burying in yellow or in red sand suggests two things. First, behavioral characters were not affected by the type of sand. Second the difference in grain size between the two types of sand was probably not great enough to observe a slower entrance into the coarser-type sand (except for the one significant difference in L. salinicola).

"Medium sand", formed by particles of approximately 0.50 to 0.25 mm (Buckman and Brady, 1969; the "red" type sand in this study), is apparently a type of sand in which lizards readily bury. In his study on the ecology of Uma, Stebbins (1944) used sand taken from the lizards' habitat. This sand contained 75% of particles slightly less than 0.5 mm in diameter. Hetherington (1989), for his part, used a commercially obtained sand with grain size ranging from 0.6 to 0.2 mm to study prey detection in the sand-swimming Scincus scincus.

Pough (1970:148-149) observed that the grain size preferred by adult lizard Uma notata had a modal grain diameter of 0.5-0.25 mm ("medium sand", Buckman and Brady, 1969), whereas hatchlings preferred "fine sand" (0.25-0.12 mm) and small adults were intermediate. Preference seems to have been established based on whether or not a lizard buried in a certain type of sand. Actual speed of burial was not reported.

In other experiments, Pough (1970) found that adults were slow to bury in sand with a modal diameter of 2.0-1.0 mm ("very coarse sand", Buckman and Brady, 1969) and frequently did not bury in sand of 0.25-0.12 mm modal diameter ("fine sand", Buckman and Brady, 1969). Stebbins (1944:314), writing on Uma, also found that "sand composed of particles greater than 2 mm in diameter is generally

avoided". It is possible that sand burying species of Liolaemus would also not bury into "very coarse" sand, although this was not tested, but they readily buried into "fine sand" (the "yellow sand").

In another article, Pough et al. (1978) specify the modal size grain for two locations (0.25 to 0.125 mm and 0.50 to 0.25 mm, similar to the modal size grain of the two types of sand used in this study) to be used in a study on Uma exsul. Unfortunately, the authors did not specify whether the lizards showed a preference for one type of sand over the other or if they were quicker in one type of sand. It is possible that no noticeable differences were observed, as was the case in this study with similar sized-grain sands.

Lizards of several species of the boulengeri group (e.g., L. scapularis) scratch the surface of the sand before burying. This may give them an indication of soil type, looseness of particles and grain size and thus help them determine whether it is appropriate or not for burying. Stebbins (1944) and Pough (1970) found that lizards belonging to the genus Uma "avoided" or "preferred" certain sand types depending on grain sizes. It would be interesting to know if these lizards had "tested" the surface by scratching it or by some other means before burying.

To conclude, behavioral characters used in burying were consistent even though the context had changed. This gave

further support for their use in a phylogenetic analysis. Although sand burying on any of the two types of sand could have been used in the Phylogenetic analysis, only the information obtained on the yellow sand was used in order to minimize the effect of characters corresponding to Time Recordings (see previous section). As mentioned earlier (Chapter 1, Part II), yellow sand was preferred over red sand because it was a more typical sand dune type sand and because it was the type of sand more commonly found in many of the habitats where lizards for this study were found.

Variability between Males and Females

No differences were found between males and females with respect to any of the behavioral characters considered in Table 5. Although males and females may differ in other behavioral patterns, such as in behaviors related to courtship (e.g., Carpenter and Ferguson, 1977), burying behavioral patterns were the same in males and females within a species.

Variability among Populations within a Species

Populations were compared within three different species (Table 6). Lizards did not differ with respect to 4 of the 5 behavioral characters used. The exception was T1, time in seconds taken to first stop. This difference occurred between two populations of L. scapularis. Lizards

from the population CF (Cafayate, Salta) were slower than lizards coming from the population PZ (Pozuelos, Catamarca). This was somewhat surprising, because if a difference had been expected, it would have been the reverse, that is, lizards from the Cafayate population would have been expected to be faster than those from Pozuelos. This is because the Cafayate population's habitat is characterized by sand dunes with loose sand whereas at the Pozuelos site, although there may be loose sand, there are no sand dunes. It is interesting to note that lizards from the third population of L. scapularis, PM (Pie de Medanos, Catamarca), is intermediate in time taken to first stop and is also intermediate geographically.

Geographical variation among populations of a species is not unusual and may indicate an incipient speciation process. Ferguson (1971) found geographical variation in the display rituals of the side-blotched lizard, Uta stansburiana. In garter snakes, Burghardt (1970) found intraspecific geographical differences in the specific chemical stimuli that elicited the basic behavioral patterns involved in the attack of prey. Arnold (1977), for his part, established that the coastal populations of Thamnophis elegans eat slugs whereas inland populations refuse them. Nevertheless, both populations of T. elegans accept anurans.

Variability between Adults and Neonates

Adult and neonate L. melanops differed significantly with respect to one character, T1, time taken to first stop. As mentioned before, this character seemed to be the most affected by variability. In this case, weight is possibly an important factor, since neonates, which are 12 to 20 times lighter than adults, were also significantly quicker.

It is not clear whether a developmental factor may be involved in another character MT, movement of tail. Although adult L. melanops all retrieve their tail to get completely covered (Fig. 23c), the three types of tail movement were observed in the neonates, i.e., FO (tail following straight), RT (tail retrieval as in adults), and also LR (tail lashing). Too little data are available for an interpretation at this point.

Experience might be involved. An example in which experience was found to be a factor in a reptile study is in prey handling in garter snakes species, Thamnophis (Halloy and Burghardt, 1990). Although the general feeding pattern was present at birth, experience affected prey handling efficiency in some species more than in others. Schleidt and Shalter (1973) found that chicks of the European quail, Coturnix c. coturnix, that were a few hours old emitted a call that occurred in adult males (presumably to attract females and repel competitors). The appearance of the call

was very similar in both the chick and the adult male although higher pitched in the former.

Neonate L. melanops buried as soon as loose sand was provided and the pattern used generally concurred with that of adults except for character MT, movement of tail. That the neonate generally used the same behavioral pattern as the adult was also observed in two other species for which I had neonates. Because I had only one individual of each species, no statistical comparisons were made. One neonate, L. xanthoviridis, was tested on sand only once. It died shortly after. This individual buried leaving its tail out. The other neonate belonged to Liolaemus canqueli. It was tested several times over several months. Its behavioral pattern mimicked that of the adult, including retrieval of the tail, location at first stop (generally the midbody) and the number of stops (generally 5 stops).

Neonates belonging to species of the outgroup (L. andinus, L. huacahuasicus, and L. ruibali), however, did not bury. Although some digging was observed when they were placed on loose sand they did not get covered by sand and neither had adults.

Klauber (1939:91) writes of a Phrynosoma orbiculare hernandesi, from Arizona, giving birth to 27 young and these tried "rather ineffectually, to bury themselves in the sand". Unfortunately, the author did not describe the

burying behavior of the adult nor how or why was the newborn's burying behavior "rather ineffectual". Klauber argued that this species should be considered one with P. douglassii. I had the opportunity to observe an adult male P. douglassii from northeastern Colorado, which was very "ineffectual" in the way it buried. By this I mean it made many stops, barely got covered (often sections of head or body could be seen), and although it used the swinging-kind of motion of the head observed in some Phrynosoma (e.g., P. modestum, Arnold, 1994a; P. platyrhinos, Klauber, 1939, and pers. obs.) it did not use the rocking movement of the hind legs observed in the latter species but pushed its way into the sand very close to the surface. The end result seemed less "efficient" than what had been observed in other sand burying lizards. Thus, the "inefficiency" observed by Klauber in the young, may well be just the way these lizards bury. Of course, systematic observations of burying behavior of both adults and neonates would be needed to support this idea.

Carpenter (1967b) suggested that stereotyped behavioral characters in lizards are inherited. Evidence for stereotypy of behavioral characters has often been shown (e.g., head bobs in lizards tend to follow a very stereotyped temporal pattern, Jenssen, 1977). Cooper (1971) observed head bobbings in hatchling Anolis carolinensis in the first few

minutes of life. He discarded learning as a possibility since the behavior occurred when no other subjects were present and concluded that the display was probably innate. Stamps (1978:27) studied spacing behavior displays and aggression in hatchlings, juveniles and adults of Anolis aeneus. She found that, "Temporal elements of the species specific bob pattern are very stereotyped in both juveniles and adults" and that hatchlings a few days old, "have nonoverlapping home ranges or participate in dominance hierarchies". Cogger (1978:666) found that head bobbing was "remarkably stable" in Amphibolurus fordi (Agaminae) and that the behavioral pattern was present in hatchlings. In a longitudinal study of display behaviors, Roggenbuck and Jenssen (1986:153) observed 36 fence lizards, Sceloporus undulatus, from 8 different clutches. They found that hatchlings "possessed almost all of their adult display patterns by the first two days of life."

In colubrid snakes, Burghardt (e.g., 1967, 1970) found that the basic behavioral patterns involved in the attack of prey are present at birth and are probably genetically coded. The consistency of the behavioral patterns used in sand burying in lizards of the boulengeri group suggests that these too are innate and species-characteristic, giving further support for their use in a phylogenetic evaluation.

CHAPTER 2

THREE BURYING MODES IN THE BOULENGERI GROUP: A PHYLOGENETIC EVALUATION

Three burying modes were observed among 18 of the 19 species of the boulengeri group. The descriptive information (e.g., Figs. 17 to 21) matches well the consensus tree obtained from a cladistic analysis of characters (Figs. 22 and 23). Results also generally agree with the indented classification proposed by Etheridge (1995) based on morphological evidence (see Chapter 3, Part I).

Entering the sand, whatever the particular method, seems to be the major behavioral synapomorphy for the species of the boulengeri group except for L. ornatus that did not enter loose sand. Eight specimens of L. ornatus had been tested (4 males and 4 females) on sand in the same conditions as all the other lizards, but none had buried. Although digging was observed in the corners of the test aquarium, they did not attempt to enter loose sand. This suggests that, based on behavioral information alone, this species might be misplaced and could belong in the functional outgroup with L. andinus, L. huacahuasicus, L. multicolor, and L. ruibali which all dug burrows but did not enter loose sand. However, this is not supported by the

morphological data (Etheridge, 1995) and further research is needed.

Within the boulengeri group, Etheridge (1995) recognized a subset of 9 species as the wiegmannii subgroup, based on sublabial-mental contact and smaller, more numerous lorilabials. A cladistic analysis based on behavioral characters also finds species of this subset clustered together (species on stem 32, Fig. 23) with the additional species L. cuyanus, the major synapomorphy of this subgroup being "tail lashing". Whether L. cuyanus belongs to this subset needs further investigation as discussed below.

In addition, results obtained discriminate among the non-wiegmannii subgroup species within the boulengeri group suggesting two subgroups of species (stems 31 and 32, Fig. 23) or one clade containing species in these two stems (Fig. 22, trees 1 to 3). These agree in part with the darwinii complex proposed by Etheridge (1993) and to the fitzingerii complex (Etheridge, pers. comm.). The difference lies in that L. boulengeri and L. donosobarrosi, instead of being associated to the fitzingerii complex (Etheridge, 1993), are associated to the darwinii complex. This indicates that more research is needed in this area in order to find the best supporting characters for different species associations.

Arnold (1994a:154, 160) suggests that "sand diving" (a term he used in a similar way that "sand burying" has been used here) has evolved at least nine times in surface-dwelling lizards belonging to six different families. These are the families Chamaeleonidae (subfamily Agaminae), Cordylidae, Lacertidae, Phrynosomatidae, Scincidae, and Tropiduridae (to which the genus Liolaemus belongs).

As summarized in Chapter 1, Part I, Arnold (1994a, 1995) described five methods of entering the sand for five of the 6 families, methods which, according to phylogenetic information, arose independently. The author did not have information available on sand burying in species belonging to the Tropiduridae. Here I will first review the results obtained on observations of sand burying in the boulengeri group, without L. ornatus (combining descriptive and cladistic results) after which I will cite the 5 methods of sand burying observed by Arnold (1994a, 1995) in 5 families of non-tropidurid lizards to compare to species of the boulengeri group (less L. ornatus).

Behavioral Characters that Support the Different Groupings of Species within the boulengeri Group (Figs. 22 and 23)

Before describing the different possible species associations, it is important to note that clades that are diagnosed on the basis of changes in the frequency of a character are considered to be very weakly supported if a

change of only 10 to 20% has occurred, weakly supported if a change of about 30 to 50% has occurred, and well supported if a change of 60% or more has occurred.

Species of the Liolaemus boulengeri group without L. ornatus (stem 33, Fig. 23):

1. Digging is partly lost (Fig. 23a).
2. Scratching before entering the sand is observed to a lesser or greater extent (varying frequencies) with no scratching observed in the darwinii complex (sensu Etheridge, 1993, Fig. 23a, stem 24).
3. Tendency (30-40% of individuals) to stop at the base of the tail at their first stop when entering sand (Fig.23d) although frequencies vary among species.
4. Most lizards get completely covered although this is partly lost in species of stem 30 (Fig. 23e) and completely lost in 2 species of the darwinii complex (L. laurenti and L. darwinii).
5. Tendency (40% of individuals) to make a total of 3 stops before settling for the night (Fig. 23f) although there is a lot of variation among species.
6. Most species enter the sand to their first stop in less than 13 seconds, and are not active more than 40 seconds (Fig. 23g). The exceptions are L. melanops and L. xanthoviridis.

Species L. cuyanus, L. wiegmannii, L. salinicola, L. scapularis, L. multimaculatus, L. riojanus (stem 32, Fig. 23)

This branch contains the wiegmannii subgroup (sensu Etheridge, 1995) plus L. cuyanus whose status in the boulengeri group with respect to the other species, is unclear (e.g., Laurent, 1995). This branch seems to be supported by:

1. Lack of digging (Fig. 23a).
2. Frequency of scratching increases (Fig. 23a) although it appears to be lost in L. multimaculatus.
3. Lashing of the tail (Fig. 23c).

Species Liolaemus cuyanus

Liolaemus cuyanus (stem 32, Fig. 23) remains a problem. Based on the behavioral analysis, it would seem to be associated with the wiegmannii subgroup (sensu Etheridge, 1995). The synapomorphy that relates L. cuyanus with species of the wiegmannii subgroup is lashing of the tail (Fig. 23c). It is basically the only synapomorphy, albeit an important one if it is considered that it occurs in all individuals of all the species on stem 32.

Liolaemus cuyanus moves its head laterally when it enters the sand compared to plunging observed in species of the wiegmannii subgroup. This behavior (lateral movement of

the head) is observed in species of stem 31. Because of the phenetic similarity of L. cuyanus to L. canqueli, L. fitzingerii, L. melanops and L. xanthoviridis, Cei (1986:87) had recognized what he called the fitzingerii group which included the above 5 species. Laurent (1983a, 1984, 1995) agrees with placing L. cuyanus in the fitzingerii group (sensu Cei, 1986) although he acknowledges the difficulty of doing so due to "intermediate characters" (1983a:9). Because of this, Laurent suggests that this species might stand out on its own. However, new information on morphological characters seems to associate this species to the wiegmannii subgroup (Etheridge, pers. comm.). The behavioral analysis would seem to support this later development.

Species L. salinicola, L. scapularis, L. multimaculatus, L. riojanus (stem 29, Fig. 23)

Within stem 32, the grouping of 4 species seems well supported by the following behavioral characters:

1. Back movement before plunging into sand (Fig. 23a). This behavior occurs also at similar frequencies in species of stem 31 but in the latter case it is immediately followed by lateral movement of the head whereas species of stem 29 thrust forward their head into the sand.

2. What is unique to the four species of stem 29 and seems to have arisen in this clade only, is back stepping before plunging into sand. It is possible that back stepping

facilitates the forward thrust into sand. It also might explain in part the fact that these species are generally quicker to enter and move into sand than other species. Three of the four species on stem 29 have the smallest averages for TIME ONE (Fig. 15), L. riojanus, L. salinicola, and L. multimaculatus from quickest to slowest. Liolaemus scapularis is also quick but it is sixth. When considering ACTIVE TIME, all four species have the lowest averages (Fig. 16), the quickest being L. multimaculatus, followed by L. riojanus, L. salinicola and L. scapularis.

3. Plunging is characteristic of species of stem 29 (Fig. 23b). Although it also occurs in L. wiegmannii, the frequency is very low. This might indicate a rudimentary stage of this behavior in this species. However, plunging is also observed in a species on another stem, L. boulengeri (stem 30). In this case, the character shows homoplasy and there might be a process of convergence or parallelism. However, the frequency being so low, any interpretation can only be uncertain.

4. Another evidence that the species of stem 29 are quick is that they take fewer stops to get completely buried when compared to species on the other stems. Generally, they are covered in only one to two stops.

Species L. fitzingerii, L. canqueli, L. melanops, L. xanthoviridis, L. boulengeri, L. donosobarrosi, L. olongasta, L. darwinii (Nihuil), L. quilmes, L. laurenti, L. darwinii, L. koslowskyi (stems 31 and 30, Fig. 23)

Several behavioral characters seem to support a clade with both stems (such as trees 1 to 3 in Fig. 22b-d). This would be in accordance with Etheridge's indentation (1995) in which species from stem 31 and 30 are not discriminated, the exceptions being L. ornatus which did not dig and L. cuyanus which appears related to the wiegmannii subgroup.

1. Introducing head into sand (Fig. 23b) is characteristic of species of stem 30 but it is also characteristic of species of stem 31, although the frequencies are lower and another method of entering the sand appears, i. e. the lateral movement of the head.

Although frequencies vary, the lateral movement of the head appears to be a synapomorphy for species of stem 31 separating them from species of stem 30. One other species exhibited lateral movement of the head as it entered the sand, L. cuyanus associated to species of stem 32. This might be a case of parallelism.

2. The general tendency for species in stems 31 and 30 is for reaching midbody at first stop (50%, Fig. 23d). Species of stem 32 go further before stopping the first time, i. e. to the base of the tail.

3. Species on stems 31 and 30 tend to make 3 or more stops before settling for the night (Fig. 23f) more than species on stem 32 (that tend to do 1 or 2 stops only).

Species L. fitzingerii, L. canqueli, L. melanops, L. xanthoviridis (stem 31, Fig. 23)

This is the clade that is perhaps the most weakly supported because several of the behavioral characters that appear in stem 31 also appear in stem 32 and/or stem 30 although at different frequencies. However, two characters seem to well support this clade.

1. Lateral movement of the head (Fig. 23b) is observed only in species of stem 31 with the one exception mentioned earlier, L. cuyanus.

2. Retrieval or pulling in of the tail in a final movement to get completely covered (Fig. 23c) is the second character that has been observed only in species of stem 31 with the exceptions of L. boulengeri and L. donosobarrosi. However, the frequency observed in the latter two species is very low (20%) and it would indicate the need for more behavioral observations in order to investigate how much more they might be related to species in stem 31, a hypothesis entertained by Etheridge (pers. comm., see comments on the fitzingerii complex in Chapter 3, Part I).

3. Within stem 31, two species, L. melanops and L. xanthoviridis form a derived dichotomy that is based on the

speed they take to enter the sand to the first stop and how long they are actively burying (Fig. 23g). These two species were observed to be slower than the rest of the species in those two characters. It is interesting to note that there is a small frequency of individuals in species L. boulengeri and L. donosobarrosi which also tend to be slower. Another case is L. quilmes. Since speed may be more affected by environmental factors (e.g., general condition of lizard at time of testing, temperature) than other characters used here (e.g., movement of the head or tail), as was discussed in the previous Chapter, it might be a weak character for interpretation of clade formation.

Species L. boulengeri, L. donosobarrosi, L. olongasta, L. darwinii (Nihuil), L. quilmes, L. laurenti, L. darwinii, L. koslowskyi (stem 30, Fig. 23)

Reaching midbody at first stop (Fig. 23d) and making 3 or more stops (Fig. 23f) were already mentioned as characters that species on this stem share with species on stem 31.

1. Introducing head straight into the sand is typical of species of this clade (Fig. 23b). Although this behavioral character is also present in species of stem 31, in stem 30 it is the only method of entering the sand with the exception of L. boulengeri where 10% of individuals were seen to plunge.

2. Tail is usually in contact with substrate in species of stem 30 (Fig. 23c). However, this behavioral character also occurs at varying frequencies in species of stem 29 and in most species of stem 31. This character might have arisen independently in each stem but it might also have been present in a common sand burying ancestor and different frequency losses are observed among different species.

3. Characteristic of species on stem 30 but mostly of species on stem 24 is tail following body as it enters sand (Fig. 23c). The only other species showing this character is L. fitzingerii on stem 31 but the frequency is low (20%).

4. Another characteristic in species of stem 30 is that they do not always get completely covered like species of stems 31 and 32 (Fig. 23e). This tendency of individuals being partly covered increases in frequency in species on stem 24 and particularly in species on stem 21.

Species L. olongasta, L. darwinii (Nihuil), L. quilmes, L. laurenti, L. darwinii, L. koslowskyi (stem 24, Fig. 23)

These species are within stem 30 and correspond to species of the darwinii complex (Etheridge, 1993). The darwinii complex seems to be supported by the following behavioral characters:

1. All species of stem 24 dig (Fig. 23a). This relates them to L. ornatus, also placed in the darwinii complex by

Etheridge (1993) and to species of the functional outgroup, L. andinus, L. huacahuasicus, L. multicolor, and L. ruibali. This may point to the primitiveness of this group of species since the plesiomorphic character "digging" is present in all individuals belonging to the outgroup.

2. All species of stem 24 show "tail following" (Fig. 23c). This may also point to the primitiveness of this group since no behavioral pattern has evolved to facilitate and speed up complete covering of the lizard, such as tail lashing or tail retrieval.

CHAPTER 3

SAND BURYING IN NON-TROPIDURID LIZARDS

From the discussion in the previous chapter, it is clear that there are three different burying styles among species of the boulengeri group: three styles, one genus. I suspect that there may be a fourth style in sand lizard species of Liolaemus that do not belong to the ingroup nor to the outgroup species considered in this study. These are the species that live on the beaches of the Pacific Ocean in Chile. Because data on these species are not reported here, it would be premature at this point to generalize the burying styles typical of species of the boulengeri group to other species of Liolaemus, to species of other genera, and even more so at higher taxonomic levels. Predictions could be attempted for other sand burying species of Liolaemus or at most for species belonging to other tropidurid genera, but not more than that.

For instance, I had occasion to observe 2 individuals from another tropidurid genus, Stenocercus doellojuradoi, (from Tucumán, Argentina), which were about the size of the bigger Liolaemus species used in this study. Preliminary results suggest that these lizards use a lateral movement of the head to enter the sand. Based on observations of species of the boulengeri group that use lateral movement of the

head, it might be expected that individuals of S. doellojuradoi might also retrieve their tail. Yet they do not, their tail follows straight. It might be expected that they might not get completely covered as species of the boulengeri group which keep their tail straight while burying and often do not get completely covered. Yet they get completely covered maybe because they bury deeper than the other species.

Arnold (1994a, 1995) tends to generalize from observations on a few species to the family level. Thus, he characterizes both the scincids and cordylids with the same type of burying behavior called "sand swimming" (described in Chapter 1, Part I). Nevertheless, there is indication in the literature that although overall patterns may be similar there are some important differences that might have important phylogenetic consequences in understanding the evolution of sand burying. These will be indicated later. In addition, Arnold (1994a, 1995) points to two burying styles within the Phrynosomatidae, represented by Uma and Phrynosoma. I suspect there are many more. I had occasion to observe two species of Phrynosoma, P. platyrhinos and P. douglassii. The first part of the burying movement involving the head is similar in both species, the last part involving the hind legs is not. Finally, Arnold (1994a, 1995) refers to two other burying styles each corresponding to a

different major taxon, the Chamaeleonidae (Agaminae) and the Lacertidae.

Although Arnold (1994a, 1995) may have generalized a little prematurely, his work is invaluable because it appears to be the first that consistently attempts to describe and interpret sand burying in lizards in a historical context. In order to follow his lead, I will now attempt to compare sand burying in the tropidurids (limited to burying styles observed within the boulengeri group) with the sand burying he observed in other lizard families. I will point out differences and similarities. Differences in burying styles, although occurring in similar habitat types, may point to lineage constraints whereas similarities may reflect processes of adaptations related to environmental conditions or possibly processes of exaptations (Arnold, 1994a, and see Chapter 1, Part I).

Species that Bury Differently than Species of the boulengeri Group

1. Phrynocephalus (Chamaeleonidae, Agaminae, central and south-west Asia, similar behavior observed in P. reticulatus, P. arabicus, and P. maculatus, Arnold, 1995): lizards descend vertically into the sand. "The body is flattened and oscillated laterally by alternate extension and contraction of the limbs on each side, and is tilted

downwards in the direction of each sideways thrust so that sand is pushed onto the back. The head and tail are subsequently buried separately by lateral movements" (Arnold, 1994a:154). Arnold (1995) finds that in Phrynocephalus the hind limbs are oscillated or vibrated laterally in a similar way to Phrynosoma modestum (see description below).

2. Scincus (Scincidae, Arabia and North Africa, observed in S. mitranus, Arnold, 1995) and Angolosaurus skoogi (Gerrhosaurinae, Cordylidae, southwest Africa, Arnold, 1995): lizards of these two families enter the sand in a similar way and Arnold (1994a, 1995) believes that this might indicate that the behavior arose in a common ancestor to both families. They "enter the sand head first, rapidly laying both pairs of hind legs along the flanks. After this they progress by rapid high-amplitude sinusoidal movement of the body, and swim through the sand rather like a fish in water" (Arnold, 1994a:155). These are what Pough (1970) called the "sand swimmers". Arnold (1995) notes that Angolosaurus submerges completely into sand in 1-2 seconds, faster than the quickest Liolaemus (Fig. 15 and 16).

According to Lang (1991), Angolosaurus skoogi is a highly derived member of the Cordylidae and although there is no phylogeny for the Scincidae, Scincus mitranus is also quite possibly a derived member of its family (Etheridge,

pers. comm.). Sand swimming in these two species appears to be derived and therefore is not likely to have arisen in a common ancestor of both families as Arnold (1994a, 1995) has suggested. Indication that sand swimming may have had independent origins in these two lizard families is also supported by the somewhat different description of sand swimming in Angolosaurus skoogi given by Steyn (1963:8, 10), "they swiftly disappear into the sand when disturbed... The depressed snout is pressed into the sand while digging with the forelimbs. The hindlimbs are used to push the body forwards, while the trunk and tail are swung rapidly and markedly from side to side in an alternating motion.... Angolosaurus skoogi thus practices a kind of sand swimming, which leaves practically no trace on the spot where the animal disappeared into the sand." The main differences between Arnold's and Steyn's descriptions seem to lie in the fact that the latter refers to use of limbs to help push the animal into the sand and refers to the tail swaying from side to side, which might be analogous to lashing of the tail seen in species on stem 32 (Fig. 23c), but which does not occur in Scincus mitranus. In addition, it has been reported in several species of sand swimming skinks that these leave tracks on the surface as they move under the surface (e.g., Chalcides sepsoides, Mosauer, 1932; Lerista bipes, Greer, 1989; Neoseps reynoldsi, Andrews, 1994)

whereas Angolosaurus skoogi does not, which is also the case for burying species of the boulengeri group.

Huey et al. (1974:304) give a description of sand swimming in two partially sympatric, legless skinks of the genus Typhlosaurus from the Kalahari Desert (T. gariepensis and T. lineatus). According to these authors, these two species are "almost completely subterranean but do not construct tunnels. They occasionally travel snake-like above ground for short distances, but normally move in a lateral sinuous path just beneath the sand." Although few descriptions of sand swimming species were found, there seem to exist differences in the way lizards sand swim in species from these two families. These differences may be related to historical constraints such as presence and size of limbs and shape of head.

None of the species of the boulengeri group show evidence for the behavioral patterns shown by the above species. The only similarity is that species of the boulengeri group (less L. ornatus) enter the sand head first as in Scincus and Angolosaurus skoogi. In addition, species of stem 32 (Fig. 23) may sway their tail in a similar way as A. skoogi if by swaying the author (Steyn, 1983) understands tail lashing as described here.

Species that Bury Similar to Some of the Species in the boulengeri Group

1. Meroles (Lacertidae, southwest Africa, similar behavior observed in M. cuneirostris, M. anchietae, and M. ctenodactylus, Arnold, 1995): "lizards dive head first into the sand using all their limbs, and flexing the head and body laterally into serpentine waves, the tail being buried by broad whip-like sweeps" (Arnold, 1994a:154). These lizards submerge in about 1 second, a little more than twice as fast than the quickest Liolaemus.

Species of the boulengeri group (less L. ornatus) also use all their limbs before burying but only species of stem 31 and L. cuyanus show lateral movement of the head (Fig. 23b) although this lateral movement is not accompanied by a great downward flexion of the head to almost a vertical position as described by Arnold (1995) for Meroles. The tail in Meroles is buried by "broad whip-like sweeps". Another species for which tail lashing is reported is in Cophosaurus texanus, Phrynosomatidae (called "tail wagging", Arnold, 1995:375). Tail lashing is typical of species of stem 32 (Fig. 23c).

An analogous behavior pattern observed in Meroles, is that, when not pursued (which is the case of lizards in this study), it usually took a few steps back before burying (Arnold, 1995:359). Arnold hypothesizes that this may ensure

the lizard that it is diving into loose sand. Species of stem 29 also took a few steps back before plunging (Fig. 23a). My impression was that back stepping helped the lizard gain the impulse necessary to dive quickly into the sand. It may have helped, in addition, to test the substrate but testing of substrate seems to have been obtained by scratching the surface, behavior observed in greater or lesser frequency in many species of stem 33 (Fig. 23).

Another lacertid that submerges into sand but for which only a partial description of its burying behavior is given is Aporosaura anchietae, from the Namib Desert. Louw and Holm (1972:81) describe its burying behavior thus, "it will disappear beneath the sand within a fraction of a second with a mere flick of the tail". The "flick of the tail" may refer to a "shimmy-type" burial as described for Uma (see further) or a lashing of the tail as in Meroles and as in species of stem 32. However, the description is too brief to be certain.

Another species that seems to slightly resemble Meroles in the way it buries is a skink, Mabuya acutilabris, whose burying behavior Arnold (1995:363) describes as being "quite different" from that of Scincus. In M. acutilabris, "The body is held more or less straight and the head is inserted in the substratum and either rocked around its longitudinal axis or moved laterally from side to side. As these small-

amplitude head movements take place, all four limbs are used to propel the animal quickly into the sand." The lateral movements of the head may be similar to lateral movements of the head observed in species of stem 31 and in L. cuyanus (Fig. 23b) but in these species the head is not rocked (as in Phrynosoma, see further) and these species also initially use their 4 limbs but soon place the front limbs along their flanks and propel themselves solely with the hind limbs.

2. Phrynosoma (e.g., P. modestum, North America): in these lizards, "the head is swung from side to side and then pushed under the surface, the forelimbs again being soon laid along the flanks as the lizard moves forward powered by the hind legs. Once the foreparts are buried, the hind quarters are rapidly oscillated from side to side, so that they sink vertically" (Arnold, 1994a:154). Another description of the burying behavior of Phrynosoma is given by Weese, cited by Mosauer (1932:74), " 'The snout is directed downward and moved from side to side, the body extremely flattened, while the legs take part in a rapid horizontally clawing movement'. This movement is aided by lateral vibrations of the posterior portion of the lizard's body extending to the tip of the tail. Simultaneously, however, the animal pushes itself forward, so that it comes to rest slightly ahead of the spot where the digging action had started."

Species of stem 33 (Fig. 23), the boulengeri group without L. ornatus, were not observed to use any of the elements used by Phrynosoma in burying into sand.

3. Uma (California and bordering Mexico, e.g., U. scoparia, Arnold 1995): these lizards bury into the sand head first but they do it a different way than Meroles, i. e., "the head is twisted rapidly about its sagittal axis like an awl and forward motion is largely produced by the hindlimbs, the forelimbs being quickly laid back along the flanks. Lateral movements are confined to low-amplitude waves passing from the head to the fore-body, which contribute to forward progress by moving the shoulders backwards and forwards alternately, so areas of large posteriorly-directed scales that they bear act like a pair of ratchets. Finally, the distal tail is concealed by a very rapid, small-amplitude vibration" (Arnold, 1994a:154). This has been called "shimmy burial", term coined by Axtell (1956) when referring to sand burying in Holbrookia species.

Species of stem 33 resemble the general pattern of burying in Uma in that they bury head first, place their front limbs along the flanks, the hind limbs pushing and helping in progressing into sand. However, none of the species of stem 33 were seen to twist their heads "like an awl" nor were they seen to shimmy their tail at the end of

burying into sand. Arnold (1995:363) mentions that Uma, like Meroles, take a few steps back before burying themselves. Axtell (1956) also reports back stepping in species of Holbrookia. Back stepping is one of the unique behavioral synapomorphies recognized in species of stem 29 (Fig. 23a).

CHAPTER 4

CONCLUSIONS AND IMPLICATIONS

Although there is much diversity in the burying patterns used among different lizard families and in the way these are combined in different species, there seem to be three major burying styles, considering species from this study and based on Arnold's work (1994a, 1995). These are:

1. Sand swimmers as exemplified by Scincus (Scincidae),
2. Vertical sand buriers such as Phrynocephalus (Chamaeleonidae, Agaminae),
3. Head first sand buriers such as Meroles (Lacertidae), and Liolaemus (Tropiduridae).

Within the third group, common elements in burying behavior can be found in genera of three families: the African Meroles, a lacertid, the North American Uma, a phrynosomatid, and the South American Liolaemus, a tropidurid. Lizards belonging to these genera have been observed to generally back step prior to submerging, enter sand head first, lay their front limbs along the flanks, and generally execute some movement of the tail. These behavior patterns may be a case of adaptive convergence where similar solutions are applied to similar problems given that no

major historical constraint, such as a blunt snout, impede head first entrance into the sand. On the other hand, behavior patterns used in sand burying may reflect the history of these lizard families. However, much more needs to be known on burying behavior in many more species within these lizard families before any interpretation can be advanced with respect to the evolution of this behavior at the family level.

The different methods used in burying into loose sand do not seem to reflect different mechanical problems. In fact, loose aeolian sand from different geographical regions and in which lizards are found to bury, is similar with respect to its physical properties (Bagnold, 1941, in Arnold, 1994a). Sand burying lizards will, therefore, probably encounter similar difficulties. This suggests that different methods of burying into sand reflect different historical heritages or lineage effects (Arnold, 1994a) rather than a response to physical properties of the sand.

For instance, Phrynocephalus has developed a very blunt snout which evolved before the appearance of its sand burying behavior. This development acted as a morphological constraint on options available to the lizard when sand burying became an alternative for predator escape. It probably explains why these lizards do not enter sand head

first but descend vertically into it. Uma, on the other hand, is characterized by a lateral ridge on the upper lip, which appears to facilitate head first entrance into the sand.

Another example of a different type of lineage effect is related to the ecology of a species. This may be shown in the lacertid Acanthodactylus schmidti, a close relative of Meroles. This species occurs on sparsely vegetated sand dunes but it does not bury into sand. Arnold (1984) found that A. schmidti did not stray far from shrubs where it could find cover and burrows and therefore might not have needed to escape predators by sand burying as the sympatric and sand burying species Scincus mitranus and Phrynocephalus arabicus which ranged further away from cover.

Species of stem 29 (Fig. 23) are characterized by keeled infra-labials. It may explain why lizards in this subgroup plunge into sand combining a forward thrusting of the head and body with the presence of these keeled labials to cut their way into sand. Species of stem 31 and L. cuyanus (Fig. 23) do not have keeled labials. They use an alternate method, i. e. lateral movement of the head which apparently facilitates entry into sand. Species of stem 30 and most individuals of L. wiegmannii (Fig. 23) enter the sand head straight without an impulse or lateral movement of the head but advance by pushing with the hind limbs. Thus,

it would seem that constraints imposed by lineage effects, in this case morphological, appear to be foremost in explaining the differences observed.

The behavioral characters used in this study combined with morphological characters will probably provide a more robust hypothesis of phylogeny for species of the boulengeri group. This will be attempted in the near future. Such an analysis will then provide a background on which other studies may be built. Almost nothing is known about such areas as life histories, mating systems, specific diets, and antipredator defense, in species of the boulengeri group. Questions in these areas could then be addressed in a phylogenetic context allowing for more insight into the evolutionary processes involved. Future studies could also incorporate information from genetic and molecular analyses of different species of the boulengeri group adding yet another perspective to phylogenetic relationships among species of this group.

REFERENCES

REFERENCES

Andrews, R. M. 1994. Activity and thermal biology of the sand-swimming skink Neoseps reynoldsi: diel and seasonal patterns. Copeia, 1994(1):91-99.

Andrews, R. M. and Kenney, B. S. 1990. Diel patterns of activity and of selected ambient temperature of the sand-swimming lizard Sphenops sepsoides (Reptilia: Scincidae). Israel J. of Zoology, 37:65-73.

Archibald, G. W. 1976. Crane taxonomy as revealed by the unison call. In: Proceedings of the International Crane Workshop, (Ed. J. C. Lewis). Oklahoma State University Publishing and Printing, pp. 225-251.

Armstrong, G. 1979. Reptiles of the Golden Grove Areas in the Adelaide Hills. South Australia Herp. Group Newsletter, pp. 5-8.

Arnold, E. N. 1984. Ecology of lowland lizards in the eastern United Arab Emirates. J. Zool. Lond., 204:329-354.

Arnold, E. N. 1992. The Rajasthan toad-headed lizard, Phrynocephalus laungwalaensis (Reptilia: Agamidae), represents a new genus. J. Herpetol., 26(4):467-472.

Arnold, E. N. 1994a. Investigating the origins of performance advantage: adaptation, exaptation and lineage effects. In: Phylogenetics and Ecology, (Eds. P. Eggleton and R. I. Vane-Wright). Linnean Society of London, Academic Press, 17:123-168.

Arnold, E. N. 1994b. Do ecological analogues assemble their common features in the same order? An investigation of regularities in evolution, using sand-dwelling lizards as examples. Phil. Trans. R. Soc. Lond. B, 344:277-290.

Arnold, E. N. 1995. Identifying the effects of history on adaptation: origins of different sand-diving techniques in lizards. J. Zool., Lond., 235:351-388.

Arnold, S. J. 1977. Polymorphism and geographic variation in the feeding behavior of the garter snake Thamnophis elegans. Science, 197:676-678.

Atz, J. W. 1970. The application of the idea of homology to behavior. In: Development and Evolution of Behavior, (Eds. L. R. Aronson, E. Tobach, D. S. Lehrman, and J. S. Rosenblatt). W. H. Freeman and Company, San Francisco, pp. 53-74.

Auffenberg, W. 1981. Behavioral Ecology of the Komodo Dragon. Univ. Presses of Florida, Gainesville, 406 pp.

Auffenberg, W. 1983. The burrows of Varanus bengalensis: characteristics and use. Rec. zool. Surv. India, 80:375-385.

Axtell, R. A. 1956. A solution to the long neglected Holbrookia lacerata problem, and the description of two new subspecies of Holbrookia. Bull. Chicago Acad. Sci., 10:163-179.

Bagnold, R. A. 1941. The Physics of Blown Sand and Desert Dunes. Lo Methuen.

Bakeman, R. and Gottman, J. M. 1989. Observing Interaction. An Introduction to Sequential Analysis (3rd ed.). Cambridge University Press, N. Y., 221 pp.

Bartlett, R. D. 1982. Initial observations on the captive reproduction of Varanus storri, Mertens. Herpetofauna, 13(2):6-7.

Bauer, A. M. and Russell, A. P. 1991. Pedal specializations in dune-dwelling geckos. J. Arid Environ., 20(1):43-62.

Boucot, A. J. 1990. Evolutionary Paleobiology of Behavior and Coevolution. Elsevier, Amsterdam, 725 pp.

Bouskila, A. 1987. Feeding in the herbivorous lizard Uromastyx aegyptius near Hazeva. Israel J. Zool., 33:122.

Bradshaw, S. D. and Main, A. R. 1968. Behavioural attitudes and regulation of temperature in Amphibolurus lizards. J. Zool., Lond., 154:193-221.

Brooks, D. R. and McLennan, D. A. 1991. Phylogeny, Ecology, and Behavior. A Research Program in Comparative Biology. The University of Chicago Press, Chicago and London, 434 pp.

Brown, J. L. 1975. The Evolution of Behavior. W. W. Norton & Company, Inc., New York, 761 pp.

Buckman, H. O. and Brady, N. C. 1969. The Nature and Properties of Soils. The Macmillan Company/Collier-Macmillan Limited, London.

Burghardt, G. M. 1967. Chemical-cue preferences of inexperienced snakes: comparative aspects. Science, 157(3789):718-721.

Burghardt, G. M. 1970. Intraspecific geographical variation in chemical food cue preferences of newborn garter snakes (Thamnophis sirtalis). Behaviour, 36(3):246-257.

Burghardt, G. M. and Gittleman, J. L. 1990. Comparative behavior and phylogenetic analyses: new wine, old bottles. In: Interpretation and Explanation in the Study of Animal Behavior. Vol. II: Explanation, Evolution and Adaptation, (Eds. M. Bekoff and D. Jamieson. Westview Press, Boulder, San Francisco and Oxford, 8:192-225.

Bustard, H. R. 1965. Observations on Australian geckos. Herpetologica, 21(4):294-302.

Bustard, H. R. 1968. The reptiles of Merriwindi State Forest, Pilliga West, Northern New South Wales, Australia. Herpetologica, 24(2):131-140.

Cabrera, A. L. and Willink, A. 1980. Biogeografía de America Latina. Secretaría General de la Organización de los Estados Americanos. Programa Regional de Desarrollo Científico y Tecnológico. Washington, D. C., 2nd ed., 122 pp.

Carpenter, C. C. 1963. Patterns of behavior in three forms of the fringe-toed lizards (Uma-Iguanidae). Copeia, 1963(2):406-412.

Carpenter, C. C. 1967a. Display patterns of the Mexican iguanid lizards of the genus Uma. Herpetologica, 23(4):285-293.

Carpenter, C. C. 1967b. Aggression and social structure in Iguanid lizards. In: Lizard Ecology: a Symposium, (Ed. W. W. Milstead). Univ. of Missouri Press, Columbia, Missouri, pp. 87-105.

Carpenter, C. C. 1978. Ritualistic social behaviors in lizards. In: Behavior and Neurology of Lizards, (Eds. N. Greenberg and P. D. MacLean). NIMH, pp. 253-267.

Carpenter, C. C. and Ferguson, G. W. 1977. Variation and evolution of stereotyped behavior in reptiles. In: Biology of the Reptilia, (Ed. C. Gans and D. W. Tinkle). Academic Press, New York, Chapter 6, pp. 335-554.

Carr, A. 1963. The Reptiles. Time-Life Books, New York, 192 pp.

Carrillo de Espinoza, N., Rothenstein, D., Salas, A. W., and Werner, Y. L. 1990. Radiation and convergence among desert geckos: Phyllodactylus species resembling both Ptyodactylus and Stenodactylus. Amphibia-Reptilia, 11:1-13.

Cei, J. M. 1979. A reassessment of the genus Ctenoblepharis (Reptilia, Sauria, Iguanidae) with a description of a new subspecies of Liolaemus multimaculatus from western Argentina. J. Herpet., 13(3):297-302.

Cei, J. M. 1986. Reptiles del Centro, Centro-Oeste y Sur de la Argentina. Herpetofauna de las zonas áridas y semiáridas. Monogr. IV, Mus. reg. Sci. nat. Torino, 527 pp.

Cei, J. M. 1993. Reptiles del Noroeste, Nordeste y Este de la Argentina. Herpetofauna de las selvas subtropicales, Puna y Pampas. Monogr. XIV, Mus. reg. Sci. nat. Torino, 949 pp.

Chapman, A. and Dell, J. 1974. Reptiles and frogs of Buntine and Nugadong Reserves. Records of the Western Australian Museum, Perth, 9:117-127.

Clarke, R. F. 1965. An ethological study of the iguanid lizard genera Callisaurus, Cophosaurus, and Holbrookia. Emporia State Research Studies, 13(4):1-66.

Coddington, J. A. 1988. Cladistic tests of adaptational hypotheses. Cladistics, 4:3-22.

Cogger, H. G. 1978. Reproductive cycles, fat body cycles and socio-sexual behaviour in the Mallee Dragon, Amphibolurus fordi (Lacertilia: Agamidae). Aust. J. Zool., 26:653-672.

Cogger, H. G. 1994. Reptiles and Amphibians of Australia. Comstock, Cornell, 6th ed., 788 pp.

Cooper, W. E. 1971. Display behavior of hatchling Anolis carolinensis. Herpetologica, 27(4):498-500.

Coventry, A. J. and Robertson, P. 1980. New records of scincid lizards from Victoria. Vic. Nat., 97(5):190-193.

Cowles, R. B. 1941. Observations on the winter activities of desert reptiles. Ecology, 22(1):125-140.

Darwin, C. 1859/1964. On the Origin of Species. A Facsimile of the First Edition with an Introduction by Ernst Mayr. Harvard University Press, Cambridge, Massachusetts, 513 pp.

Davey, K. 1970. Australian Lizards. Lansdowne Press Pty. Ltd., Melbourne.

de Queiroz, A. 1989. Morphological and biochemical evolution in the sand lizards. Unpubl. PhD Thesis, Univ. Calif. Berkeley, 490 pp.

de Queiroz, A. 1993. For consensus (sometimes). Syst. Biol., 42(3):368-372.

de Queiroz, A., and Wimberger, P. H. 1993. The usefulness of behavior for phylogeny estimation: levels of homoplasy in behavioral and morphological characters. Evolution, 47(1):46-60.

Dobson, F. S. 1985. The use of phylogeny in behavior and ecology. Evolution, 39(6):1384-1388.

Donoso-Barros, R. 1966. Reptiles de Chile. Ediciones de la Universidad de Chile, Santiago de Chile, 459 pp.

Duellman W. E. 1985. Reproductive modes in anuran amphibians: phylogenetic significance of adaptive strategies. South African J. of Science, 81:174-178.

Dunford, C. and Davis, R. 1975. Cliff chipmunk vocalizations and their relevance to the taxonomy of coastal sonoran chipmunks. J. of Mammalogy, 56(1):207-212.

Ehmann, H. and Swan, G. 1987. Microsympatry, limb characteristics and tail colour in burrowing skinks of the genus Anomalopus. Herpetofauna, 17(2):25-27.

Etheridge, R. 1992. A new psammophilus lizard of the genus Liolaemus (Squamata: Tropiduridae) from Northwestern Argentina. Boll. Mus. reg. Sci. nat., Torino, 10(1):1-19.

Etheridge, R. 1993. Lizards of the Liolaemus darwinii complex (Squamata: Iguania: Tropiduridae) in Northern Argentina. Boll. Mus. reg. Sci. nat., Torino, 11(1):137-199.

Etheridge, R. 1995. Redescription of Ctenoblepharys adspersa Tschudi, 1845, and the taxonomy of Liolaeminae (Reptilia: Squamata: Tropiduridae). Am. Mus. Nat. Hist. Novitates, 3142:1-34.

Etheridge, R. and de Queiroz, K. 1988. A phylogeny of Iguanidae. In: Phylogenetic Relationships of Lizard Families: Essays Commemorating Charles L. Camp, (Eds. R. Estes and G. Pregill). Stanford Univ. Press, pp. 283-368.

Ferguson, G. W. 1971. Variation and evolution of the pushup displays of the side-blotched lizard genus Uta (Iguanidae). Syst. Zool., 20(1):79-101.

Ford, J. 1963. The distribution and variation of the skinks Egernia pulchra and E. bos in Western Australia. W. Aust. Nat., 9(2):25-29.

Ford, J. 1965. The Reptilian fauna of the islands between Dongara and Lancelin, Western Australia: additional notes. W. Aust. Nat., 9(7):174-175.

Forey, P. L., Humphries, C. J., Kitching, I. L., Scotland, R. W., Siebert, D. J., and Williams, D. M. 1994. Cladistics. A Practice Course in Systematics. Systematics Association Publication, n° 10, Oxford University Press Inc., New York, 191 pp.

Frost, D. R. and Etheridge, R. 1989. A phylogenetic analysis and taxonomy of Iguanian lizards (Reptilia: Squamata). Museum of Nat. History, Univ. Kansas, 81:1-65.

Gallardo, J. M. 1977. Reptiles de los Alrededores de Buenos Aires. E.U.D.E.B.A., Buenos Aires, 213 pp.

Galliford, M. 1978. A brief study of Nephrurus stellatus in captivity. South Australia Herp. Group Newsletter, pp.1-2.

Gans, C. 1974. Biomechanics. An Approach to Vertebrate Biology. The Univ. of Michigan Press, Ann Arbor, 261 pp.

Gans, C., Morgan, W. K., and Allen, E. S. 1992. Surface locomotion of the elongate and limbless lizard Anniella pulchra (Anguidae). Herpetologica, 48(2):246-262.

Gittleman, J. L. 1981. The phylogeny of parental care in fishes. Anim. Beh., 29:936-941.

Gittleman, J. L. and Decker, D. M. 1994. The phylogeny of behaviour. In: Behaviour and Evolution, (Eds. P. J. B. Slater and T. R. Halliday). Cambridge University Press, pp. 81-105.

Gittleman, J. L., Anderson, C. G., Kot, M., and Luh, H-K. 1996 (in press). Comparing behavioral and morphological evolution: Using molecular phylogenies to measure phylogeny, plasticity and rates. In: Phylogenies and the Comparative Method, (Ed. E. P. Martins). Oxford University Press, Oxford.

Greene, H. W. 1977. Phylogeny, Convergence, and Snake Behavior. Doctoral Thesis, University of Tennessee, Knoxville, 112 pp.

Greene, H. W. 1994. Homology and behavioral repertoires. In: Homology: The Hierarchical Basis of Comparative Biology, (Ed. B. K. Hall). Academic Press, Inc., San Diego, pp. 369-391.

Greene, H. W. and Burghardt, G. M. 1978. Behavior and phylogeny: Constriction in ancient and modern snakes. Science, 200:74-77.

Greer, A. E. 1989. The Biology and Evolution of Australian Lizards. Surrey Beatty & Sons Pty Limited, 264 pp.

Haacke, W. D. 1964. Description of two new species of lizards and notes on Fitzsimonsia brevipes (FitzSimons) from the central Namib desert. Scient. Pap. Namib Desert Res. Stn., 25:1-15.

Haacke, W. D. 1975. The burrowing geckos of Southern Africa, 1 (Reptilia: Gekkonidae). Ann. Transv. Mus., 29(12):197-243.

Haacke, W. D. 1976a. The burrowing geckos of Southern Africa, 2 (Reptilia: Gekkonidae). Ann. Transv. Mus., 30(2)13-29.

Haacke, W. D. 1976b. The burrowing geckos of Southern Africa, 4 (Reptilia: Gekkonidae). Ann. Transv. Mus., 30(5):53-70.

Halloy, M. and Burghardt, G. M. 1990. Ontogeny of fish capture and ingestion in four species of garter snakes (Thamnophis). Behaviour, 112(3-4):299-318.

Halloy, M., Grosse, C., and Laurent, R. F. 1991. Liolaemus andinus (Iguanidae) des deux cotés des Andes. Revue fr. Aquariol., 18(2):61-64.

Halloy, M. and Halloy, S. In press. Parental care and social organization in Liolaemus huacahuasicus (Tropiduridae), a high altitude viviparous lizard. J. of Herpetology.

Halloy, S. 1985. High Mountain Climatology and Edaphology in Relation to the Composition and Adaptations of Biotic Communities (with special reference to the Cumbres Calchaquíes, Tucumán, Argentina). [Spanish text]. Doctoral Thesis. Fac. C. Nat. Univ. Nac. Tucumán, Argentina, 839 pp. [University Microfilm International publ. # 85-02967. Ann Arbor, MI.]

Halloy, S. and Laurent, R. F. 1988. Notes éco-éthologiques sur Liolaemus huacahuasicus Laurent (Iguanidae) du Nord-Ouest argentin. Revue fr. Aquariol., 14(4):137-144.

Hamilton, W. J. III and Coetzee, C. G. 1969. Thermoregulatory behaviour of the vegetarian lizard, Angolosaurus skoogi, on the vegetationless northern Namib desert dunes. Scientific Papers of the Namib Desert Research Station, 47:95-103.

Heath, J. E. 1965. Temperature regulation and diurnal activity in horned lizards. Univ. Calif. Pub. Zool., 64(3):97-136.

Heatwole, H. 1970. Thermal ecology of the Desert Dragon Amphibolurus inermis. Ecological Monographs, 40(4):425-455.

Heinroth, O. 1911/1985. Contributions to the biology, especially the ethology and psychology of the Anatidae. In: Foundations of Comparative Ethology, (Ed. G. M. Burghardt). Van Nostrand Reinhold Company, New York, pp. 246-301.

Hetherington, T. E. 1989. Use of vibratory cues for detection of insect prey by the sandswimming lizard Scincus scincus. Anim. Behav., 37:290-297.

Hickman, J. L. 1960. Observation on the skink lizard Egernia whitii (Lacépède). Papers and proceedings of the Royal Society of Tasmania, 94:111-118.

Hinde, R. A. 1966. Animal Behaviour. A Synthesis of Ethology and Comparative Psychology. McGraw-Hill Book Co., 534 pp.

Hinde, R. A. and Tinbergen, N. 1958. The comparative study of species-specific behavior. In: Behavior and Evolution, (Eds. A. Roe and G. G. Simpson). Yale University Press, New Haven, pp. 251-268.

Houston, T. F. 1978. Dragon Lizards and Goannas. Special Educational Bulletin Series, South Australian Museum, Adelaide.

Huey, R. B., Pianka, E. R., Egan, M. E., and Coons, L. W. 1974. Ecological shifts in sympatry: Kalahari fossorial lizards (Typhlosaurus). Ecology, 55:304-316.

Hunsaker II, D. 1962. Ethological isolating mechanisms in the Sceloporus torquatus group of lizards. Evolution, 16:62-74.

James, C. D. and Losos, J. B. 1991. Diet and reproductive biology of the australian sand-swimming lizards, Eremiascincus (Scincidae). Wildl. Res., 18:641-654.

Jenkins, R. and Bartell, R. 1979. A Field Guide to Reptiles of the Australian High Country. Inkata Press.

Jenssen, T. A. 1977. Evolution of Anoline lizard display behavior. Amer. Zool., 17:203-215.

Keller, C. and Krause, L. 1986. The appendicular skeleton of Liolaemus occipitalis Boulenger, 1885 (Sauria, Iguanidae). Rev. Brasil. Biol., 46(4):727-740.

Klauber, L. M. 1939. Studies of Reptile life in the arid Southwest. Part III. Notes on some lizards of the southwesten United States. Bull. Zool. Soc. San Diego, 14:80-100.

Klopfer, P. H. 1969. Instincts and chromosomes: what is an "innate" act? Amer. Nat., 103:556-560 (letter to the editor).

Klopfer, P. H. 1975. (Review of) J. Alcock. Animal Behavior: An Evolutionary Approach. Am. Sci., 63:578-579.

Kluge, A. G. 1983. Cladistics and the classification of the great apes. In: New Interpretations of Ape and Human Ancestry, (Eds. R. L. Ciochon, and R. S. Corruccini). Plenum Press, New York, pp. 151-177.

Kluge, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among Epicrates (Boidae, Serpentes). Syst. Zool., 38(1):7-25.

Lang, M. 1991. Generic relationships within Cordyliformes (Reptilia: Squamata). Bull. Inst. Royal Sci. Nat. Belgique, Biol., 61:121-181).

Lauder, G. V. 1986. Homology, analogy, and the evolution of behavior. In: Evolution of Animal Behavior. Paleontological and Field Approaches, (Eds. M. H. Nitecki, and J. A. Kitchell). Oxford University Press, New York, pp. 9-40.

Laurent, R. F. 1983a. Sinonimia del género Pelusaurus Donoso-Barros con Liolaemus (Sauria, Iguanidae). Bol. As. Herp. Arg., 1(1):9-10.

Laurent, R. F. 1983b. Contribución al conocimiento de la estructura taxonómica del género Liolaemus Wiegmann (Iguanidae). Bol. As. Herp. Arg., 1(3):15-18.

Laurent, R. F. 1984. On some iguanid genera related to or previously confused with Liolaemus Wiegmann. J. Herpetol., 18(4):357-373.

Laurent, R. F. 1985. Segunda contribución al conocimiento de la estructura taxonómica del género Liolaemus Wiegmann (Iguanidae). Cuad. Herp. Asoc. Herp. Arg., 1(6):1-37.

Laurent, R. F. 1992. On some overlooked species of the genus Liolaemus Wiegmann (Reptilia Tropiduridae) from Peru. Breviora, 494:1-33.

Laurent, R. F. 1995. A tentative arrangement of subgenera of the genus Liolaemus Wiegmann (Reptilia: Squamata: Tropiduridae). Bulletin of the Maryland Herpetological Society, 31(1):10-14

Lorenz, K. 1941. Vergleichende Bewegungsstudien an Anatinen. J. Orn., 89:194-294.

Lorenz, K. 1971. Studies in Animal and Human Behaviour. Vol. II, Harvard University Press, Cambridge, Mass., 366 pp.

Lorenz, K. 1981. The Foundations of Ethology. Springer-Verlag, New York, 380 pp.

Louw, G. N. and Holm, E. 1972. Physiological, morphological and behavioural adaptations of the ultrapsammophilous, Namib Desert lizard Aporosaura anchietae (Bocage). Madoqua, Series II, 1(54-62):67-85.

Lynn, R. T. 1965. A comparative study of display behavior in Phrynosoma (Iguanidae). The Southwestern Naturalist, 10(1):25-30.

McGinnis, S. M. 1966. Sceloporus occidentalis: preferred body temperature of the western fence lizard. Science, 152:1090-1091.

McLennan, D. A. 1993. Phylogenetic relationships in gasterosteidae: an updated tree based on behavioral characters with a discussion of homoplasy. Copeia, 1993(2):318-326.

McLennan, D. A., Brooks, D. R., and McPhail, J. D. 1988. The benefits of communication between comparative ethology and phylogenetic systematics: a case study using gasterosteid fishes. Can. J. Zool., 66:2177-2190.

Maddison, W. P., Donoghue, M. J., and Maddison, D. R. 1984. Outgroup analysis and parsimony. Syst. Zool., 33(1):83-103.

Mayhew, W. W. 1963. Observations on captive Amphibolurus pictus. An Australian agamid lizard. Herpetologica, 19(2):81-88.

Mayhew, W. W. 1964. Photoperiodic responses in three species of the lizard genus Uma. Herpetologica, 20(2):95-113.

Mayhew, W. W. 1966. Reproduction in the psammophilous lizard Uma scoparia. Copeia, 1966(1):114-122.

Mayr, E. 1958. Behavior and systematics. In: Behavior and Evolution, (Eds. A. Roe and G. G. Simpson). Yale University Press, New Haven, pp. 341-362.

Mitchell, A. J. L. and Steyn, W. 1967. Further distribution records of reptiles in South West Africa. Cimbebasia, 21:23-26.

Mitchell, D., Seely, M. K., Roberts, C. S., Pietruszka, R. D., McClain, E., Griffin, M., and Yeaton, R. I. 1987. On the biology of the lizard Angolosaurus skoogi in the Namib Desert. Madoqua, 15(3):201-216.

Miyamato, M. M. 1985. Consensus cladograms and general classifications. Cladistics, 1(2):186-189.

Mosauer, W. 1932. Adaptive convergence in the sand reptiles of the Sahara and California: a study in structure and behavior. Copeia, 1932(2):72-78.

Mosauer, W. 1936. The reptilian fauna of sand dune areas of the Vizcaino Desert and of north-western lower California. Occasional Papers of the Museum of Zoology, University of Michigan Press, Ann Arbor, Michigan, 329:1-25.

Murthy, T. S. N. and Arockiasamy, R. A. A. 1977. Observations on the spiny-tailed lizard Uromastix hardwicki Gray in captivity. Geobios, 4:167-168.

Norris, K. S. 1949. Observations on the habits of the horned lizard Phrynosoma m'callii. Copeia, 1949(3):176-180.

Norris, K. S. 1953. The ecology of the desert iguana, Dipsosaurus dorsalis. Ecology, 34(2):265-287.

Norris, K. S. 1958. The evolution and systematics of the iguanid genus Uma and its relation to the evolution of other North American desert reptiles. Bull. Amer. Mus. Nat. Hist., 114(3):247-326.

Norris, K. S. and Kavanau, J. L. 1966. The burrowing of the Western shovel-nosed snake, Chionactis occipitalis Halowell, and the undersand environment. Copeia, 1966(4):650-664.

Packer, L. 1991. The evolution of social behavior and nest architecture in sweat bees of the subgenus Evylaeus (Hymenoptera: Halictidae): a phylogenetic approach. Behav. Ecol. Sociobiol., 29:153-160.

Pianka, E. R. 1986. Ecology and Natural History of Desert Lizards. Princeton University Press, 208 pp.

Pianka, E. R. and Giles, W. F. 1982. Notes on the biology of two species of nocturnal skinks, Egernia inornata and Egernia striata, in the Great Victoria Desert. W. Aust. Nat., 15(2):8-13.

Pough, F. H. 1969a. Physiological aspects of the burrowing of sand lizards (Uma, Iguanidae) and other lizards. Comp. Biochem. Physiol., 31:869-884.

Pough, F. H. 1969b. The morphology of undersand respiration in reptiles. Herpetologica, 25(3):216-223.

Pough, F. H. 1970. The burrowing ecology of the sand lizard, Uma notata. Copeia, 1970(1).:145-157.

Pough, F. H., Morafka, D. J., and Hillman, P. E. 1978. The ecology and burrowing behavior of the Chihuahuan fringe-footed lizard, Uma exsul. Copeia, 1978(1):81-86.

Prum, R. O. 1990. Phylogenetic analysis of the evolution of display behavior in the neotropical manakins (Aves: Pipridae). Ethology, 84:202:231.

Rankin, P. R. 1977. Burrow plugging in the netted dragon Amphibolurus nuchalis with reports on the occurrence in three other Australian agamids. Herpetofauna, 9(1):18-22.

Rankin, P. R. 1978. A new species of lizard (Lacertilia: Scincidae) from the Northern Territory, closely allied to Ctenotus decaneurus Storr. Records of the Australian Museum, 31(10):395-409.

Reeve, W. L. 1952. Taxonomy and distribution of the horned lizard genus Phrynosoma. The Univ. Kansas Science Bul., 34(2):817-960.

Rocha, C. F. D. 1993. The set of defence mechanisms in a tropical sand lizard (Liolaemus lutzae) of southeastern Brazil. Ciencia e Cultura (J. of the Brazilian Association for the Advancement of Science), 45(2):116-122.

Rocha, C. F. D., and Bergallo, H. G. 1992. Population decrease: The case of Liolaemus lutzae, an endemic lizard of Southeastern Brazil. Ciencia e Cultura (J. of the Brazilian Association for the Advancement of Science), 44(1):52-54.

Roggenbuck, M. E. and Jenssen, T. A. 1986. The ontogeny of display behaviour in Sceloporus undulatus (Sauria:Iguanidae). Ethology, 71:153-165.

Russell, A. P. and Bauer, A. M. 1990. Substrate excavation in the Namibian web-footed gecko, Palmatogecko rangei Andersson 1908, and its ecological significance. Tropical Zoology, 3:197-207.

Schleidt, W. M. and Shalter, M. D. 1973. Stereotypy of a fixed action pattern during ontogeny in Coturnix coturnix coturnix. Z. Tierpsychol., 33:35-37.

Schmida, G. E. 1975. Däumlinge aus der Familie der Riesen. Kurzschwanz-, Gillen- und Schwanzstrichwaran. Aquar. Mag., 9(1):9-11.

Schmidt, K. P. and Inger, R. F. 1957. Living Reptiles of the World. Hanover House, Garden City, New York, 287 pp.

Seilacher, A. 1967. Fossil behavior. Scientific American, 217:72-80.

Shammakov, S., Sopyev, O. S., and Fedorova, N. M. 1981. Ecology of the Teratoscincus Scincus scincus Schlegel in the Karakum. UDK 598.112:591.5(575.4):36-42 [in Russian].

Siegel, S. and Castellan, N. J., Jr. 1988. Nonparametric Statistics for the Behavioral Sciences (2nd ed.). McGraw-Hill, Inc., N. Y., 399 pp.

Simonetti, J. 1984. Utilización de refugio por Liolaemus nigromaculatus: compromiso entre riesgos de predación y necesidades termorregulatorias. Studies on Neotropical Fauna and Environment, 19(1):47-51.

Smith, L. A. 1976. The reptiles of Barrow Island. West. Aust. Nat., 13(6):125-136.

Stamps, J. A. 1978. A field study of the ontogeny of social behavior in the lizard Anolis aeneus. Behaviour, 66:1-31.

Stamps, J. A. and Barlow, G. W. 1972. Variation and stereotypy in the displays of Anolis aeneus (Sauria: Iguanidae). Behaviour, 47:67-94.

Stebbins, R. C. 1944. Some aspects of the ecology of the iguanid genus Uma. Univ. of California, Los Angeles. Ecological Monographs, 14(3):311-332.

Stebbins, R. C. 1963. Activity changes in the striped plateau lizard with evidence on influence of the parietal eye. Copeia, 1963(4):681-691.

Stevens, P. F. 1991. Character states, morphological variation, and phylogenetic analysis: a review. Systematic Botany, 16(3):553-583.

Steyn, W. 1963. Angolosaurus skoogi (Andersson) - A new record from South West Africa. Cimbebasia, 6(1):8-11.

Steyn, W., Finkeldey, H., and Buys, P. J. 1963. Agama hispida makarikarica FitzSimons. A preliminary note on its occurrence in South West Africa and behaviour. Cimbebasia, 6:12-15.

Storr, G. M. 1960. Egernia bos a new skink from the south coast of Western Australia. West. Aust. Nat., 7(4):99-103

Storr, G. M. 1966. The Amphibolurus reticulatus species-group (Lacertilia, Agamidae) in Western Australia. Journal of the Royal Society of Western Australia, 49(1):17-25.

Swofford, D. L. and Berlocher, S. H. 1987. Inferring evolutionary trees from gene frequency data under the principle of maximum parsimony. Syst. Zool., 36(3):293-325.

Tanner, W. W. and Krogh, J. E. 1973. Ecology of Phrynosoma platyrhinos at the Nevada test site, Nye County, Nevada. Herpetologica, 29(4):327-342.

Tanner, W. W. and Krogh, J. E. 1975. Ecology of the zebra-tailed lizard Callisaurus draconoides at the Nevada Test Site. Herpetologica, 31(3):302-316.

Taylor, J. A. 1984. Burrow construction and utilisation by the lizard Ctenotus taeniolatus. Herpetofauna, 15(2):44-47.

Telford, S. R., Jr. 1959. A study of the sand skink, Neoseps reynoldsi Stejneger. Copeia, 1959(2):110-119.

Thiele, K. 1993. The holy grail of the perfect character: the cladistic treatment of morphometric data. Cladistics, 9:275-304.

Tinbergen, N. 1951. The Study of Instinct. Clarendon Press, Oxford, 228 pp.

Tinbergen, N. 1960. Comparative studies of the behaviour of gulls (Laridae): a progress report. Behaviour, 15:1-70.

Vanzolini, P. E. 1977. An Annotated Bibliography of the Land and Freshwater Reptiles of South America (1758-1975). Museu de Zoologia, Universidade de Sao Paulo, Vol. I. (1758-1900).

Vanzolini, P. E., Ramos Costa, A. M. M., and Vitt, L. J. 1980. Repteis das Caatingas. Acad. brasil. Cien., Rio de Janeiro, 161 pp.

Watrous, L. E. and Wheeler, Q. D. 1981. The out-group comparison method of character analysis. Syst. Zool., 30(1):1-11.

Webber, P. 1979. Burrow density, position and relationship of burrows to vegetation coverage shown Rosen's desert skink Egernia inornata (Lacertilia: Scincidae). Herpetofauna, 10(2):16-20.

Werner, Y. L. 1977. Ecological comments on some gekkonid lizards of the Namib Desert, South West Africa. Madoqua, 10(3):157-169.

Whitman, C.O. 1898/1985. Animal behavior. In: Foundations of Comparative Ethology, (Ed. G. M. Burghardt). Van Nostrand Reinhold Company, New York, pp. 141-194.

Wiley, E. O. 1981. Phylogenetics. The Theory and Practice of Phylogenetic systematics. A Wiley-Interscience Publication. John Wiley and Sons, 439pp.

APPENDICES

APPENDIX A

List of species used in the study, number of individuals, measurements. The 23 *Liolaemus* species (455 lizards) that were used are listed following the taxonomic arrangement proposed by Etheridge (1995). LOC = location. Codes used for location names are explained in Appendix B. Under the column M/F/J/B are given the number of males for that species at that location (M), number of females (F), number of juveniles and/or subadults (J), and finally neonates measured within 24 hours of birth (B) [except in a few cases when the neonate was caught in the field, it might have been a few weeks old and those were marked B* as in *L. melanops*]. Weight = average weight in grams ± a standard deviation. SVL = average snout vent length in centimeters ± a standard deviation. TL = average total length in centimeters ± a standard deviation (this last measurement is affected by the lizard's proneness of losing parts of their tail when predated upon).

	LOC	M/F/J/B	Weight	SVL	TL
Liolaemus (*signifer* group; N = 455)					
L. montanus supergroup (not including *boulengeri* group, n = 77)					
L. andinus (1 location; 21 lizards)					
	JG	6 M	7.16±2.02	6.72±0.66	14.23±3.30
		3 F	5.93±0.46	6.40±0.52	11.27±3.70
		3 J	2.40±0.38	4.57±0.21	8.50±2.93
		9 B	0.53±0.04	2.62±0.04	5.84±0.13

LOC	M/F/J/B	Weight	SVL	TL
L. huacahuasicus (1 location; 25 lizards)				
HU	3 M	9.75±2.05	7.17±0.32	16.53±0.70
	7 F	5.12±0.93	6.20±0.59	13.07±2.07
	15 B	0.53±0.09	2.60±0.08	6.19±0.21
L. multicolor (1 location; 7 lizards)				
AB	4 M	10.80±1.93	7.27±0.51	10.92±2.12
	3 F	9.40±0.33	7.00±0.26	14.13±0.87
L. ruibali (4 locations; 5 M, 14 F, 2 J, 3 B; 24 lizards) (Figs. 1a, 1b)				
JA	1 M	8.32	6.5	7.7
	3 F	7.40±0.50	6.60±0.10	14.07±1.20
	2 J	4.73±1.75	5.50±0.42	9.80±5.10
	3 B	0.57±0.04	2.60±0	6.07±0.06
NA	1 M	5.03	5.1	9.3
	5 F	3.28±0.48	4.90±0.35	9.44±2.45
NC	1 M	4.48	5.1	12.8
	2 F	3.76±0.31	5.10±0	12.15±0.78
PA	2 M	6.29±0.39	6.00±0.14	10.40±4.52
	4 F	4.03±0.52	4.92±0.26	9.65±2.09
A. boulengeri group (not including wiegmannii subgroup, n = 240)				
L. boulengeri (5 locations; 1 M, 6 F, 1 B, 8 lizards) (Figs. 2a, 2b)				
BP	2 F	6.75±0.28	5.55±0.35	13.85±0.64
	1 B	0.59	2.8	7.7
CR	1 M	8.42	7.0	14.9
CT	1 F	5.30	5.6	14.8
LN	1 F	4.22	5.6	10.9
MT	2 F	4.47±1.11	5.70±0.85	13.45±0.07

LOC	M/F/J/B	Weight	SVL	TL
L. canqueli (1 location; 12 lizards) (Fig. 3)				
IN	2 M	18.71±4.54	8.55±0.50	20.60±1.13
	6 F	16.36±2.31	8.67±0.50	17.00±3.75
	3 J	12.31±1.41	7.73±0.30	18.97±0.90
	1 B	0.84	3.1	8.0
L. cuyanus (4 locations; 9 M, 5 F, 3 J; 17 lizards) (Figs. 4a, 4b)				
BA	1 FJ	8.37	6.9	14.5
MN	1 M	26.05	9.4	11.5
	2 F	19.96±6.48	8.75±1.63	20.45±2.05
	1 J	3.54	5.1	11.8
PI	7 M	20.59±3.47	8.74±0.30	18.97±1.39
	2 F	17.49±1.43	8.30±0	14.65±6.01
TI	1 M	13.56	7.9	17.9
	1 F	10.54	7.3	17.4
	1 MJ	4.68	5.7	13.4
L. darwinii (1 location; 2 lizards)				
MZ	1 M	3.88	5.0	14.3
	1 F	3.89	5.1	13.5
L. darwinii Nihuil (undescribed species belonging to the darwinii complex, Etheridge, 1993, and first located near Lago Nihuil; 4 locations; 7 M, 6 F; 13 lizards)				
CR	1 M	3.91	5.3	14.5
	1 F	2.72	5.2	8.6
CT	1 M	--	--	--
LN	4 M	3.40±0.37	4.95±0.10	10.55±2.07
	5 F	3.12±0.60	4.90±0.20	9.52±2.97
MT	1 M	4.56	5.5	15.0
L. donosobarrosi (1 location; 11 lizards) (Figs. 5a, 5b)				
MA	4 M	6.36±0.72	5.95±0.19	14.17±1.62
	7 F	4.79±0.60	5.60±0.35	12.41±1.40

LOC	M/F/J/B	Weight	SVL	TL
L. fitzingerii (1 location; 11 lizards) (Figs. 6a, 6b)				
CH	3 M	23.74±0.42	9.20±0.35	18.07±1.19
	4 F	18.31±1.28	8.80±0.34	20.62±0.46
	4 J	12.95±2.27	8.02±0.56	15.25±3.90
L. koslowskyi (1 location; 2 lizards)				
NT	2 M	4.33±0.78	5.00±0.28	13.65±0.07
L. laurenti (3 locations; 15 M, 13 F, 14 J; 42 lizards)				
BA	1 MJ	2.50	4.8	13.3
PI	10 M	4.29±1.22	5.42±0.45	14.71±1.83
	6 F	5.16±0.96	5.80±0.25	12.63±4.30
	13 J	2.01±0.46	4.26±0.29	11.41±1.21
TI	5 M	5.11±0.45	5.58±0.18	14.90±1.09
	7 F	5.29±1.33	5.61±0.37	13.17±1.58
L. melanops (2 locations; 11 M, 10 F, 1 J, 13 B; 35 lizards) (Figs. 7a, 7b)				
PP	1 FJ	6.13	6.3	10.7
PV	11 M	9.98±2.25	7.17±0.44	15.84±2.30
	9 F	7.74±1.06	6.60±0.19	14.44±1.97
	1 J	5.58	5.6	14.3
	5 B*	1.06±0.12	3.34±0.11	7.56±1.36
	8 B	0.56±0.09	2.89±0.12	6.69±1.36
L. olongasta (1 location; 7 lizards) (Fig. 8)				
TA	2 M	5.04±0.04	5.90±0.14	12.70±1.56
	3 MJ	2.38±0.93	4.43±0.50	12.50±1.34
	2 FJ	2.35±0.85	4.35±0.49	11.50±3.54
L. ornatus (1 location; 8 lizards)				
AB	4 M	6.69±1.39	6.40±0.22	14.05±2.48
	4 F	8.41±1.52	6.67±0.27	12.07±3.87

LOC	M/F/J/B	Weight	SVL	TL
L. quilmes (7 locations; 22 M, 19 F, 10 J, 7 B; 58 lizards) (Fig. 9)				
AN	2 M	4.75±0	5.30±0.28	9.85±1.48
	2 F	3.07±0.79	4.90±0	10.60±3.96
	1 J	3.04	4.6	12.1
CA	3 F	3.98±0.14	5.27±0.06	10.10±3.80
PB	6 M	4.83±0.72	5.72±0.19	13.57±0.66
	2 F	3.76±0.16	5.2	10.60±1.56
	2 J	2.58±0.20	4.70±0.28	9.05±4.74
PZ	1 M	5.67	5.9	15.2
	2 F	4.56±0.16	5.60±0.28	13.20±0.13
QU	5 M	4.04±1.59	5.36±0.61	9.58±3.23
	4 F	2.89±0.55	4.82±0.39	11.32±1.36
	2 J	1.56±0.06	4.00±0.14	8.05±3.32
SM	3 M	3.98±0.22	5.33±0.11	11.73±2.10
TF	5 M	7.68±1.30	6.28±0.33	15.06±1.52
	6 F	6.65±0.29	5.97±0.10	13.03±2.21
	5 J	3.53±0.45	5.02±0.26	12.08±3.24
	7 B	0.45±0.09	2.51±0.18	5.57±1.29
L. xanthoviridis (1 location; 14 lizards)				
LI	6 M	14.25±3.57	7.62±0.48	18.12±2.04
	7 F	9.99±1.66	7.29±0.38	16.26±1.51
	1 B	0.83	3.0	8.0

1. *wiegmannii* subgroup (n = 138)

L. multimaculatus (2 locations; 1 F, 2 J; 3 lizards) (Fig. 10)

AL	1 MJ	2.57	4.3	9.7
FQ	1 F	7.81	6.0	12.0
	1 FJ	5.12	5.4	11.3

LOC	M/F/J/B	Weight	SVL	TL
L. riojanus (2 locations; 9 M, 9 F, 14 J; 32 lizards)				
BA	6 M	5.16±1.60	5.48±0.50	11.17±1.34
	6 F	4.44±1.32	5.30±0.39	10.67±0.56
	13 J	2.39±0.74	4.27±0.46	8.91±0.82
VU	3 M	6.30±1.35	5.83±0.45	11.83±1.86
	3 F	4.27±1.04	5.10±0.44	9.77±1.59
	1 J	1.82	3.8	8.0
L. salinicola (2 locations; 3 M, 4 F, 7 J; 14 lizards)				
MN	2 M	12.45±1.82	7.80±0.42	17.20±0.71
	4 F	4.25±0.73	5.35±0.17	12.27±1.32
	6 J	2.45±0.67	4.55±0.34	8.92±2.02
TI	1 M	6.99	6.1	14.2
	1 JF	2.86	4.6	10.2
L. scapularis (6 loc.; 21 M, 11 F, 19 J; 51 lizards) (Figs. 11a, 11b)				
CF	9 M	8.66±1.63	6.38±0.43	12.79±1.91
	3 F	4.89±0.84	5.53±0.40	10.20±1.49
	5 J	3.56±0.83	4.86±0.54	9.76±1.89
IT	2 FJ	3.30±0.96	4.60±0.42	9.45±0.64
PE	3 M	6.06±1.30	6.07±0.45	11.93±1.91
	2 MJ	3.52±0.32	4.95±0.07	9.5
PM	1 M	6.25	6.4	13.6
	2 F	4.86±0.24	5.55±0.35	11.05±1.91
	2 J	3.05±1.25	4.60±0.57	9.85±1.06
PZ	7 M	6.03±0.96	6.03±0.43	11.30±0.87
	6 F	5.05±0.95	5.45±0.57	10.80±1.73
	6 J	2.10±0.76	4.23±0.38	8.35±1.76
SM	1 M	5.71	5.9	12.90
	2 J	3.51±1.24	4.95±0.49	10.35±0.92
L. wiegmannii (1 location; 38 lizards) (Figs. 12a, 12b)				
MD	11 M	3.92±1.06	5.09±0.41	10.52±1.96
	21 F	4.02±1.14	5.00±0.32	9.45±1.96
	6 J	2.17±0.21	4.20±0.17	8.48±0.86

APPENDIX B

List of locations for Liolaemus species. Locations where Liolaemus species were found are listed in alphabetical order by the two letter codes used in Appendix A. All locations are within Argentina except for location NC which is in Chile. Habitats were selected in order to collect as many species belonging to the boulengeri group (the ingroup) as possible, and a few species belonging to the outgroup (listed in Appendix A). The biogeographic province to which each location corresponds is identified in parentheses (a brief description of the different provinces is given in Appendix C, after Cabrera and Willink, 1980). Elevation is then indicated, also in parentheses. Maps used for location specifications were from the Sector de Cartografía Vial y Turística del Automóvil Club Argentino and from Turistel: Guía Turística de Todo Chile. Following this information, a brief description of the local habitat is provided except in 3 cases when it was unknown. When known, type of substrate and name of a few characteristic plants are given.

AB (Puna, 3500 m) = Abrapampa, ruta nacional 9, Jujuy: mountainous, open area, hard ground, stones; dry tussock grassland.

AL (Monte, 200-600 m) = Alto Limpio, Departamento Lavalle, northern Mendoza: local habitat unknown.

AN (Monte, 1700 m) = 3.4 Km South of Animaná (± 10 km North of Cafayate), for males (Fig. 9), and 9.1 Km South of Animaná (± 4 km North of Cafayate), for females, ruta nacional 40, Salta: firm substrate with rocks; shrubs 1 to 1.5 m high, a few trees (e. g. algarrobo, Prosopis, Leguminosae).

BA (Monte, 1000-2000 m) = 3-5 Km north Baldecitos, ruta provincial 26, La Rioja: reddish fine sand mixed with stones, low selection; shrubs about 2 m high.

BP (Patagonia, < 500 m) = Bosque Petrificado, intersection of rutas provinciales 27 and 29, Chubut: mostly firm substrate, flat, open area, small stones, petrified wood from small to large trunks; very low shrubs (up to 20 cm high).

CA (Monte transition to Prepuna, 2100 m) = San José, about 15 km south of Cachi, ruta nacional 40, Salta: hard ground, stones; shrubs.

CF (Monte, 1700 m) = Los Medanos, Cafayate, near ruta nacional 40, Salta (Fig. 11b): sand dunes, fine loose light greyish, highly selected sand; scattered tall yellowish grass, Sporobolus rigens (Graminea); 30-40 cm high shrubs (e. g. Atripplex, Chenopodiaceae; Prosopis, Leguminosae; Zuccagnia, Leguminosae).

CH (Monte, 250 m) = ruta provincial 32, close to intersection ruta provincial 1, Chubut (Fig. 6b): mostly firm sandy clayey soil with small stones mixed with earth; grasses, spiny shrubs about 1 m high; non-spiny shrubs, Baccharis divaricata (Compositae), and Colliguaya integerrima (Euphorbiaceae).

CR (Monte, 1100 m) = 7 Km SW Cortadera, ruta provincial 180 to Matancilla, Departamento Malargüe, Mendoza (Fig. 2b): sand dunes, mostly fine loose sand; small shrubs some with spines.

CT (Patagonia transition to Monte, 1380 m) = 18 Km NE of Cueva del Tigre, SW of Laguna Llancanelo, ruta provincial 186, Departamento Malargüe, Mendoza: firm sandy soil with volcanic rocks; abundant low spiny shrubs.

FQ (Pampa, about 100 m) = Faro Querandí, between Villa Gesell and Mar Chiquita, Buenos Aires: fine loose sand; shrubs, grasses, Spartina coarctata (Gramineae).

HU (Altoandino Calchaquí, 4000 m) = Lagunas de Huaca-Huasi, Cumbres Calchaquies, Tucumán: mountainous, open areas, firm substrate; sparse low vegetation (see Halloy, 1985, for details).

IN (Monte, 380 m) = 20 Km Southeast of Paso de los Indios, ruta provincial 53, going towards El Sombrero, Chubut (Fig. 3): usually firm substrate but some loose greyish sand mixed with small stones (low selection), open spaces; herbs, Hoffmancegia trifoliata (Leguminosae); shrubs about 50-70 cm high, Atriplex aff. lampa (Chenopodiaceae), Chuquiraga cf. ruscifolia (Compositae), Lycium aff. chilense (Solanaceae).

IT (Monte, about 1500 m) = 5.6 Km north from intersection 307 & 40, Tucumán: small area covered with sand dunes, fine loose sand; low shrubs on the side (up to 50 cm), trees further away.

JA (Puna or Monte, 3000 m) = 47 km northwest of Alto Jagüe, Agua Quemada, ruta a Laguna Brava, Departamento Vinchina, La Rioja: mountainous, firm substrate, stones, rocks; sparse vegetation, cacti.

JG (Puna or Monte, 3250 m) = 55 km northwest of Alto Jagüe, Pampa del Leoncito, Dpto Vinchina, ruta a Laguna Brava, La Rioja: mountainous, firm substrate, stones, rocks; sparse vegetation, cacti.

LI (Monte, < 100 m) = Establecimiento Laguna de los Indios, ruta provincial 1, about 20 Km south of Rawson, Chubut: very fine silty sand highly selected, other parts with firm soil; shrubs, Leguminosae, cf Grindelia chiloensis (Compositae), Mulinum spinosum (Umbelliferae).

LN (Monte, 1300 m) = Lago Embalse Nihuil, South of San Rafael, near ruta provincial 186, Mendoza: sandy shores on lake (some areas with loose sand, others with firm substrate, low selection, stones (some volcanic in origin); grasses, Sporobolus riges (Gramineae), shrubs about 50 cm tall and 1 m wide, Rubiaceae and Compositae.

MA (Monte, 1110 m) = Matancilla, 4 Km SE of ruta provincial 180, Departamento Malargüe, Mendoza (Fig. 5b): open area of salty patches and short spiny grasses, surrounded by a zone of volcanic (basalt) rocks, boulders of varying sizes and some areas with light greyish fine sand; shrubs of up to 80 cm high.

MD (Chaco, 500-1000 m) = Sierra de Medina, ruta provincial 310, Departamento Burruyacú, Tucumán (Fig. 12b): firm red clay and sand, low selection, medium sized sand grain, sandstone rocks; grasses (e. g. Stipa, Graminea) and shrubs (e. g. Acacia, Leguminosae).

MN (Monte, 1500-2100 m) = Los Medanitos, ruta 34, North of Fiambalá, Departamento Tinogasta, Catamarca: local habitat unknown.

MT (Monte, 1100 m) = 4 Km NW of Matancilla, intersection of ruta provincial 180 with ruta to Matancilla (no number), Departamento Malargüe, Mendoza: firm substrate, stones, small spiny shrubs.

MZ (Monte, 900-1200 m) = 27 Km northwest of Mendoza city, ruta to Termas de Villavicencio, Departamento Las Heras, Mendoza: firm substrate, small stones, spiny shrubs (up to 1 m high), cacti (up to 50 cm high).

NA (Puna or Altoandino, 3000 m) = 33-36 km East of Paso Aguas Negras, ruta nacional 150, San Juan (Fig. 1b): mountainous, firm substrate, stones; sparse vegetation, grass "paja brava", Festuca (Graminea), small shrubs, "cuerno de cabra", Adesmia (Leguminosae) and Artemisia cf. mendozana, (Compositae).

NC (Puna or Altoandino, about 3000 m) = 41 Km west Paso Aguas Negras, ruta nacional 41, Región de Coquimbo, Departamento Elquí, Chile: same as for NA.

NT (Monte, 1500-2100 m) = 3 Km south of Los Nacimientos, ruta nacional 40, Catamarca: undulating terrain, firm substrate with rocks, generally small spiny shrubs.

PA (Monte transition Altoandino, 3000 m) = Paramillo, ruta nacional 7, Sierra de Uspallata, Mendoza: mountainous, firm substrate, stones; small shrubs, some spiny, sparse.

PB (Monte, 1900-2100 m) = 7 Km SW of Punta de Balasto, ruta nacional 40, Catamarca: flat, sandy, with shrubs.

PE (Monte, 2200-2500 m) = 2 Km east Pie de Medanos, Departamento Santa María, Catamarca: undulated terrain, areas with loose sand; shrubs.

PI (Monte, 900-1500 m) = 5-10 Km NE of Pituil, ruta nacional 40, el Barrial, Departamento Famatina, La Rioja: fine

reddish loose sand; shrubs as high as 2 m forming islands to which lizards escaped.

PM (Monte, 2200-2500 m) = Pie de Medanos, Campo de los Pozuelos, Departamento Santa María, Catamarca: firm substrate but with areas with loose sand, stones, shrubs sparsely distributed.

PP (Monte, < 100 m) = Punta Pirámide, near ruta provincial 2, Peninsula Valdés, Chubut (near "lobería"): sand mixed with stones, shrubs about 1 m high.

PV (Monte, 50 m) = Caleta Valdés, ruta provincial 47, Peninsula Valdés, Chubut (Fig. 7b): not far from ocean with penguins coming to nest on the shore; clayey-silt type soil, dark earth full of plant detritus; herbs, Glandularia (Verbenaceae); small shrubs up to 30 cm, rarely 50 cm high, Chuquiraga cf. ruscifolia (Compositae), Lycium (Solanaceae).

PZ (Monte, 1500-2100 m) = Km 900 and 904, ruta nacional 40, east of Hualfín, Pozuelos, Departamento Santa María, Catamarca: flat, open areas, some loose sand mixed with stones, some sections of firm substrate; small shrubs.

QU (Monte, about 1600 m) = Quilmes, about 3 Km west of intersection of ruta nacional 40 and ruta to Ruinas de Quilmes, Departamento Tafí del Valle, Tucumán: mostly firm sand with stones and rocks; shrubs, jume, Suaeda divaricata (Chenopodiaceae); trees (e. g. algarrobos, Prosopis, Leguminosae).

SM (Monte, about 1700 m) = Santa María, ruta provincial 337, Catamarca: mostly loose sand; shrubs, jume, Suaeda divaricata (Chenopodiaceae), Lycium (Solanaceae), jarilla, Larrea divaricata (Zygophyllaceae); small trees, algarrobo, Prosopis sp. (Leguminosae).

TA (Monte, 900-1500 m) = Talampaya, 50 km south of Villa Unión, ruta provincial 26, La Rioja: some open areas, fine reddish silty sand, stones, shrubs.

TF (Prepuna, 2700-3000 m) = Km 98, ruta provincial 307, Tafí del Valle to Amaicha del Valle, Tucumán: lichen, Rhizocarpon; shrubs, Adesmia horridiuscula (Leguminosae), Baccharis sp. (Compositae), chilca, Flourencia sp. (Compositae), Junellia sp. (Verbenaceae), Justicia sp. (Acanthaceae), Senecio (Compositae), el cardón, Trichocereus pasacana (Cactaceae).

TI (Monte, 900-1500 m) = 20 Km SE of Tinogasta (Medanos), ruta nacional 60, Catamarca (Fig. 4b): sand dunes, fine reddish-beige loose sand, highly selected; small and large shrubs; breas, Cercidium australe (Leguminosae).

VU (Monte, 1000-2000 m) = Villa Unión (km 110.7), ruta provincial 26, Departamento Independencia, La Rioja: local habitat unknown.

APPENDIX C

Biogeographical provinces corresponding to different *Liolaemus* habitats. A brief description of each biogeographical province cited in Appendix B is given (after Cabrera and Willink, 1980, with page numbers given in parentheses).

I. NEOTROPICAL REGION

A. Amazonian Domain

1. Province of the YUNGAS (p. 54): This province extends along the eastern slopes of the Andes, in a narrow band, from Venezuela to northeast Argentina. The climate is humid. Las Yungas Province expands between 500 and 3500 m elevation depending on the latitude. Predominant vegetation is cloud forest, rich in lauraceae and mirtaceae. Above these forests, deciduous woods of *Alnus acuminata*, perennial *Podocarpus* and tussock grasslands are found.

B. Chaqueño Domain

1. CHACO Province (p. 72): In Argentina, it extends from the northern part to the provinces of Córdoba, San Luis and Santa Fé, and from the base of the Cordillera in the West to the Paraná River in the East. It includes aluvial plains and hills of low elevation. The climate is continental and summer rains vary between 500 mm in the west to 1200 m per year in the east. The average yearly temperature is 20 to 23°C. The predominant vegetation is xerophilous deciduous woods, with an undergrowth of grasses, cacti and terrestrial bromeliads. There are also palm trees and shrubs.

2. PREPUNA Province (p. 76): It encompasses dry valleys and slopes in northwest Argentina from Jujuy to La Rioja, between 1000 and 3400 m above sea level. The climate is dry with a short wet and warm season and a long dry and cold season. The vegetation is mostly shrubs mixed with candelabra cacti called cardones.

3. MONTE Province (p. 77): It includes arid areas of Argentina approximately between parallels 27 and 44°, from Salta to northeast Chubut. Sandy plains, dry inland basins,

low mountain slopes are typical. The climate is dry and warm in the northern section and cooler in the southern part. Precipitation varies between 80 and 250 mm per year, whereas the average yearly temperature oscillates between 13 and 15.5°C. Vegetation is mostly shrublands that can reach 1 to 2 meters of height but are much lower (only a few centimeters high) in areas exposed to a lot of wind. Cacti are also present as well as riverine woods (e. g. algarrobo, Prosopis).

4. PAMPA Province (p. 79): It occurs between 30 and 39° south latitude extending over the plains of eastern Argentina. The climate is mild, with rains throughout the year (between 600 and 1200 mm per year depending on the area). The average yearly temperature oscillates between 13 and 17°C. The dominant vegetation is steppe or pseudosteppe of tussock grasses 60 to 100 cm high. There are numerous forb species, and some subshrubs and shrubs as well as some riverine woods.

C. Andino-Patagonic Domain

1. ALTOANDINE Province (p. 84): It includes the high mountains of the Andean Cordillera from Venezuela to Tierra del Fuego. The climate is cold all year long and precipitations are in the form of snow or hail. Average temperatures are low but this is compensated during clear days by the intense solar radiation. Winds can be strong. Soils are loose, sandy or with rocks, totally immature. Vegetation is poor. Scherophyllous grasses, cushion, rosette and creeping plants are typical. There are many endemic genera.

2. PUNA Province (p. 87): It extends between 15 and 27° south latitude between the two arms of the Andean Cordillera. It is usually between 3200 and 4400 m above sea level. The climate is cold and dry with extreme temperatures throughout the year (average yearly temperature 8.5 to 9.5°C). Rains occur during the summer and average between 50 and 700 mm depending on the region. Vegetation is characterized by sparse or open shrublands with bushes of 40 to 150 cm high. In more humid areas grasslands and open woods of queñoas (Polylepis tomentella) are found.

3. DESERT Province (p. 89-90): It occurs on the Pacific coast from a latitude of 5° to 30°. This extensive territory is characterized by a warm climate that is extremely dry due to the effects of Humboldt's cold current. Within this Province is the Coastal Desert District which

corresponds to the most arid zone of the Province and which has very little vegetation. Plants that can be found are species associated with the genus Tillandsia (bromeliads), grasses such as Distichlis spicata and Sporobolus virginicus, and a few small trees such as Prosopis limensis and Salix humboldtiana.

4. CHILENO CENTRAL Province (p. 92): It occurs in central Chile with the exception of the high Cordillera, between parallels 32 and 38° approximately. The climate is Mediterranean. Shrublands are common and alternate with small woods of low trees. There are many endemic species.

5. PATAGONIAN Province (p. 93): Mostly in southern Argentina, it is characterized by plateaus, hills and valleys, with soil usually a mixture of sand and stones, poor in organic matter. The climate is dry and mild to cold, with very strong winds from the west. Precipitation in the form of snow occurs in winter. Average yearly temperature varies between 5 and 13.4°C depending on the area and rainfall oscillates between 100 and 270 mm per year and up to 500 mm in the west. Shrubs alternate with cushion plants. In more humid regions in the west, grass steppes are typical. There are several endemic genera. The most important plant family is Compositae with about 50 genera.

II. Antarctic Region

A. Subantarctic Domain

a. SUBANTARCTIC Province (p. 97): It extends over mountains and valleys in Argentina and Chile between the southern latitudes 35 and 38°. The climate is cool and humid. The average yearly temperature is 9.5°C in the North and 5.4°C in the South. In some regions, precipitation may exceed 5000 mm per year. It rains throughout the year especially in the Summer. In the eastern part of this province, rainfall usually does not go over 700 to 800 mm per year. Vegetation is mostly forest, deciduous or evergreen. There are also meadows and extensive areas of bogs. This province is characterized by plants of austral distribution (e. g. Dacrydium, Laurelia, Lomatia, Nothofagus, etc.). There are many endemic genera.

VITA

Monique Halloy was born in Ixelles, Belgium, on May 25, 1949. She attended elementary school in Zaire and in Belgium, Junior High School in Belmont, Massachusetts, and High School in Tucumán, Argentina, where she graduated in December 1967. She entered the National University of Tucumán and obtained a degree in Psychology in December 1972. For the next few years, she worked part time and had a family. In 1985 she entered the Master's Program in Life Sciences at the University of Tennessee, Knoxville, obtaining her degree in August 1987. She then spent a year in Washington D. C. working at the National Zoo with golden lion tamarins. In 1988 she returned to Tucumán, Argentina, where she worked on lizard behavior at the Fundación Miguel Lillo. In January 1993 she returned to the University of Tennessee, to pursue a doctoral degree in Life Sciences.