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EVOLUTION OF THE BISEXUAL SPECIES OF CAUCASIAN ROCK LIZARDS: A PHYLOGENETIC EVALUATION OF ALLOZYME DATA

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The phylogeny of 12 species of Caucasian rock lizards and ground lizards, genus *Lacerta*, subgenus *Archaeolacerta*, was determined from allozyme data. Three additional species of *Lacerta* formed the outgroup. Of the 35 loci resolved, 20 were phylogenetically informative. Permutation tail probabilities calculated using Hennig86 and RandomCladistics and g_1 statistics obtained in PAUP revealed significant pattern in the data. Our analysis resolved 12 most parsimonious trees, among which were three well-supported monophyletic groups: 1) (*Lacerta alpina, L. caucasica, L. daghestanica)* [the *L. caucasica* group]; 2) (*L. mixta, L. saxicola, L. raddei-nairensis*) [the *L. saxicola* group]; and 3) (*L. parvula, L. portschinskii* (*L. valentini, L. rudis*)) [the *L. rudis* group]. The second and third groups formed a clade. The ground lizards *L. praticola* and *L. derjugini* were resolved as ingroup members, but their placement in the globally most parsimonious trees was ambiguous. A preferred tree was chosen by alternately pruning *L. praticola* and *L. derjugini* from the tree. In doing so, *L. praticola* was resolved as the sister taxon of the *L. caucasica* group, and *L. derjugini* was resolved as the sister taxon of the clade containing the *L. saxicola* and *L. rudis* groups. Our results are somewhat congruent with the morphology-based phylogeny of Darevsky (1967).

Key words: Reptilia, Lacertidae, *Lacerta, Archaeolacerta,* phylogeny, systematics, genetics, Caucasus Mountains, allozymes.

INTRODUCTION

Few assemblages of reptiles have made as strong an impact on our understanding of evolutionary mechanisms and reproduction as have the rock lizards of the Caucasus Mountains. Within this gathering of lacertid lizards of the genus *Lacerta*, subgenus *Archaeolacerta*, unisexuality in reptiles first became known (Darevsky, 1958, 1967) and numerous other investigations have derived from this discovery, for example studies of unisexuality of American whiptail lizards, genus *Cnemidophorus* (e.g., Wright and Lowe, 1968). Perhaps no other species aggregate has had its ecology and behavior so thoroughly described. Yet, with all this wealth of knowledge, there has never been a rigorous evaluation of the phylogenetic relationships of the taxa. Consequently, explanations about the evolution of behavior and ecology have not had the benefit of being based on the evolution of the taxa.

In 1992, we initiated a molecular investigation of the genealogical relationships of the subgenus *Archaeolacerta* from the Caucasus Mountains of southern Russia (Daghestan), Armenia, and Georgia. However, before attempting a reconstruction of the phylogeny of the bisexual species, we investigated the level of population differentiation among the various species of rock lizards. Our investigations have included an examination of population differentiation of *L. caucasica* and *L. daghestanica* (Fu et al., 1995), population genetics of the *L. raddei-nairensis* complex (Bobyn et al., in press), and differentiation among isolated populations within the *rudis* group (MacCulloch et al., 1995a).

Although the maternal parentage of many unisexual Caucasian lacertids has been established (e.g., Moritz et al., 1992), paternal contributions remain to be confirmed, and the phylogenetic constraints on the evolution of unisexuality has never been adequately addressed. Consequently, one of our ultimate goals is to examine this aspect of lacertid evolution, and the potential occurrence of multiple clones within each of the seven unisexual species. We have proceeded by evaluating the occurrence of multiple clones within the parthenogenetic species (e.g., MacCulloch et al., 1995b, in press; Murphy et al., unpublished data). Al-

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though the evolution of unisexuality is intriguing, in this paper, we will address the issue of the phylogeny of most recognized bisexual species as discerned from allozymes.

History of Taxonomy

The Caucasian rock lizards of the subgenus *Archaeolacerta* are a taxonomically challenging assemblage of Palaearctic reptiles. Some of the difficulties stem both from the number of parthenogenetic forms, these readily hybridizing with males of sympatric bisexual species to form sterile progeny, as well as bisexual species hybridizing in contact zones.

The history of our knowledge of the Caucasian rock lizards dates to the nineteenth century, when Eversmann (1834) first described *Lacerta saxicola* from the north Caucasus (in Kislovodsk). Subsequently, a number of new species were described: *Podarcis deflilppii* (Camerano 1877) from northern Iran, *L. portschinskii* (Kessler 1878) from Tbilisi, Georgia, and *L. rudis* (Bedriaga 1886) from the southwestern Caucasus. Judging from the descriptions of these species, the authors doubted the independence of these species. Although Boulenger (1887, 1913, 1920) attached significance to a considerable morphological similarity of these lizards, he considered them only as subspecies of varieties of the widely-distributed southern European species *Lacerta muralis* Laurenti, now placed in the genus *Podarcis* (Arnold, 1989).

The Hungarian herpetologist Méhely (1909) contributed much to returning a species rank to *Lacerta saxicola*. He strongly substantiated the species' independence and proposed to distinguish it with as many as six subspecies and several varieties. In addition, Méhely described a new species, *L. caucasica* from the central Caucasus (Table 1).

Lantz and Cyrén (1936) performed the next revision of the assemblage. They distinguished 14 subspecies in the Caucasus and mountainous regions of Crimea, Asia Minor, and northern Iran (Table 1).

Darevsky (1958, 1967) noted that many of the subspecies of Lantz and Cyrén (1936) retained their distinctiveness in areas of sympatry. He regarded them as species, rather than subspecies. In his monograph, Darevsky (1967) recognized eight polymorphic bisexual species, and 4 parthenoforms (Table 1). He reported that the latter can readily hybridize with sympatric bisexual forms. Based primarily on morphological characters, including body dimensions and numbers of particular scales, Darevsky proposed a speculative phylogenetic scheme, taking into account the phenomenon of partial pholidosis oligomerization that occurred in the evolution of the *Lacerta saxicola* group.

Recently, univariate and multivariate statistical methods have been applied to the study of these lizards and the recognition of both new subspecies and two new parthenogenetic species (Darevsky and Eiselt, 1980; Eiselt and Darevsky, 1991; Eiselt et al., 1992, 1993; Schmidtler et al., 1994). Molecular studies have made further progress in understanding the bisexual and parthenogenetic species of the *L. saxicola* group. Uzzell and Darevsky (1975) used allozymes to demonstrate species independence of *L. parvula*, *L. portschinskii*, *L. raddei*, and *L. valentini*. They also provided the first evidence of the earlier presumed (Darevsky, 1962) hybrid origin of 4 parthenogenetic species. The presumed bisexual maternal parents of the unisexuals was generally confirmed by Moritz et al. (1992) for five different parthenoforms. Fu et al. (1995) used morphological and allozyme data to document the species status of *L. caucasica*, *L. daghestanica*, and *L. alpina*. Their conclusions were congruent with recent morphological studies (Roytberg and Lotiev, 1992; Roitberg, 1994).

Arnold (1989) used morphological data, and Mayer and Lutz (1989) employed albumin immunology to investigate several different species and subspecies of *Lacerta*. Significantly, both found that two Caucasian "ground species," *L. derjugini* and *L. praticola*, that did not formally belong to the rock lizards, were very similar to them. Mayer and Benyr (1994) differentiated the Caucasian *Archaeolacerta* from those of Europe.

Recently, relatedness of the unisexual species and their presumed parental bisexual species was investigated using polymerase chain reaction amplified products obtained by single-primers (Grechko et al., 1993). They demonstrated a close relationship among all bisexual and unisexual species of rock lizards, including the "ground species" *L. derjugini* and *L. praticola*. And with some reservations, this evidence supported the earlier schemes (Darevsky, 1962; Uzzell and Darevsky, 1975) of the hybrid origins of some unisexual *Lacerta*. It now seems that the unisexual species *L. unisexualis* and *L. uzzelli* resulted from hybridizations between the same parental pairs, *L. nairensis* and *L. valentini*, where *L. nairensis* was the maternal parent of *L. unisexualis*, and the paternal parent of *L. uzzelli*, and *L. valentini* the matriarch of

TABLE 1. Historical Overview of Current Species Names of Caucasian Rock Lizards

Méhely, 1909	Lantz and Cyrén, 1936	Darevsky, 1967	Darevsky, 1993 (with modifications)
L. saxicola saxicola (**forma typica**)	*L. saxicola saxicola*	**Bisexual species:**	**Superspecies:**
	L. s. armeniaca	*L. saxicola saxicola*	***L. saxicola*** **Eversmann**
L. s. var. *brauneri*	*L. s. bithynica*	*L. s. bithynica*	
L. s. var. *chalybdea*	*L. s. brauneri*	*L. s. brauneri*	**Bisexual species:**
L. s. var. *defilippii*	*L. s. caucasica*	*L. s. darevskii*	***L. caucasica*** **complex**
L. s. armeniaca	*L. s. defilippii*	*L. s. daghestanica*	*L. alpina*
L. s. bithynica	*L. s. lindholmi*	*L. s. defilippii*	*L. caucasica*
L. s. gracilis	*L. s. mehelyi*	*L. s. lantzicireni*	*L. daghestanica*
L. s. rudis	*L. s. mixta*	*L. s. lindholmi*	*L. clarkorum*
L. s. valentini	*L. s. parvula*	*L. s. nairensis*	*L. defilippii*
	L. s. portschinskii	*L. s. parvula*	*L. mixta*
L. caucasica	*L. s. obscura*	*L. s. portschinskii*	
L. mixta	*L. s. rudis*	*L. s. raddei*	
	L. s. tristis	*L. s. szczerbaki*	
		L. s. tristis	***L. parvula*** **complex**
		L. s. valentini	*L. p. parvula*
			L. p. adjarica
		L. rudis rudis	
		L. r. macromaculata	***L. portschinskii*** **complex**
		L. r. obscura	*L. p. portschinskii*
			L. p. nigrita
		L. caucasica caucasica	
		L. c. alpina	***L. raddei*** **complex**
			L. r. raddei
		L. mixta	*L. r. vanensis*
			L. r. nairensis
		Unisexual species:	***L. rudis*** **complex**
		L. armeniaca	*L. r. rudis*
		L. dahli	*L. r. bithynica*
		L. rostombekovi	*L. r. bischoffi*
		L. unisexualis	*L. r. chechenica*
			L. r. macromaculata
			L. r. obscura
			L. r. svanetica
			L. saxicola **complex**
			L. s. saxicola
			L. s. brauneri
			L. s. darevskii
			L. s. lindholmi
			L. s. szczerbaki
			L. valentini **complex**
			L. v. valentini
			L. v. lantzicireni
			L. v. spitzenbergerae
			Unisexual hybridogenous species:
			L. armeniaca
			L. dahli
			L. rostombekovi
			L. unisexualis
			L. uzzelli
			L. sapphirina
			L. bendimahiensis

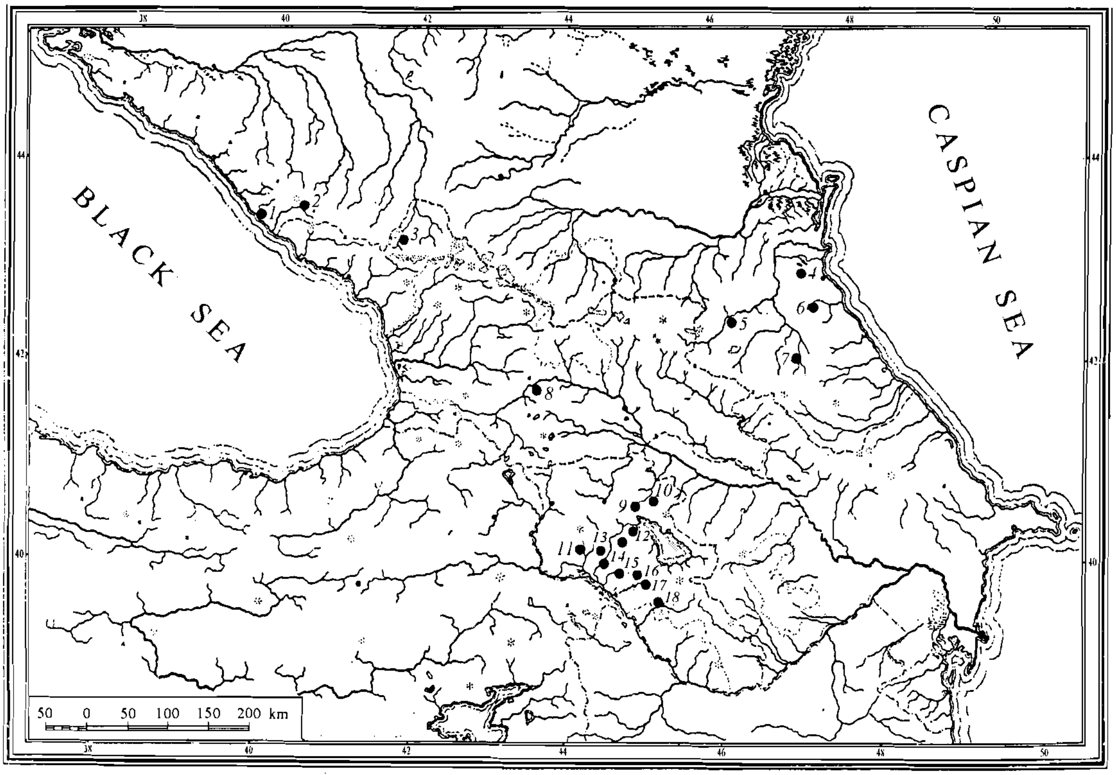

Fig. 1. Map of the Caucasus showing localities of collections. Numbers refer to names provided in Table 2.

L. uzzelli and patriarch of *L. unisexualis* (Moritz et al., 1992).

In virtually all previous studies of *Archaeolacerta*, the practice of phylogenetic systematics has rarely made an impact. Most of the species associations have been made by highly educated guesses, but without the benefit of a formal treatment of the characters and their states deemed to unite groups of lizards. The single application of phylogenetic theory to Caucasian lacertids is that of Moritz et al. (1992).

MATERIALS AND METHODS

Fieldwork in the Caucasus Mountains was conducted from 1992 – 1994. In 1992, we collected in the Republics of Armenia and Georgia, although the frozen tissue samples were subsequently lost in shipment. In 1993, we made collections in southern Russia (Daghestan), and portions of Armenia. Political instabilities prevented collecting in Georgia. In 1994, we made further collections in Armenia, but again political instabilities prevented re-collecting key sites along the border of Armenia and Azerbaijan. Some additional material was made available to us by colleagues. A summary of both ingroup and outgroup taxa included in this study, their localities of collecting (Fig. 1), and sample sizes used in our data gathering is provided in Table 2. Three species of related lacertids, two from the Caucasus Mountains, were used as the outgroup, including *L. media*, *L. strigata*, and *L. vivipara*. As supported by Mayer and Lutz (1989), we assume that none of these taxa are members of our ingroup.

Within two days of collecting, most lizards were euthanized by an overdose of sodium pentobarbital following accepted animal welfare protocols. Blood, heart, liver, and tail muscle were dissected and frozen in liquid nitrogen. Most juvenile lizards were frozen whole in LN2. Subsequent to return to the laboratory, tissue samples were maintained at – 75°C until processing. All processing occurred within one year of collecting.

Voucher specimens were initially preserved in 10% formalin, and subsequently transferred to 65% ethanol. All voucher specimens are deposited in the

TABLE 2. Species of *Lacerta* Examined in This Study, Sample Size (*n*), Locality Shown in Fig. 1 (Map), and Locality by Name and Coordinates

Species	*n*	Map	Locality
L. alpina	5	*2*	Russia, Krasnodar, Aishkho Mountain, 45°02′ N, 39°00′ E
L. caucasica	11	*4*	Russia, Daghestan, Khvarshi, 42°21′ N, 46°06′ E
L. daghestanica	32	*5*	Russia, Daghestan, Gengutai, 42°40′ 36″ N, 47°14′07″ E
	30	*7*	Russia, Daghestan, Kuli, 42°01′18″ N, 47°14′42″ E
	15	*4*	Russia, Daghestan, Khvarshi, 42°21′ N, 46°06′ E
L. derjugini	2	*8*	Georgia, Achaldaba, 41°54′24″ N, 43°30′05″ E
L. media	7	*17*	Armenia, Azat River near Geolazar, 40°18′ N, 44°46′ E
	3	*13*	Armenia, Abovyan, Arailer Mountain, 40°24′ N, 44°29′ E
	1	*16*	Armenia, Vartashen, 40°00′ N, 44°52′ E
L. mixta	6	*8*	Georgia, Achaldaba, 41°54′24″ N, 43°30′05″ E
L. nairensis	33	*14*	Armenia, Yerevan, 40°11′50″ N, 44°29′48″ E
	8	*19*	Armenia, Adis Mountain, 40°23′ N, 44°42′ E
	30	*11*	Armenia, Aragatz Mountain, Bjurakan, 40°21′54″ N, 44°15′12″ E
L. parvula	9	*8*	Georgia, Achaldaba, 41°54′24″ N, 43°30′05″ E
L. portschinskii	39	*10*	Armenia, Gosh, 40°44′51″ N, 45°01′26″ E
L. praticola	1	*9*	Armenia, Papanino, 40°44′39″ N, 44°49′14″ E
	10	*1*	Russia, vicinity of Sochi, 43°35′ N, 39°46′ E
L. raddei	3	*18*	Armenia, Yekhegnadzor, 39°45′ N, 45°08′ E
	30	*16*	Armenia, Geghart, 40°08′15″ N, 44°49′06″ E
	30	*17*	Armenia, Chosrov National Park, 40°00′54″ N, 44°54′36″ E
	30	*10*	Armenia, Gosh, 40°44′51″ N, 45°01′26″ E
L. rudis	26	*8*	Georgia, Achaldaba, 41°54′24″ N, 43°30′05″ E
L. saxicola	3	*3*	Russia, Dombay, 43°15′ N, 41°45′ E
L. strigata	3	*4*	Russia, Daghestan, Kumtorkala, 43°00′50″ N, 47°14′45″ E
L. valentini	26	*19*	Armenia, Gegam Range, Adis Mountain, 40°23′ N, 44°42′ E
	33	*12*	Armenia, Sevan, 40°30′58″ N, 44°56′26″ E
L. vivipara	1	–	Sweden, Uppsala, 59°55′ N, 17°38′E

herpetological collections of the Royal Ontario Museum (specific data available on request).

Protein electrophoresis, staining protocols, and enzyme and locus nomenclature follow Murphy et al. (1996). Buffer combinations for resolving locus products are given in Fu et al. (1995), MacCulloch et al. (1995a), and Bobyn et al. (in press). We attempted to resolve each locus product on a minimum of two different buffer systems to minimize hidden variation. All allelic products were required to have a minimum of 1-cm migration from the origin before scoring.

In one instance, the data for two putative species were combined. Bobyn et al. (in press) could not differentiate unequivocally the species *L. nairensis* and *L. raddei* with allozymes. No fixed allelic differences separate the two taxa, and, in fact, a "phylogenetic" clustering of the populations based of the allelic frequency data resulted in polyphyletic relationships in both taxa. Therefore, we have combined the allelic data for these two taxa. It should be noted, however, that in the interest of nomenclatoral stability we recommend recognition of these two taxa as species pending the results of further investigations. Eiselt et al. (personal communication) are evaluating morphological characteristics, and Fu et al. are completing a mitochondrial DNA cytochrome b gene sequence investigation.

Our phylogenetic analysis followed the recommendations of Murphy (1993) and Murphy and Lovejoy (in press). The following rules for coding allelic combinations were used: 1) unique alleles in polymorphic arrays were ignored when they could be interpreted as autapomorphies and contribute nothing to branching patterns [e.g., mIdh-A (a), (c), (d); Table 3]. The alleles remaining were used in the phylogenetic analysis; 2) when multiple alleles were shared between the ingroup and outgroup, the hypothetical ancestor was allowed to be polymorphic. In order to avoid the coding of loss events (Murphy, 1993; Murphy and Lovejoy, in press), the presence of either allele was considered as the same state for data analysis (e.g., sAcoh-A; Table 3); 3) losses of relatively plesiomorphic alleles were ignored in the first two levels (Murphy, 1993) of analysis; 4) when allelic arrays could be unambiguously ordered using functional ingroups and outgroups (Watrous and Wheeler, 1981; Murphy et al., 1983), these were evaluated as additive (ordered) states; 5) for those arrays in which partial ordering was possible, these were evaluated using Sankoff (step function) matrices following Siddall and Murphy (unpublished); 6) multiple allelic arrays were evaluated as nonadditive (unordered) when no alleles were shared among the defined arrays. In our evaluation, all alleles were considered, regardless of their frequency of occurrence.

To facilitate comparisons, we constructed a hypothetical ancestor to represent all defensible ancestral allelic compositions. This approach to data analysis also serves to delete from analyses multiple trees arising from ambiguous relationships among outgroup members, and to allow fit measures of the data to reflect ingroup taxa only. These considerations are significant when multiple taxa are used in the outgroup, as is preferred.

Two tests were used to examine the strength of pattern in our data. Permutation tail probability tests (PTP; Faith, 1991; Faith and Cranston, 1991) were accomplished using RandomCladistics (Siddall, 1995) in association with Hennig86 (Farris, 1988). As an alternative, g_1 statistics (Sokal and Rohlf, 1981) were examined using PAUP ver. 3.1.1 (Swofford, 1993) based on the calculation of 100,000 randomly generated trees.

The re-coded data were heuristically evaluated using PAUP ver. 3.1.1 (Swofford, 1993). In some evaluations, multistate characters were treated as having nonadditive (unordered) states (Table 3). Heuristic searches involved keeping minimal length trees only, stepwise addition performed as random additions with an eight digit integer seed number, 10 repeats, and 20 equally parsimonious trees held for branch swapping. Branch swapping was performed using tree bisection – reconnection, steepest descent, and holding all most parsimonious trees (MPTs). Examination of character state optimizations and tree branch lengths was accomplished using MacClade ver. 3.04 (Maddison and Maddison, 1992).

Following initial evaluation, all synapomorphic and basally symplesiomorphic alleles were re-examined using additional electrophoretic buffer combinations to assure estimates of homology and further minimize artificial homoplasy resulting from an incorrect identification of homologues. The original data base was subsequently modified, and the data were re-coded for a final evaluation.

Final trees were examined using a variety of tree selecting methods, including successive approximations (Farris, 1969), functional ingroup – functional outgroup (Watrous and Wheeler, 1981; Fu and Murphy, in press), taxon pruning, and the addition of losses of relatively plesiomorphic alleles (Murphy, 1993). The latter was accomplished by including all allelic arrays in the data matrix thereby having polymorphic states, and evaluating all characters as nonadditive. Tree comparisons and evolution of specific characters was examined using MacClade.

Bootstrap (BS) values (Felsenstein, 1985) were calculated for the nodes on the preferred tree using RandomCladistics ver. 3.0 (Siddall, 1995) to examine relative strength of support. We do not believe that low BS values necessarily indicate a lack of confidence in a node, but rather that relatively few character state transformations occur. A single, highly conserved transformation may support a node, but if this is the only support, then BS evaluations incorrectly may deem the support insignificant.

RESULTS

Table 3 summarizes the 35 loci encoding 178 alleles resolved for the 12 ingroup taxa, and the 3 outgroup species. Discontinuous alphabetic series of alleles owe to the presence of hybrid individuals not considered further in this study; these will be dealt with in a subsequent report. Genotypic frequencies for *L. caucasica*, *L. daghestanica*, and *L. alpina* are given in Fu et al. (1995), *L. valentini*, *L. rudis*, and *L. portschinskii* in MacCulloch et al. (1995a), and *L. nairensis* and *L. raddei* in Bobyn et al. (in press). The unpublished genotypic data are available on request.

Upon examination, 13 loci are seen to be phylogenetically uninformative, including Ada-A, Ck-A, Gda-A, βGlur-A, Gtdh-A, G6pdh-A, βGa-A,

TABLE 3. Loci and Alleles Resolved Among 15 Species of *Lacerta*. Alleles in Parentheses were Eliminated from the Phylogenetic Evaluation Because Their Presence either would be Interpreted as Autapomorphic, or Their Loss Events would be Considered Synapomorphic States (Murphy, 1993; Murphy and Lovejoy, in press)

Species	Loci								
	sAat-A	mAat-A	sAcoh-A	mAcoh-A	Acp-B	Ada-A^1	Cat-A	Cpb-A	Ck-A^1
Ingroup taxa									
L. alpina	g	b	b	a	c	b	f	c	b
L. caucasica	b, (e)	b	d^5	g	j	b	?	d	b
L. daghestanica	b, (e, g)	b	(b, d), f	g	(a), j	b	f	d	b
L. derjugini	g	c	g	d	d	b	f	c	c
L. mixta	b, (e)	c	a, (b, d)	b	k	b	a	c	b
L. parvula	g	c	b	d	i	b	f	c	b
L. portschinskii	d	c	h	d	i	b	f	c	b
L. praticola	g	c	b	a	?	b	f	c	b
L. raddei–nairensis	(e), g	c	(b, d), e	d, (e)	(b), c	b	c, (e)	c	b
L. rudis	d	c	(b), c, (d)	d	g	b	d	c	b
L. saxicola	e	c	b	d	d	b	a, (f)	c	b
L. valentini	d	c	(b), c, (d)	i	h	b	d	c	b
Outgroup taxa									
L. media	f	c	b	f	e	a	g, (h)	(a), c	b
L. strigata	f	c	b, (d)	c	f	c	g	c	a
L. vivipara	a	a	b	h	d	c	?	b	b
Hypothetical ancestor^2	e	c	b, (d)	d	d	?	f	c	b
Level of resolution^3	2	1	1	2	1	1	2	1	1
Character type^4	O	O	U	U	U	Del	O	O	Del

Species	Loci								
	Ck-C	Est-D	Gta-A^1	βGlus-A^6	βGlur-A^1	Gpi-A	Gpi-B	Gtdh-A^1	G6pdh-A^1
Ingroup taxa									
L. alpina	c	c	a	b	d	b	e	b	c
L. caucasica	b, (c)	c	a	b	d	(b), d	d	a	b
L. daghestanica	b	c	a	b	d	(b), d	d	a	b
L. derjugini	c	c	a	b	d	c	i	a	b
L. mixta	b	d	a	b	d	b	b	a	b
L. parvula	b	c	a	b	d	b	k	a	b
L. portschinskii	b	c	a	b	d	b	h	a	b
L. praticola	b	c	a	b	d	f	a	a	b
L. raddei–nairensis	(a), b	(a), (c), d	a	(a), b, (c)	d	(b), c, (e)	j	a	b
L. rudis	c	c	a	b	d	a, (b)	h	a	b
L. saxicola	b	c	a	b	d	(b), f	g	a	b
L. valentini	c	c	a	b	d	b	h	a	b
Outgroup taxa									
L. media	c	c	a	c	a	b	l	a	d
L. strigata	c	c	a	c	c	b	c	a	a
L. vivipara	c	(b), c	a	d	b	b	f	a	b
Hypothetical ancestor^2	c	c	a	c	?	b	?	a	b
Level of resolution^3	1	1	1	1	1	1	2	1	1
Character type^4	O	O	Del	Del	Del	U	U	Del	Del

TABLE 3. (continued)

Species	Loci							
	βGa-A[1]	mIdh-A[1]	sIdh-A[1]	Ldh-A[1]	Ldh-B	sMdh-A[1]	mMdh-A[1]	sMdhp-A
Ingroup taxa								
L. alpina	a	b	e	b	f	a	d	f
L. caucasica	a	b	e	b	f	a	d	f
L. daghestanica	a	b	e	b, c	f	a	d	f
L. derjugini	a	b	e, f	b	a	a	d	h
L. mixta	a	b, c	e	b	d	a	d	g
L. parvula	a	e	b	b	e	a	d	f
L. portschinskii	a	b	e	b	e	a	d	f
L. praticola	a	b	e	b	f	a	d	f
L. raddei–nairensis	a	a, b	a, e	a, b	d	a	d	g
L. rudis	a	b	e	b	e	a	d	f
L. saxicola	a	b	e	b	d	a	d	d
L. valentini	a	b	e	b	e	a	d	f
Outgroup taxa								
L. media	a	e	e	d	b	a	b	b
L. strigata	a	f	d	d	c	a	c	a
L. vivipara	a	b	g	b	c	a	a	c
Hypothetical ancestor[2]	a	b, e	e	b	c	a	?	f
Level of resolution[3]	1	1	1	1	1	1	1	2
Character type[4]	Del	Del	Del	Del	U	Del	Del	U

Species	Loci								
	mMdhp-A	Mpi-A	Pep-B	Pgm-A[6]	Pk-A[1]	Pnp-A	sSod-A	mSod-A	Tpi-A
Ingroup taxa									
L. alpina	c	h	d, (g)	d	a	b, (d)	b	a	d
L. caucasica	c	f	k	d	a	b, (d)	c	a	g
L. daghestanica	c	c	(h), k	(b), d	a	b, (d)	c	a	g
L. derjugini	d	j	c	d	b	d	b	c	f
L. mixta	c	g	n	d	a	d	c	b	d
L. parvula	e	e	e	d	a	d	b	c	c
L. portschinskii	e	i	(b), c	(b), d	a	e	b	c	d
L. praticola	g	k	l	d	a	d	b	c	d
L. raddei–nairensis	h	l	c, (j)	(b), d	a	b, (c), (d)	c	c	a, (d)
L. rudis	f	i	c	d	a	(d), e	b	c	d
L. saxicola	c	l	c	d	a	d	c	c	a, (d)
L. valentini	f	i	c	(a), d	a	e	a, (b)	?	d
Outgroup taxa									
L. media	c	a	m	b	a	d	b	d	b
L. strigata	a	d	i	b	a	a	b	d	b
L. vivipara	b	b	a	b, (c)	a	d	b	d	e
Hypothetical ancestor[2]	c	?	c	b	a	d	b	c	d
Level of resolution[3]	1	3	2	1	1	2	1	2	3
Character type[4]	U	U	U	Del	Del	O	O	O	U

[1] Void of phylogenetic information and deleted from analyses.

[2] Based on alleles shared between either the taxonomic ingroup and outgroup, or functional ingroup and outgroup.

[3] 1) Character states polarized by taxonomic outgroups; 2) polarization by functional outgroups; 3) character status determined during third pass through data.

[4] Del) Deleted from phylogenetic evaluation; O) character states evaluated as ordered (additive); U) character states evaluated as unordered (nonadditive).

[5] Plesiomorphic allele "d" was coded as the alternative plesiomorphic "b" for the parsimony analysis.

[6] This locus provides a synapomorphic allele diagnosing the ingroup. However, in terms of ingroup relationships the locus is uninformative and, therefore, it was deleted from the phylogenetic treatment.

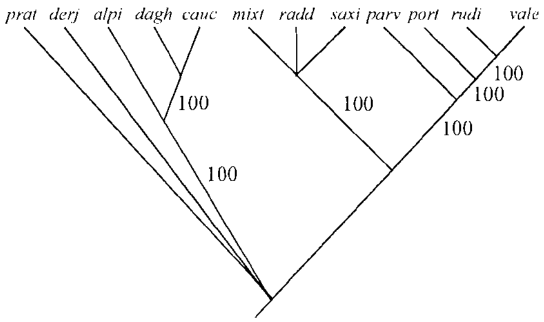

Fig. 2. A 50% majority rule consensus tree derived from 12 most parsimonious solutions resolved from Caucasian rock lizards, genus *Lacerta*, subgenus *Archaeolacerta*. Numbers indicate the frequency of occurrence of nodes. Abbreviations are as follows: *prat*) *Lacerta praticola*; *derj*) *L. derjugini*; *alpi*) *L. alpina*; *dagh*) *L. daghestanica*; *cauc*) *L. caucasica*; *mixt*) *L. mixta*; *radd*) *L. raddei* and *L. nairensis*; *saxi*) *L. saxicola*; *parv*) *L. parvula*; *port*) *L. portschinskii*; *rudi*) *L. rudis*; and *vale*) *L. valentini*.

mIdh-A, sIdh-A, Ldh-A, sMdh-A, mMdh-A, Pk-A. In these loci, either no variation occurs among ingroup members, or all variation can be interpreted as autapomorphic. Alleles at two loci, Glus-A(b) and Pgm-A(d) serve as unambiguous synapomorphies for the ingroup because of polymorphic allelic arrays in one or more ingroup members in which the plesiomorphic allele is shared with an outgroup member. However, these two loci add no information about ingroup member relationships and therefore both are deleted from the phylogenetic analyses. The remaining 20 potentially informative loci are coded for phylogenetic evaluation. Table 3 gives the coding of these loci, designation as to the use of functional outgroups to polarize the states (level 2 of Murphy, 1993), and whether or not the characters are evaluated as having either additive (ordered) or nonadditive (unordered) states.

Following coding, the data are analyzed for pattern. Our PTP test, which includes 999 randomizations of the data, revealed significant pattern to the data ($p < 0.001$). The shortest tree found by Hennig86 had a length of 85 steps, whereas the shortest tree based on a randomization of the data had a length of 94 steps. However, our simulation tests have shown that even one well-resolved branch among 10 taxa can result in a significant PTP. As an independent measure of pattern in the data, we calculated the g_1 statistic based on 100, 000 randomly chosen trees and found the value to be -1.057 ($p < 0.01$; Hillis and Huelsenbeck, 1992; Huelsenbeck, 1991; see Källersjö et al., 1992 for a criticism of the significance of this approach). Consequently, these measures provided evidence that we may confidently make some phylogenetic inference from the data, and that further analyses of the data were warranted. Because both indices indicated the presence of structure in the data, we proceeded with our evaluation.

Our initial estimations of relationships resulted in the resolution of 12 most parsimonious trees (length = 85 steps, CI = 0.871, RI = 0.771). A 50% majority rule consensus tree is shown in Fig. 2. Three stem monophyletic groups were resolved, including the following sets of relationships: 1) (*alpina*(*caucasica*, *daghestanica*)), 2) (*mixta*, *raddei-nairensis*, *saxicola*), and 3) (*parvula*(*portschinskii*(*rudis*, *valentini*))). Successive approximations evaluations based on the retention index and the rescaled consistency index, and with a maximum scaled weight of 10, failed to reduce the number of MPTs. All characters retained a weight of greater than 50% except for Gpi-A, which received a weight of 30%. Characters receiving less than maximum weight (i.e., characters with homoplastic states) included sAat-A, mAcoh-A, Acp-B, Ck-C, Pnp-A, and sSod-A.

Examination of all trees showed that much of the instability was owing to unstable relationships of the two ground species, *L. derjugini* and *L. praticola*, both to one another and to the 3 stable clades. Because the ambiguous relationships of one taxon can cause great tree instability, especially if this is depicted in a consensus tree (Miyamoto, 1985), we performed analyses pruning each and both of these species. Elimination of *L. derjugini* resulted in the resolution of 18 trees with relationships identical to previous analyses with one exception; *L. praticola* was resolved as the sister taxon of the *caucasica* group in 10 trees, as was *L. mixta* with *L. raddei-nairensis*. Upon pruning *L. praticola* and reinstating *L. derjugini*, 2 MPTs were resolved, the lack of resolution owing to the *saxicola* group. In this analysis, *L. alpina*, *L. caucasica* and *L. daghestanica* formed the sister group to the remaining lizards, *L. praticola* was next to branch off, and the *saxicola* group was the sister group to the *rudis* group, including *L. valentini*, *L. rudis*, *L. portschinskii*, and *L. parvula*.

Upon deleting both *L. praticola* and *L. derjugini*, 2 trees were resolved. The instability owed to the relationships of *L. mixta*, *L. saxicola*, and *L. raddei-nairensis* where the latter was resolved as the sister taxon of either one or the other of the remaining two species in the clade. In both trees the *saxicola* and *rudis* groups were resolved as sister taxa. Together, they formed the sister group of the *caucasica* group.

In an attempt to further resolve the relationships among the ingroup taxa, the *caucasica* group, including *L. praticola*, was used as a functional outgroup, and the hypothetical ancestor was deleted from the data set. A parsimony analysis yielded 11 MPTs. Among these trees, *L. derjugini* was most frequently (6 of 11 trees) resolved as the sister taxon of the stable clade containing *L. parvula*, *L. portschinskii*, *L. valentini*, and *L. rudis*.

Finally, we allowed for allozyme loss data to be incorporated into our analysis by evaluating the unedited data set (including all alleles), and evaluating all characters as nonadditive. Our parsimony evaluation resolved 73 MPTs. The relationships resolved in this evaluation differed significantly from those that considered derived states only. For example, not only were far more MPTs resolved, but *L. alpina* was no longer unambiguously resolved as the sister taxon of *L. caucasica* and *L. daghestanica*. These latter 2 taxa were the sister group of the *L. saxicola* clade and not basal to all other taxa. The clade containing *L. parvula* was resolved as before. Although similarities such as this latter example exist, the exclusion of *L. alpina* from the *L. caucasica – L. daghestanica* association is problematic, as is the association of *L. daghestanica* and *L. caucasica* with the *saxicola* group. Thus, we believe that, as warned by Murphy (1993) and expanded by Murphy and Lovejoy (in press), allozyme loss data should not be used in phyletic analyses of allozyme data.

Figure 3 shows our preferred tree. It reflects relationships resulting from the alternate pruning of both *L. praticola* and *L. derjugini*. In this figure, *L. praticola* is resolved as the sister taxon of the *caucasica* group. *Lacerta derjugini* is resolved as the sister taxon of the clade uniting the *saxicola* and the *rudis* groups. The sister relationship of *L. raddei-nairensis* with *L. saxicola* reflects our incomplete mtDNA sequence data. BS values are given at the base of each node.

No characters unambiguously associated *L. raddei-nairensis* with either *L. mixta* or *L. saxicola*. Preference for a sister relationship of *L. raddei-nairensis* with *L. mixta* would be based on an absence of variation in their common ancestor in Est-D, and a variable ancestor in Tpi-A. Alternatively, the association of *L. raddei-nairensis* with *L. saxicola* would be based on the opposite scenario. We cannot choose between these two scenarios. *Lacerta mixta* and *L. saxicola* were never resolved as sister taxa in our evaluations. A preliminary evaluation of a mtDNA cytochrome b sequence data set (Fu et al., unpublished data) associated *L. nairensis* with *L. saxicola*, and this tentative association is depicted in our preferred tree.

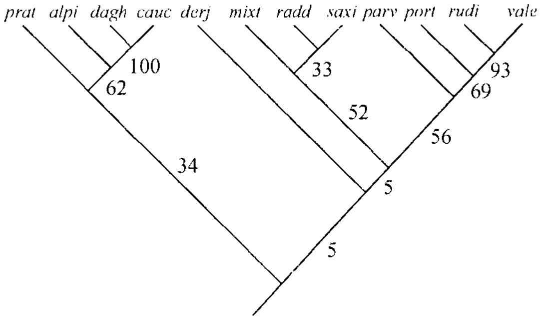

Fig. 3. Our preferred cladogram depicting the relationships among Caucasian rock lizards included in this study. Numbers give the bootstrap values. Abbreviations as in Fig. 2.

DISCUSSION

Our tree provides a reasonably robust explanation of the phylogenetic relationships of the Caucasian *Archaeolacerta*. Most nodes in the cladogram are unambiguously supported. However, we would consider the placements of *L. praticola* and *L. derjugini* tentative, as is the association of the *saxicola* clade with the remaining lizards exclusive of the *caucasica* group. Further refinements in relationships must await additional data, preferably both morphological and molecular in nature. Although additional molecular data are highly desirable, we are doubtful that significant additional information will be derived from allozymes.

Comparison of Hypotheses

The only previous assessment of evolutionary relationships of the Caucasus *Archaeolacerta* is that of Darevsky (1967) based largely on morphology. Our hypothesis is compared to his in Fig. 4. For taxa common to both hypotheses, Darevsky's tree requires 78 steps (allowing for the most parsimonious resolution of his unresolved nodes) whereas our tree(s) requires only 67 steps (a reduced number of steps from our global trees due to deleted taxa in comparison to Darevsky, 1967). The retention index (Farris, 1989) increases from 0.57 for Darevsky's hypothesis to

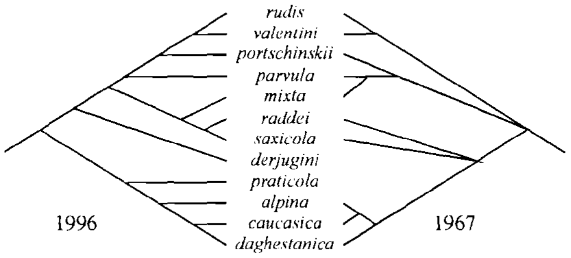

Fig. 4. A comparison of our preferred tree (1996) with that of Darevsky (1967) (right).

0.86. Our cladogram is identical to Darevsky's tree in several respects. First, Darevsky (1967), like us, also believed that *L. rudis* and *L. valentini* were sister taxa. Second, both Darevsky (1967) and this study included *L. alpina*, *L. caucasica*, and *L. daghestanica* as sister taxa. The two differences in this group are the taxonomic level assigned to the taxa, and the association of *L. caucasica* with *L. daghestanica*. Darevsky (1967) believed the taxa to be subspecies whereas recently it has been demonstrated that all three should be considered as species on both molecular (Fu et al., 1995) and morphological bases (Roytberg and Lotiev, 1992; Roitberg, 1994; Fu et al., 1995). Apart from these associations, few similarities occur.

Darevsky (1967) considered *L. mixta* to be the closest relative of *L. parvula*, and together these were the sister group of *L. portschinskii*. Our analysis supports this association only in the inclusion of *L. parvula* and *L. portschinskii* in the same clade, but not as sister taxa. We found *L. mixta* to be excluded from this clade, and *L. rudis* and *L. valentini* to be the terminal sister taxa.

Darevsky (1967) depicted *L. raddei* and *L. saxicola* as sister taxa to the *caucasica* group, but the relationships of *L. saxicola* to *L. raddei* were unresolved. Our analysis differs in two respects. First, the *saxicola* and *caucasica* groups are not considered sister groups. Second, *L. raddei* and *L. saxicola* also have *L. mixta* as a sister taxon; *L. mixta* does not appear to be closely related to either *L. derjugini* or *L. portschinskii*. The relationships among the three members of the *saxicola* group, however, are uncertain and must be resolved with additional data. This lack of accord between results based on molecular and morphological data likely illustrates differences in methods of analyses, and not the superiority of one form of data.

Hybridization, Homoplasy, and Ambiguous Nodes

Hybridization among bisexual species of sympatric Caucasian *Archaeolacerta* is common place, at least in some populations. Both morphological data (Darevsky and Danielyan, 1968; Darevsky et al., 1978, 1985) and molecular markers (Fu et al., 1995; Murphy et al. unpublished data) have documented instances of hybridization and backcrossing. Consequently, homoplasy resulting from the acquisition of derived alleles though introgressive hybridization might be expected. If the acquisition of alleles through introgressive hybridization has occurred recently, then we would expect to observe the homoplastic occurrence in sympatric populations of different species, or within single, sympatric species only. We would not expect to find homoplastic alleles among sister taxa within two different clades. If the hybridization events are much older, then the homoplasy might be more widespread. Because the former pattern was found, our data seem to reflect that such events are very limited.

Among vertebrates, creatine kinase (CK) is one of the best studied enzyme systems. Ck-C allozymes appear homoplastic on our preferred tree. Plesiomorphic Ck-C(c) is fixed in *L. alpina*, *L. derjugini* and the clade uniting *L. rudis* and *L. valentini*. An established trend of CK allozymes is the absence of heterozygotes among squamate reptiles (Buth et al., 1985). In Caucasian *Archaeolacerta*, Ck-C is no exception to this rule. Among the bisexual and parthenogenetic unisexual species of *Lacerta* evaluated to date, we have observed CK heterozygosity only in either (1) parthenoforms whose parents express different alleles, or (2) bisexual individuals that (a) have an excess of heterozygotes, and (b) occur sympatrically with another bisexual species expressing an alternative allele. In such cases hybridity is implicated. Given the exceptional absence of heterozygotes concomitant with interspecific variability, we believe that the allelic distributions from Ck-C may be unreliable due to an apparently strong selection pressure for the occurrence of a single allele only. Ck-C heterozygotes have been reported in *L. caucasica* and it seems likely that this derives from hybridization with sympatric *L. alpina*. Fixation of the plesiomorphic allele in *L. derjugini*, and the clade uniting *L. rudis* and *L. valentini* would seem to reflect either a reversal to the plesiomorphic allozyme, or a more ancient hybridization event.

At mAcoh-A, *L. raddei-nairensis* and *L. saxicola* share the apomorphic allele mAcoh-A(d). In addition, mAcoh-A(a) occurs in both *L. alpina* and *L. praticola.* However, if widespread (d) were considered as plesiomorphic, making the hypothetical ancestor polymorphic, then no homoplasy would be observed.

In every other instance of homoplasy in our data set, recent introgressive hybridization is not a viable explanation. For example, sAat-A(b) is homoplastic in being shared among *L. caucasica*, *L. daghestanica* and *L. mixta.* Because *L. mixta* does not occur sympatrically with either *L. caucasica* or *L. daghestanica*, recent hybridity is not a viable explanation for this homoplasy. Most other homoplastic distributions of alleles have similar patterns occurring in the absence of sympatry. Consequently, if our allelic homologies are certain, then it seems likely that the homoplasy represents former distributions of species, such as those that might have occurred during Pleistocene glacial maxima. Nonetheless, for most bisexual populations, hybridization is not commonplace, or if it is, then there is little gene flow among the species. To this extent, hybridizations may be highly localized and serving as "hybrid sinks," while unintentionally acting as "hybrid reserves," not only to keep, but also, through intercistronic recombination and other cytogenetic mechanisms, to be a source of novel genetic alternatives.

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