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SPECIES LIMITS, PHYLOGENETIC RELATIONSHIPS, AND ORIGINS OF VIVIPARITY IN THE *SCALARIS* COMPLEX OF THE LIZARD GENUS *SCELOPORUS* (PHRYNOSOMATIDAE: SAURIA)

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ABSTRACT: We electrophoretically assayed 32 gene loci in the *Sceloporus scalaris* complex. We sampled 208 animals from 22 localities representing the following: *Sceloporus aeneus* (12 localities), *S. bicanthalis* (five localities), *S. chaneyi* (one locality), *S. goldmani* (one locality), and *S. scalaris samcolemani* (two localities), and we used *Sceloporus parvus* and *S. variabilis* as outgroups. Of the 32 gene loci, 11 were uninformative, 10 were polymorphic both within and among species, and 11 were polymorphic among species but monomorphic within species. Thirteen diagnostic loci, plus two morphological characteristics (number of canthal scales and male belly patterns) and the type of parity mode present, define a total of eight genetically and/or morphologically distinct ingroup units. Cladistic analysis of these markers suggests at least two separate origins of viviparity within the complex (based on the most parsimonious trees from the cladistic analysis), as well as the possibility of reproductively bimodal groups within the complex. A phylogenetic hypothesis of the complex is presented.

Key words: *Sceloporus scalaris* complex; Species boundaries; Viviparity; Phylogeny; Isozyme electrophoresis

IT HAS generally been hypothesized that the development of viviparity from egg-laying ancestors in squamates is a gradual process (Shine and Bull, 1979) preceded by varying degrees of egg-shell thinning and egg retention (Guillette, 1993). Reptiles having pronounced egg retention may demonstrate some of the steps towards the evolution of viviparity (Guillette, 1993; Shine, 1985). In total, viviparity is believed to have evolved independently in the squamates almost 100 times (Shine and Guillette, 1988).

The genus *Sceloporus* is a New World radiation that contains approximately 70 species (Flores-Villela, 1993; Sites et al., 1992), of which at least 28 are viviparous (Guillette et al., 1980). *Sceloporus* can be divided into a number of different complexes (or species groups) on the basis of presumed phylogenetic relationships (reviewed by Sites et al., 1992). Both egg retention and viviparity can be seen in several of these groups, but with the single exception of the *S. scalaris* complex, all these groups as defined by earlier studies (reviewed by Sites et al., 1992) are either wholly viviparous or wholly oviparous (though some of the latter may show egg retention).

The *S. scalaris* complex contains at least 4–6 species (depending on how certain subspecies are viewed) confined largely to regions of high elevation in northern and central Mexico (Fig. 1). Currently recognized species in the *S. scalaris* complex are *Sceloporus chaneyi* (Liner and Dixon, 1992), *S. goldmani*, *S. scalaris*, and *S. aeneus*, with *S. aeneus bicanthalis* and *S. aeneus subniger* being treated either as additional species (Davis and Smith, 1953; Guillette, 1993), or as subspecies of *S. aeneus* (with a third subspecies being *S. aeneus aeneus*: see Smith and Hall, 1974; Thomas and Dixon, 1976). *Sceloporus scalaris* also has been divided into the subspecies *S. scalaris scalaris*, *S. s. slevini*, *S. s. unicanthalis*, and *S. s. samcolemani* (Guillette and Smith, 1985), but these have generally been accepted as geographic variants of the same species (see also Thomas and Dixon, 1976). The species of

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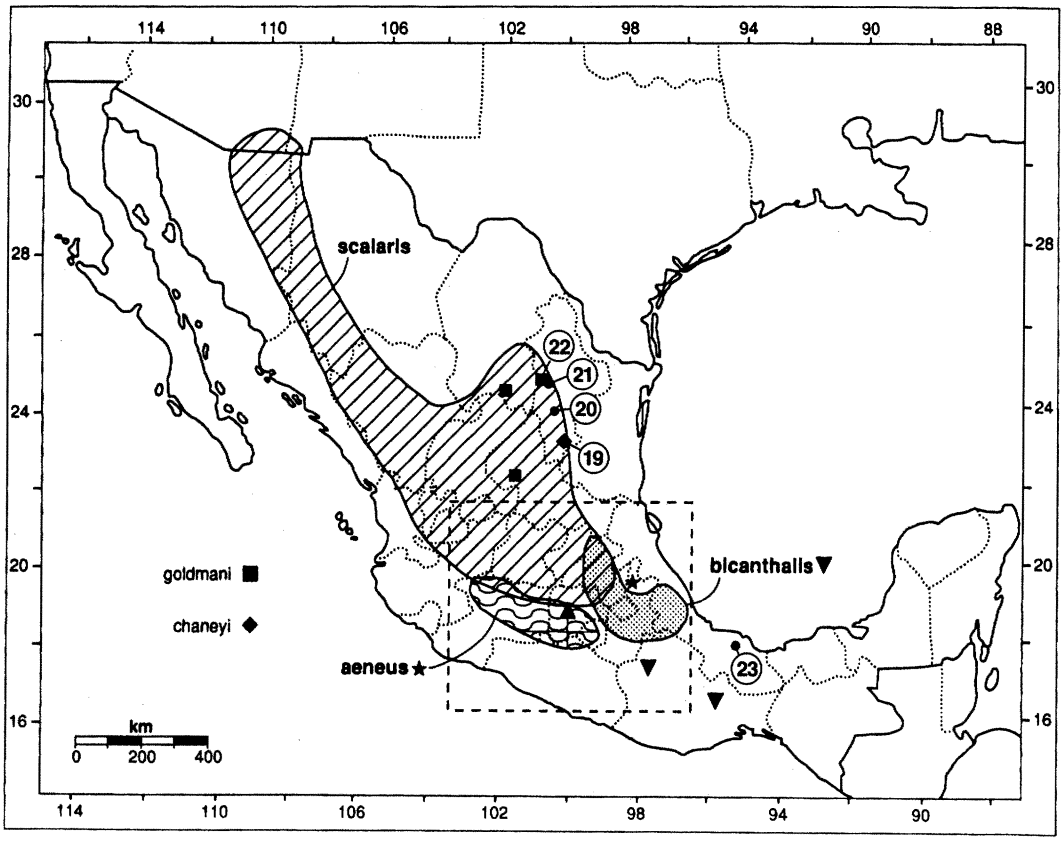

FIG. 1.—Ranges of the members of the *S. scalaris* complex and collection sites for those populations not collected within the rectangular area (see Fig. 2 for remaining collection sites). Table 1 gives exact localities and sample sizes for all populations.

the *S. scalaris* complex are commonly known as "bunch grass" lizards because of their montane distributions and confinement to high elevation open grasslands. Monophyly of the *S. scalaris* complex (except for the newly described *Sceloporus chaneyi*, which has not been cytogenetically studied) is strongly supported by a uniquely derived karyotype (Cole, 1978).

Within *Sceloporus*, one feature unique to this group is its bimodal reproductive parity. *Sceloporus scalaris* (all subspecies), *S. a. aeneus*, and *S. chaneyi* are oviparous, whereas *S. goldmani*, *S. a. subniger*, and *S. a. bicanthalis* are generally considered viviparous (Guillette and Smith, 1985; Mink, personal observation). *Sceloporus scalaris* and *S. a. aeneus* may have fairly prolonged egg retention (Guillette and Gongora, 1986; Shine, 1983), but both appear to be totally oviparous. If *S. a. bicanthalis* and *S. a. subniger* are conspecific with *S. a. aeneus*, then the species *S. aeneus* is reproductively bimodal (Guillette and Jones, 1985).

The objectives of this paper are to (1) test previously described species limits within the *S. scalaris* complex on the basis of isozyme and morphological characters, (2) develop a well corroborated phylogenetic hypothesis for this complex on the basis of a multilocus isozyme data and morphological data set, and (3) infer the evolution of viviparity in an historical context (Brooks and McLennan, 1991).

MATERIALS AND METHODS

Collection of Animals

We collected 247 specimens over two summers of field work (1991 and 1992), representing from 1–12 populations of

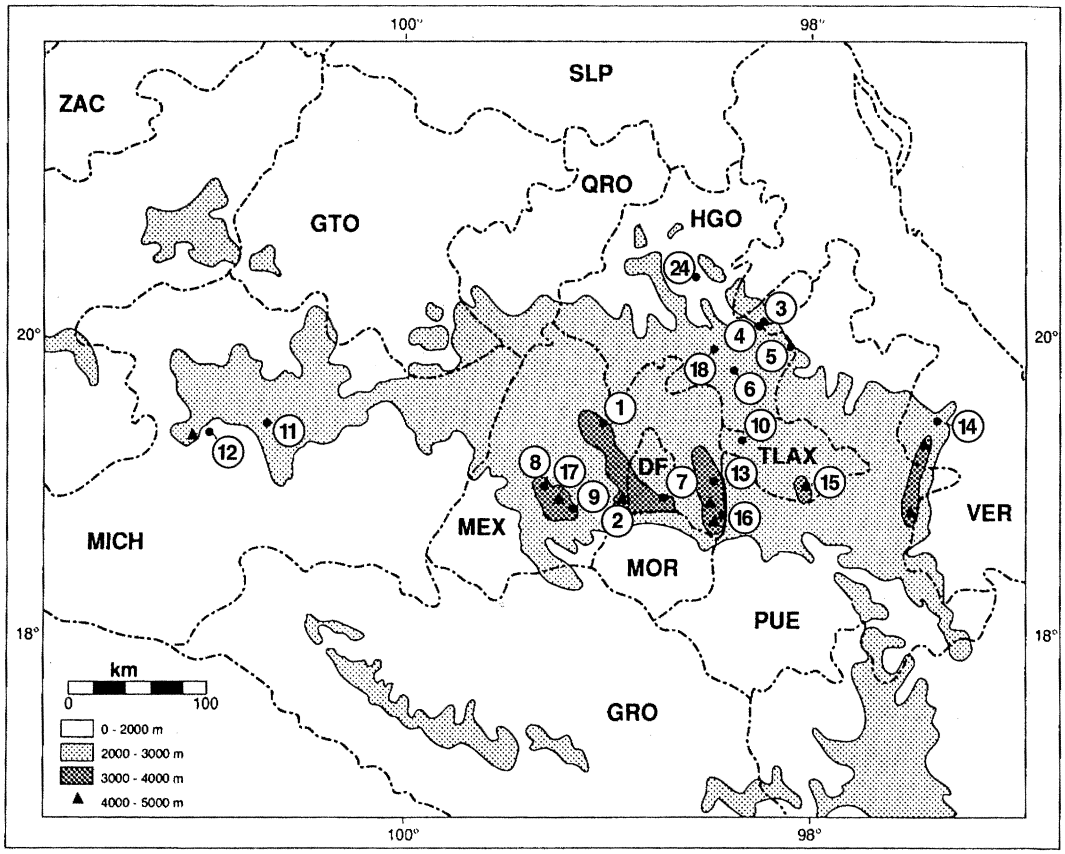

FIG. 2.—Collecting sites for populations of the *S. scalaris* complex taken from the rectangular area shown in Fig. 1; numbers correspond to those in Table 1. Abbreviations identify the following political units: DF = Federal District, GRO = Guerrero, GTO = Guanajuato, HGO = Hidalgo, MEX = México, MICH = Michoacan, MOR = Morelos, PUE = Puebla, QRO = Querétaro, TLAX = Tlaxcala, VER = Veracruz, ZAC = Zacatecas.

many of the recognized taxonomic units (Figs. 1, 2, Table 1). Lizards were collected during the day with nooses, rubber bands, or by hand, and we attempted to collect 12–15 lizards per locality. However, fewer individuals were collected if lizards were not abundant at a particular site, and in two cases more were taken.

We initially identified specimens by geographic distribution, morphological characteristics, and parity modes, which we determined by dissection of gravid females. Populations with gravid females that contained well developed embryos (which in some cases moved on their own once removed from the mothers, and in a few cases, survived the premature birth) were classified as viviparous. Populations that contained shelled, well developed eggs (vitellogenic eggs were not used in these determinations) were classified as oviparous, following the most stringent criteria suggested by Blackburn (1993). One sample of *S. scalaris samcolemani* contained no gravid females (locality 21) but was classified as oviparous because another sample of the same taxon (locality 20) did include gravid females, thus meeting the criterion for oviparity. Because only a single subadult female *S. goldmani* was collected, parity mode for this taxon was not established by us, but was based on a previous report (Guillette and Smith, 1985). All other population samples included gravid females, and parity modes for all are given in Table 1. The population of *S. a. bicanthalis* from Las Vegas, Veracruz (locality 14) was classified as viviparous, but both

TABLE 1.—Localities and sample size (n) for all populations of the *S. scalaris* complex sampled in this study. Localities are plotted in Figs. 1 and 2, and voucher specimens are identified by taxa [SAA = *S. aeneus aeneus*; SAB = *S. aeneus bicanthalis*; SCH = *S. chaneyi*; SGO = *S. goldmani*; SSS = *S. scalaris*; SVA = *S. variabilis*; and SPA = *S. parvus*], parity mode [O = oviparous; V = viviparous], total number of canthals, and male belly pattern [A = solid, dark pattern; B = blue venter and throat, barred; C = plain pattern (no markings); D = rose and blue venter].

Locality	n	Habitat	Voucher number	Taxon	Parity	No. canthals	Male belly
1. 3.5 km NE Cahuacan, state of México.	11	Bunch grass, open pine forest	MZFC 05784 BYU 45299–45304	SAA	O	2	A
2. Between km 18 and km 20, El Ajusco Highway, El Ajusco D. F.	12	Bunch grass in open fields	MZFC 05789 MZFC 05783 BYU 45309–13 BYU 45385–86	SAA	O	2	A
3. Linda Vista, 3.5 km N of La Cruz on state highway Metepec—Tenango de Doria, Hidalgo.	3	Brush and rocks by stream bed	MZFC 05778	SAA	O	2	A
4. Palo Gacho, 2 km NE of La Cruz on state highway Metepec—Tenango de Doria, Hidalgo.	9	Edges of corn fields, brush and rocks by stream bed	MZFC 05779	SAA	O	2	A
5. Campestre Las Truchas (Río Topolapo), Puebla, off Mexico Highway 130 by the Puebla—Hidalgo border.	6	Brush and rocks along field edges	MZFC 05775 BYU 45305–06 BYU 45383–84	SAA	O	2	A
6. El Autodromo Bosques El Angel, Hidalgo, off Mexico Highway 132.	3	Bunch grass in fields and open pine forest	MZFC 05785 BYU 45307–08	SAA	O	2	A
7. Km 28 of Mexico Highway 28, between Milpa Alta and Oaxtepec, state of México.	9	Brush around field edges	MZFC 05780 BYU 45314–16 BYU 45387–88	SAA	O	2	A
8. El Mapa, km 23 of Mexico Toluca—Temascaltepec highway, state of Mexico.	9	Bunch grass and brush	MZFC 05788 BYU 45317–19 BYU 45389–90	SAA	O	2	A
9. 2.8 km S–SW of Zaragoza, state of México.	10	Bunch grass and brush	MZFC 05786 BYU 45320–24	SAA	O	2	A
10. Junction of Mexico Highway 136 with road to Españita, Tlaxcala.	9	Bunch grass and agave bases lining open fields	MZFC 05686 MZFC 05687 BYU 45405 BYU 45371–73	SAA	O	2	A
11. 8.5 km S of Patzcuaro on Mexico Highway 120, Michoacan.	13	Bunch grass and brush around open fields	MZFC 05836 BYU 45330–35	SAA	O	2	A
12. 4 km N of Uruapan on Mexico Highway 37, Michoacan.	6	Brush around open fields	MZFC BYU 45336–38	SAA	O	2	A
13. Km 3 of road from Llano Grande to Zoquiapan, state of México.	13	Bunch grass and brush in fields and open pine forest	MZFC 05787 BYU 45344–51 BYU 45395	SAB	V	4	B
14. Km 125 of Mexico Highway 140, 2 km E of Las Vigas, Veracruz.	21	In rocks and plants of open pine forest on lava flow	MZFC 05776 MZFC 05688 BYU 45357-58 BYU 45398	SAB	V	4	B
15. Volcán La Malinche, the area around the swimming pool, Tlaxcala.	10	Bunch grass of open pine forest	MZFC 05774 BYU 45352–56 BYU 45396–97	SAB	V	4	B
16. El Paso de Cortés, at the México—Puebla border.	8	Bunch grass of fields and open pine forest	MZFC 05777 BYU 45359–62	SAB	V	4	B
17. El Nevado de Toluca, from 4050 to 4250 m elevation, state of Mexico.	18	Bunch grass, rocks	MZFC 05762 BYU 45339–40 BYU 45342–43 BYU 45393–94	SAB	V	4	B

TABLE 1.—Continued.

Locality	n	Habitat	Voucher number	Taxon	Parity	No. canthals	Male belly
18. 2 km NE of Nopalillo (5 km from turnoff of Mexico Highway 130), Hidalgo.	12	Bunch grass, brush, bases of agaves around open fields	MZFC 05685 BYU 45325–28 BYU 45391 BYU 45342	SAB	O	4	B
19. 18 km NE of San Antonio, Peña Nevada, Nuevo Leon.	9	Brush, rocks, and around agave bases	MZFC 05473 BYU 45393 BYU 45364–65 BYU 45399–400	SCH	O	2	C
20. 1.2 km NW Mimbres, at road junction to San Juan de Mimbres, Nuevo Leon.	10	Under rocks in open field at edge of open pine forest	MZFC 05349 BYU 45366–68 BYU 45402–03	SSS	O	2	B
21. 14.4 km E of San Antonio de las Alazanes, Coahuila.	6	Bunch grass on slope by road	MZFC 05350 BYU 45369–70 BYU 45404	SSS	O	2	B
22. Junction of road from San Antonio de las Alazanes with Mexico Highway 57, Coahuila.	1	On rock by bunch grass	MZFC 05458	SGO	V	4	B
23. Catemaco, by the Lago de Catemaco, Veracruz.	3	Brush by road facing beach	MZFC 05819	SVA	O	4	D
24. San Cristobal (highway from Ixmilquilpan to Tolantongo), Hidalgo.	2	Thorn scrub	MZFC 05509	SPA	O	4	B

parity modes were found in this population (see below).

After capture, we dissected all animals in the field and removed tissues for molecular studies. The heart and part of the liver were frozen in a single cryogenic tube for DNA extraction, whereas the duodenum, stomach, kidneys, remaining liver, and skeletal muscle were put in a separate tube for isozyme analysis. We stored tissues in liquid nitrogen in the field and later stored them at −80 C in an ultralow freezer at Brigham Young University. All voucher specimens were fixed in 10% formalin, transferred to 70% ethanol, and deposited in collections either at the Museo de Zoología—Facultad de Ciencias (MZFC), at the Universidad Nacional Autónoma de Mexico, Mexico City, or the Monte L. Bean Life Science Museum, Brigham Young University (BYU), Provo, Utah. Catalogue numbers and locality data are given in Table 1.

Protein Electrophoresis

We separated tissue samples into three portions for laboratory analysis: (1) skeletal muscle, (2) duodenum and stomach (flushed free of contents), and (3) liver and kidney. Each portion was added to an equal volume of grinding solution (0.01 M Tris/0.03 M NaCl/0.001 M EDTA, pH 6.8) and homogenized. We then stored the liquid homogenate at −80 C until electrophoresis.

Horizontal starch gel electrophoresis was carried out in 12.5% (w/v) starch gels (1:1 Sigma Starch—Electrostarch) at 5–7 C. Enzymes resolved and the tissue-buffer combinations used for specific loci are given in Table 2. General histochemical staining protocols followed Murphy et al. (1990). Of the 247 animals collected, we used 208 for isozyme electrophoresis, along with three individuals of *Sceloporus variabilis* and two individuals of *S. parvus* combined to form a monophyletic outgroup.

We considered electromorphs of any given locus to be homologous if they had the same mobility. We designated those with differing mobilities as different alleles using alphabetic designations ("A"–"G") based on their order of appearance; the first allele resolved for any locus was designated "A", the second "B", and so forth. An appendix available from either author

TABLE 2.—Enzymes and electrophoretic conditions for isozyme surveys of the *Sceloporus scalaris* complex. Names, abbreviations, and enzyme commission (EC) numbers follow Murphy et al. (1990), after those recommended by the International Union of Biochemistry (1984). Tissue symbols are: D = duodenum and stomach, L = liver and kidney, and M = skeletal muscle.

Enzyme	EC number	Locus	Tissue	Buffer*
Aconitase hydratase	4.2.1.3	M-Acoh-A	L	A
		S-Acoh-A	L	A, B
Adenylate kinase	2.7.4.3	Ak-A	M	A, E
Aspartate aminotransferase	2.6.1.1	M-Aat-A	L	A
		S-Aat-A	L	A
Creatine kinase	2.7.3.2	Ck-A	M	A, E
		Ck-C	D	C
Dihydrolipoamide dehydrogenase	1.8.1.4	Ddh-A	L	B
Fructose-bisphosphate aldolase	4.1.2.13	Fba-1	L	B
Glucose-6-phosphate isomerase	5.3.1.9	Gpi-A	D	A
alpha-glucosidase	3.2.1.20	Glus-1	L	A
Glutamate dehydrogenase	1.4.1.2	Gtdh-A	L	B
Glycerol-3-phosphate dehydrogenase	1.1.1.8	G3pdh-A[1]	L	A
		G3pdh-A[2]	L	A
Isocitrate dehydrogenase	1.1.1.42	M-Idh-A	M	A, E
		S-Idh-A	L	A
L-lactate dehydrogenase	1.1.1.27	Ldh-A	L	A
		Ldh-B	L	A
Malate dehydrogenase	1.1.1.37	S-Mdh-A	L	A, B
Malate dehydrogenase (NADP+)	1.1.1.40	S-Mdhp-A	L	A
Mannose-6-phosphate isomerase	5.3.1.8	Mpi-A	L	A, B, C
alpha-Mannosidase	3.2.1.24	Man-A	L	A, B
Peptidases	3.4.-.-			
Glycyl-L-leucine		Pep-A(GL)	D	A, C, D
L-leucylglycylglycine		Pep-B(LGG)	D	A, C, D
DL-alanyl-DL-methionine		Pep-C(AM)	D	A
L-phenylalanyl-L-proline		Pep-D(PAP)	D	A, C, D
L-leucyl-L-alanine		Pep-?(LA)	M	B
Phosphoglucomutase	5.4.2.2	Pgm-A	L	A, C
Purine-nucleoside phosphorylase	2.4.2.1	Pnp-A	D	A, B
Pyruvate kinase	2.7.1.40	Pk-A	M	A, D
Superoxide dismutase	1.15.1.1	M-Sod-A	L	A
Triose-phosphate isomerase	5.3.1.1	Tpi-A	D	A

* A: Starch gel, Tris-citrate II, pH 8.0, 10 h at 75 mA; B: Starch gel, Tris-citrate III, pH 8.0, 20 h at 75 mA; C: Starch gel, Lithium-borate/Tris-citrate, pH 8.3, 10 h at 75 mA; D: Cellulose acetate gel, 0.01 M Citrate phosphate, pH 6.4, 30 min at 75 mA; E: Cellulose acetate gel, 0.025 M Tris-glycine, pH 8.5, 30 min at 75 mA [starch gels following Murphy et al. (1990); cellulose acetate gels following Richardson et al. (1986)].

gives all individual genotypes, by locality, for all polymorphic loci.

We compared and verified allelic mobilities in separate side-by-side electrophoretic runs. We tested for hidden heterogeneity (cryptic enzyme variation) by sequential electrophoresis (Coyne, 1982; Highton and Hedges, 1995). Sequential runs were carried out for some protein systems on a different type of gel (cellulose acetate), on a different starch-gel buffer system, or at a different pH, in order to resolve a greater portion of charge variation in the electromorphs.

Data Analysis

Allozyme data were analyzed with the BIOSYS-1 program of Swofford and Selander (1981) and the PAUP (Phylogenetic Analysis Using Parsimony) program (Swofford, 1993), version 3.1.1. We obtained estimates of overall genetic variability, which included allele frequencies, heterozygosities, and chi-square tests for deviation from Hardy-Weinberg equilibrium, and then used allele frequencies to obtain a matrix of pair-wise distance and identity coefficients (Nei, 1978).

Because isozyme data sets are problematic to code for phylogenetic studies (Buth, 1984; Mabee and Humphries, 1993; Mardulyn and Pasteels, 1994; Murphy, 1993), we carried out two different analyses. In both cases, we did not use loci that were monomorphic across all populations (and thus uninformative), and we polarized all informative characters by rooting to *S. parvus* and *S. variabilis*. For simplicity, we constrained these taxa to be monophyletic with respect to the ingroup taxa, but tree topologies were identical when the outgroup taxa were made paraphyletic to the ingroup. Two morphological features (number of canthal scales and male belly patterns) and parity modes were also included in a "total evidence" (Kluge, 1989) analysis. Some investigators have argued that the inclusion of the character(s) of interest (parity mode in this case) in the data matrix is circular (Coddington, 1988) if one wishes to draw inferences about the evolution of the character from the phylogenetic hypothesis. Others have argued that, as long as an evolutionary model (other than outgroup rooting) is not used to establish the direction of character evolution a priori (thus constraining the pathway of change for that character during the analysis), then including that character in the data matrix is not circular (Deleporte, 1993). We accommodated both concerns by running all analyses first with and then without parity mode in the data matrix.

In the first analysis, the matrix included only 12 "conservative" loci that were polymorphic among but monomorphic (or predominantly so, see below) within population samples (at this point, each population was considered separately). One of the two exceptions was the G3pdh-A^2 locus (column E in Tables 4 and 5), in which one population (locality 5, the sample of *S. a. aeneus* from Campestre Las Truchas, Table 1) segregated for both alleles seen at this locus (these alleles were alternatively fixed and unambiguously separated all other samples into two groups). In this analysis, this variable sample was coded for the high frequency allele [G3pdh-A^2(a)] as if it was fixed. The second exception is the M-Aat-A locus (column J in Tables 4 and 5), in which one population (locality 17, the sample of *S. a. bicanthalis* from El Nevado de Toluca) segregated for an autapomorphic allele. The M-Aat-A locus was coded only for the non-autapomorphic (i.e., phylogenetically informative) allele and included in the same analysis.

Samples that were identical in their allozyme genotypes at these 12 loci (Table 4) and in the three morphological characters (Table 1), were then grouped together into larger aggregates, which were separated from other such aggregates on the basis of fixed differences. In other words, we used fixed allelic differences at isozyme loci or fixed differences in morphology or parity mode as absolute diagnostic characters to delimit phylogenetic species, as recommended by Davis and Nixon (1992). Of the 22 ingroup samples initially screened, eight diagnosable groups were resolved by this procedure on the basis of this subset of 12 isozyme loci (Table 4) and the three morphological/parity characters. Omission of parity mode as a diagnostic marker collapses all populations of *S. a. bicanthalis* (BICANTHAL1 and BICANTHAL2 in Table 4) into a single terminal taxon.

The cladistic analysis consisted of an exhaustive search for minimum parsimony trees (using version 3.1.1 of PAUP: Swofford, 1993) for these eight units; in all cases, the 12 loci were considered as characters and fixed allozyme differences were coded as unordered states (0, 1, 2, etc.). Differences in the morphological characters were also treated as unordered states, and all characters were weighted equally.

In the second set of runs, we included in an expanded data matrix some of the loci that were polymorphic within as well as among populations, thereby providing additional characters whose states could be coded on the basis of unique combinations of alleles for step matrix analyses described by Mabee and Humphries (1993; see also Wiens and Titus, 1991). The step matrix procedure of PAUP provides coding options that maximize retention of character homology information while retaining bi-

ologically relevant definitions of isozyme characters. These polymorphic loci (characters M–Q in Table 5) provided additional character states either in the form of synapomorphic alleles, or autapomorphic alleles that further split out new OTU's within *S. aeneus*. We included the latter to provide another measure of taxonomic diversity. In both sets of analyses, the bootstrap (Felsenstein, 1985) with 1000 replications was used to evaluate the strength of support for each node.

We did not use five additional polymorphic loci in any phylogenetic analyses, because all or almost all ingroup samples shared the same electromorphs. These additional loci complicate phylogenetic analyses because they are polymorphic and multistate within samples, and individuals may possess more than one character state. This problem is common to most isozyme data sets (Mabee and Humphries, 1993; Murphy, 1993), and no consensus exists on a single best method for ordering and coding such data sets (see also Buth, 1984). We do not consider electromorph frequencies appropriate for phylogenetic analyses (contra Rogers, 1984, 1986; Swofford and Berlocher, 1987) because sampling is usually inadequate (Crother, 1990) and frequencies in and of themselves are not heritable characters (Jones et al., 1993; Murphy, 1993; but see Wiens, 1995).

Results

Patterns of Variability and Divergence

Of the 32 gene loci resolved (Table 2), 11 were monomorphic or essentially monomorphic (i.e., possessed a second allele in low frequency at a single locality) across all populations sampled. These were Gpi-A, Ck-C, Pep-C (AM), Tpi-A, Pep-F (LA), M-Sod-A, S-Aat-A, Ddh-A, Gtdh-A, Fba-1, and S-Idh-A. Eleven loci were monomorphic within populations but polymorphic among populations, including Ck-A, Ak-A, M-Idh-A, Pk-A, G3pdh-A^2, M-Acoh-A, Mpi-A, Ldh-A, Ldh-B, S-Mdh-A, and S-Mdhp-A. The enzyme G3PDH appears to have been duplicated in some populations surveyed, because it displayed the multiple-banded phenotype described by Sites and Murphy (1991) for some populations of the *Sceloporus grammicus* complex. In these cases, the electromorph having the same mobility as the single electromorph present in some samples is designated as "$-A^1$," while the second electromorph representing the presumably duplicated locus is designated "$-A^2$". For G3pdh-A^2, therefore, the character state "AA" denotes presence of the locus and "BB" its absence. The remaining 10 loci were polymorphic both within and among populations to various degrees, including M-Aat-A (but see paragraph three under the "Data Analysis" section above), Pep-D (PAP), Pnp-A, αMan-A, Pgm-A, G3pdh-A^1, Pep-A (GL), Pep-B (LGG), S-Acoh-A, and αGlus-1.

Table 3 summarizes the mean numbers of alleles per locus (A), percentages of loci polymorphic (P), and direct counts of mean heterozygosities (H) for all samples. Intersample variation is seen in these genetic variability estimates. A values range from 1.1 (at three localities) to 1.4 (at two localities), P values from 6.3 (locality 6) to 28.1 (localities 1 and 14), and H estimates from 0.026 (locality 6) to 0.108 (locality 16). Genotype frequencies across loci and populations were almost always in Hardy-Weinberg (HW) equilibrium, based on the chi-square tests available in BIOSYS.

Table 3 also presents the unbiased estimates of genetic identity and distance (both after Nei, 1978) for all pairwise combinations of samples. Genetic identity estimates range from 0.491 (locality 21 versus 23) to 1.000 (locality 3 versus 4), and distance estimates range from 0.000 (locality 3 versus 4) to 0.712 (locality 21 versus 23).

Phylogenetic Relationships

A total of eight different units was diagnosed on the basis of the more conservative data set (Table 4 plus the two morphological and the parity mode characteristics given in Table 1; also see the Appendix available from the authors). The eight terminal units are AENEUS 1 (localities 1, 2, 5–9, and 11–12), AENEUS 2

(localities 3–4), AENEUS 3 (locality 10), BICANTHAL1 (localities 13–17), BICANTHAL2 (locality 18), CHANEYI (locality 19), SCALARIS (localities 20–21), and GOLDMANI (locality 22). Each group is diagnosed by a unique combination of fixed electromorphs across the 12 conservative loci given in Table 4 and/or one or more fixed states in the three other characters.

The conservative data set was used to perform an exhaustive search, which evaluated a total of 2,027,025 trees ranging in length from 25–47 steps. One most parsimonious tree (Fig. 3A) of 25 steps was found, and it contained strong phylogenetic signal as assessed by an extremely right-skewed distribution ($g1 = -1.184762$, $P \ll 0.01$). The significant negative g1 value obtained here indicates tree length distributions are skewed more than would be expected from random data, which indicates that the data contain strong phylogenetic signal (Hillis, 1991; Hillis and Huelsenbeck, 1992). When parity mode is detected from the matrix, the same analysis evaluates the same number of trees, ranging in length from 23–45, and it recovers a single tree with significant phylogenetic signal ($g1 = -1.204$, $P \ll 0.01$). The topology identical to the one recovered from the full matrix and bootstrap proportions are not appreciably altered by the presence or absence of this character in the matrix. In both cases, only the *Aeneus* and (*Chaneyi* + *Scalaris*) clades are strongly supported by the criterion of Hillis and Bull (1993); bootstrap proportions of 70% or higher are considered to have a high probability (>95%) of being correct.

In the expanded data set, the αMan-A locus (column O in Table 5) is binary; character state B denotes the presence of one electromorph (B) only, while state E denotes the presence of this electromorph plus a second electromorph (A). This locus represents a relatively simple transition (either a gain of A or a loss of B), but the remaining four highly polymorphic loci in Table 5 (Pep-D, column M; Pnp-A, column N; Pgm-A, column P; and G3pdh-A^1, column Q) represent more complex characters with multiple possible transitions between states. These four loci were coded in the form of a single symmetrical step matrix (Table 6) reflecting reticulate character state transitions, because this retains all hypotheses of homology among alleles of all allelic combinations and still allows the locus to be considered the character (Mabee and Humphries, 1993). This was done instead of formulating a separate matrix with all possible combinations of alleles for each locus, to reduce computer analysis time. We assume that character state combinations not found in extant populations may have been present in ancestral taxa, for any of these markers. The number of steps required in a transition between any two allelic combinations represents the weighted value in the step matrix. Morphological and parity mode characters were assigned a weight of 1, as it would be difficult to assign them weights using the same criteria as those for the loci.

Using this expanded data matrix, 11 ingroup units are diagnosed. These are: AENEUS 1 (localities 1 and 9), AENEUS 2 (localities 3 and 4); AENEUS 3 (locality 10), AENEUS 4 (localities 11 and 12), AENEUS 5 (localities 2 and 6–8), AENEUS 6 (locality 5), BICANTHAL1 (localities 13–17), BICANTHAL2 (locality 18), CHANEYI (locality 19), SCALARIS (localities 20 and 21), and GOLDMANI (locality 22). These groups are diagnosed by the unique set of character states given in Table 5, plus the three morphological/parity characters from Table 1. A branch-and-bound search was carried out on this expanded matrix and recovered eight equally parsimonious trees of 64 steps. Despite the absence of complete resolution (a consensus tree is shown in Fig. 3B), strong phylogenetic signal is evident ($g1 = -0.992$, $P \ll 0.01$), and most of the same groups are recovered as in the first round of analyses, both with and without the parity character in the matrix. Bootstrap proportions again strongly support monophyly of the *Aeneus* and (*Chaneyi* + *Scalaris*) clades, and within the former, there is strong support for a partially resolved nested structure (*Aeneus*3 (*Aeneus*1, *Aeneus*4, *Aeneus*5 (*Aeneus*2 + *Aeneus*6))). Bootstrap proportions approach 70% for both the more inclusive "northern" (*Goldmani*

TABLE 3.—Matrix of genetic identity (above diagonal) and distance (below; both unbiased estimates of Nei, 1978) for all pairwise combinations of *Sceloporus* examined in this study. Also the mean number of alleles per locus (A); percentage of loci polymorphic (P); and direct count of the mean heterozygosity (H) are given below, with standard errors in parentheses. Population numbers and abbreviations are from those listed in Table 1.

Population	SAA							
	1	2	3	4	5	6	7	8
1. Cahuacan	—	0.99	0.92	0.91	0.97	0.97	0.98	1.00
2. El Ajusco	0.01	—	0.91	0.90	0.96	0.96	0.98	0.99
3. Linda Vista	0.08	0.10	—	1.00	0.98	0.94	0.94	0.94
4. Palo Gacho	0.09	0.10	0.00	—	0.98	0.94	0.93	0.93
5. Río Totolapa	0.03	0.04	0.01	0.02	—	0.99	0.99	0.99
6. Autódromo	0.03	0.04	0.06	0.07	0.01	—	1.00	0.98
7. Milpa Alta	0.02	0.02	0.06	0.07	0.01	0.00	—	0.99
8. El Mapa	0.00	0.01	0.06	0.08	0.01	0.02	0.01	—
9. Zaragoza	0.00	0.01	0.07	0.08	0.02	0.03	0.02	0.00
10. Españita	0.14	0.14	0.21	0.22	0.16	0.16	0.14	0.14
11. Patzcuaro	0.04	0.06	0.12	0.14	0.06	0.08	0.06	0.05
12. Uruapan	0.05	0.06	0.12	0.13	0.06	0.09	0.07	0.04
13. Zoquiapan	0.18	0.19	0.30	0.32	0.23	0.24	0.23	0.20
14. Las Vigas	0.18	0.20	0.31	0.32	0.24	0.25	0.24	0.20
15. Malinche	0.17	0.19	0.26	0.27	0.20	0.20	0.19	0.19
16. P de Cortés	0.18	0.18	0.28	0.29	0.21	0.21	0.20	0.18
17. N. Toluca	0.19	0.22	0.24	0.26	0.19	0.18	0.19	0.19
18. Nopalillo	0.19	0.20	0.28	0.29	0.21	0.22	0.21	0.19
19. SAPN	0.31	0.33	0.42	0.43	0.35	0.35	0.34	0.30
20. Mimbres	0.34	0.33	0.42	0.44	0.35	0.34	0.32	0.32
21. Alaz	0.34	0.32	0.42	0.43	0.34	0.33	0.31	0.32
22. Alaz	0.29	0.29	0.38	0.39	0.30	0.29	0.29	0.29
23. Catemaco	0.59	0.63	0.58	0.57	0.59	0.63	0.61	0.60
24. S. Cristobal	0.56	0.57	0.54	0.55	0.54	0.54	0.55	0.54
A	1.4	1.3	1.2	1.3	1.3	1.1	1.2	1.3
	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)	(0.0)	(0.1)	(0.1)
P	28.1	21.9	18.8	18.8	18.8	6.3	15.6	18.8
H	0.08	0.05	0.08	0.06	0.05	0.03	0.04	0.07
	(0.03)	(0.02)	(0.04)	(0.03)	(0.03)	(0.02)	(0.02)	(0.03)

(*Chaneyi* + *Scalaris*)) and "southern" (*Aeneus* + *Bicanthalis*) clades. The cladograms in Fig. 3 are entirely consistent with each other, although bootstrap proportions are generally lower for the groups recovered from the smaller data set (Fig. 3A).

Because *S. parvus* had missing data, all matrices were run again under two different sets of conditions in which the two outgroups were structured to be paraphyletic with respect to the ingroup. First, the missing data for *S. parvus* were filled in with "dummy" variables identical to the alleles at homologous loci found in *S. variabilis*. Second, the missing data were filled in with alleles unique (autapomorphic) to *S. parvus*. In both instances, the trees resolved were identical to those resolved from the original matrices with missing data points.

DISCUSSION

Species Limits

Over the years, various species concepts have been proposed (see Endler, 1989, for an overview). According to the biological species concept (Mayr, 1963), species are groups of entities that are reproductively isolated from all other such groups. Ghiselin (1974) and Paterson (1985) defined species as groups of entities that are able to reproduce among themselves. Templeton (1989) has argued that, instead of looking mainly at reproductive factors, we should concentrate on all the factors and

TABLE 3.—Extended.

SAA				SAB				
9	10	11	12	13	14	15	16	17
1.00	0.87	0.96	0.95	0.83	0.83	0.84	0.84	0.83
0.99	0.87	0.94	0.94	0.83	0.82	0.82	0.83	0.80
0.93	0.81	0.88	0.89	0.74	0.73	0.77	0.75	0.78
0.92	0.80	0.87	0.87	0.73	0.72	0.76	0.75	0.77
0.98	0.85	0.94	0.94	0.79	0.78	0.82	0.81	0.82
0.97	0.85	0.93	0.92	0.78	0.77	0.81	0.81	0.83
0.98	0.87	0.94	0.93	0.80	0.79	0.82	0.82	0.83
1.00	0.87	0.95	0.96	0.82	0.82	0.83	0.83	0.83
—	0.87	0.96	0.96	0.84	0.83	0.84	0.84	0.83
0.14	—	0.90	0.89	0.85	0.85	0.87	0.87	0.87
0.03	0.10	—	0.98	0.85	0.85	0.85	0.86	0.84
0.04	0.11	0.01	—	0.84	0.84	0.85	0.85	0.83
0.18	0.16	0.16	0.17	—	1.00	0.98	0.99	0.94
0.18	0.16	0.17	0.18	0.00	—	0.99	0.99	0.95
0.18	0.14	0.16	0.17	0.01	0.01	—	1.00	0.98
0.19	0.14	0.15	0.16	0.01	0.01	0.00	—	0.97
0.19	0.14	0.17	0.18	0.06	0.05	0.02	0.03	—
0.18	0.10	0.16	0.15	0.05	0.06	0.05	0.05	0.08
0.31	0.23	0.31	0.34	0.26	0.25	0.24	0.25	0.23
0.33	0.20	0.33	0.34	0.28	0.29	0.27	0.27	0.24
0.32	0.21	0.33	0.34	0.28	0.29	0.27	0.26	0.26
0.28	0.26	0.29	0.31	0.23	0.25	0.24	0.23	0.25
0.62	0.54	0.57	0.58	0.62	0.61	0.57	0.56	0.55
0.56	0.68	0.61	0.64	0.70	0.71	0.67	0.65	0.64
1.3	1.3	1.3	1.2	1.3	1.4	1.3	1.3	1.3
(0.1)	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)
21.9	25.0	18.8	12.5	25.0	28.1	15.6	18.8	25.0
0.08	0.06	0.08	0.10	0.07	0.06	0.07	0.11	0.07
(0.03)	(0.02)	(0.03)	(0.05)	(0.03)	(0.02)	(0.04)	(0.05)	(0.03)

processes that maintain similarity among groups of organisms in their morphology, biology, behavior, ecology, etc.; in other words, a cohesion species concept. This has some similarities to Wiley's (1981) evolutionary species concept, which define species as single lineages of populations which have a unique identity from all other such lineages. Nixon and Wheeler's (1990) phylogenetic species concept defines a phylogenetic species as "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals." In an extension of this idea, Davis and Nixon (1992) have argued that the character states that support hypothesized species boundaries should be unique characters that are fixed in all individuals, as compared to characters that are present in only some portion of the population. These "frequency" characters are called traits instead of characters by Davis and Nixon (1992). For the purposes of this project, we will use the following criteria for identifying species boundaries: a species will be a group of individuals united by a unique set of character states different from all other character sets of other groups of individuals. The emphasis here is not so much on the fixed condition emphasized by Nixon and Wheeler (1992), but rather on geographic concordance displayed by two or more (presumably) independent characters (Avise and Ball, 1990). This approach takes advantage of the fact that

TABLE 3.—Extended.

Population	SAB	SCH	SSS		SGO	SVA	SPA
	18	19	20	21	22	23	24
1. Cahuacan	0.83	0.74	0.71	0.71	0.74	0.55	0.57
2. El Ajusco	0.82	0.72	0.72	0.72	0.75	0.53	0.57
3. Linda Vista	0.76	0.66	0.65	0.66	0.69	0.56	0.58
4. Palo Gacho	0.75	0.65	0.65	0.65	0.68	0.57	0.57
5. Río Tolopapo	0.81	0.70	0.70	0.71	0.74	0.55	0.58
6. Autódromo	0.80	0.70	0.71	0.72	0.75	0.53	0.58
7. Milpa Alta	0.81	0.71	0.73	0.73	0.74	0.54	0.58
8. El Mapa	0.83	0.72	0.72	0.72	0.74	0.55	0.58
9. Zaragoza	0.83	0.72	0.72	0.72	0.76	0.54	0.57
10. Españita	0.90	0.80	0.82	0.81	0.77	0.58	0.50
11. Patzcuaro	0.85	0.73	0.72	0.72	0.75	0.57	0.54
12. Uruapan	0.86	0.71	0.71	0.71	0.73	0.56	0.52
13. Zoquiapan	0.95	0.77	0.75	0.76	0.79	0.54	0.50
14. Las Vigas	0.94	0.78	0.75	0.75	0.78	0.56	0.49
15. Malinche	0.95	0.78	0.77	0.76	0.78	0.57	0.51
16. P de Cortés	0.95	0.78	0.76	0.77	0.79	0.57	0.52
17. N. Toluca	0.92	0.80	0.78	0.77	0.78	0.57	0.52
18. Nopalillo	—	0.79	0.79	0.79	0.81	0.58	0.52
19. SAPN	0.23	—	0.94	0.92	0.87	0.54	0.53
20. Mimbres	0.23	0.06	—	1.00	0.86	0.50	0.53
21. Alaz	0.23	0.08	0.00	—	0.87	0.49	0.53
22. Alaz	0.21	0.14	0.15	0.13	—	0.67	0.67
23. Catemaco	0.55	0.61	0.69	0.71	0.51	—	0.74
24. S. Cristobal	0.65	0.63	0.64	0.63	0.51	0.30	—
A	1.3	1.3	1.3	1.3	1.2	1.1	1.1
	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)
P	21.9	21.9	18.8	15.6	12.5	9.4	9.4
H	0.07	0.06	0.05	0.07	0.06	0.05	0.09
	(0.03)	(0.02)	(0.02)	(0.04)	(0.03)	(0.03)	(0.05)

reproductive isolation is the only process that *guarantees* the "individuality" (e.g., evolutionary independence) of lineages of bisexual organisms, and this process is expected to sometimes be reflected by the "capture" of unique character states that have not achieved fixation (see also Kluge, 1990). O'Hara (1993), Graybeal (1995), and Frost and Kluge (1995) treated these and related issues in greater depth.

Previous species deliminations of the *Sceloporus scalaris* complex have been based mostly on morphological characteristics (Liner and Dixon, 1992; Poglayen and Smith, 1958; Smith, 1939; Smith and Hall, 1974; Smith et al., 1993; Thomas and Dixon, 1976). Smith (1939) presented a key to the taxa of the *scalaris* complex described at that time, based on such characteristics as number of canthals and dorsal scales, tibia/head proportions, and coloration. *Sceloporus aeneus subniger* was described by Poglayen and Smith (1958), and more recently *S. scalaris samcolemani* was described by Smith and Hall (1974). Thomas and Dixon (1976) re-evaluated Smith's (1939) groupings of the *scalaris* complex and removed *S. jalapae* from the group.

There has been some debate on whether *S. a. aeneus* and *S. a. bicanthalis* should both be given full species status. Davis and Smith (1953) suggested according both *S. a. aeneus* and *S. a. bicanthalis* separate species status on the basis of their presumed parity differences. Smith and Hall (1974) rejected this separation, but they did propose using parity types to assess phylogenetic relationships within the *S. scalaris* complex. Thomas and Dixon (1976), on failing to find consistent morphological differences between *S. a. aeneus* and *S. a. bicanthalis*, recommended continued recognition of a single species,

TABLE 4.—Data matrix for the eight terminal units diagnosed by the method of Davis and Nixon (1992). The samples included are each given in the text, and the characters are coded as: A = Ck-A; B = Ak-A; C = M-Idh-A; D = Pk-A; E = G3pdh-A²; F = M-Acoh-A; G = Mpi-A; H = Ldh-A; I = Ldh-B; J = M-Aat-A; K = S-Mdh-A; L = S-Mdhp-A; R = parity mode (O = oviparous, V = viviparous); S = total number of canthals (2 × number on each side of head); and T = male belly pattern (A = solid dark venter; B = blue venter and throat with bars; C = no coloration; D = rose and blue venter). Outgroups are identified by *, and in each character column, fixed electromorphs are followed (in parentheses) by the state used in the PAUP analysis (A, B, etc.); missing data are identified by "?".

Terminal unit	Character states														
	A	B	C	D	E	F	G	H	I	J	K	L	R	S	T
AENEUS1	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	0	2	A
	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)
AENEUS2	AA	AA	AA	AA	BB	AA	AA	AA	AA	AA	AA	AA	0	2	A
	(A)	(A)	(A)	(A)	(B)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)
AENEUS3	AA	AA	AA	AA	AA	BB	AA	AA	AA	AA	AA	AA	0	2	A
	(A)	(A)	(A)	(A)	(A)	(B)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)
BICANTHAL1	BB	AA	AA	AA	AA	BB	AA	AA	AA	BB	AA	AA	V	4	B
	(B)	(A)	(A)	(A)	(A)	(B)	(A)	(A)	(A)	(B)	(A)	(A)	(B)	(B)	(B)
BICANTHAL2	BB	AA	AA	AA	AA	BB	AA	AA	AA	BB	AA	AA	0	4	B
	(B)	(A)	(A)	(A)	(A)	(B)	(A)	(A)	(A)	(B)	(A)	(A)	(A)	(B)	(B)
CHANEYI	BB	BB	AA	BB	AA	BB	BB	AA	AA	AA	AA	AA	0	2	C
	(B)	(B)	(A)	(B)	(A)	(B)	(B)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(C)
SCALARIS	BB	BB	AA	BB	AA	BB	BB	AA	AA	AA	AA	AA	0	2	B
	(B)	(B)	(A)	(B)	(A)	(B)	(B)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(B)
GOLDMANI	BB	CC	—	BB	AA	BB	BB	AA	AA	AA	—	—	V	4	B
	(B)	(C)	(?)	(B)	(A)	(B)	(B)	(A)	(A)	(A)	(?)	(?)	(B)	(B)	(B)
VARIABILIS	CC	CC	CC	CC	BB	BB	AA	BB	BB	DD	BB	CC	0	4	D
	(C)	(C)	(C)	(C)	(B)	(B)	(A)	(B)	(B)	(D)	(B)	(C)	(A)	(B)	(D)
PARVUS	CC	DD	—	CC	BB	CC	CC	BB	BB	DD	BB	DD	0	4	B
	(C)	(D)	(?)	(C)	(B)	(C)	(C)	(B)	(B)	(D)	(B)	(D)	(A)	(B)	(B)

but they did acknowledge the presence of reproductive bimodality within this species. Guillette and Smith (1985) showed that differences in canthal scale numbers and reproductive mode gave 100% resolution between *S. a. aeneus* and *S. a. bicanthalis*, and they argued for separate species level recognition of the two.

Most recently, Smith et al. (1993) treated *S. bicanthalis* and *S. aeneus* as separate

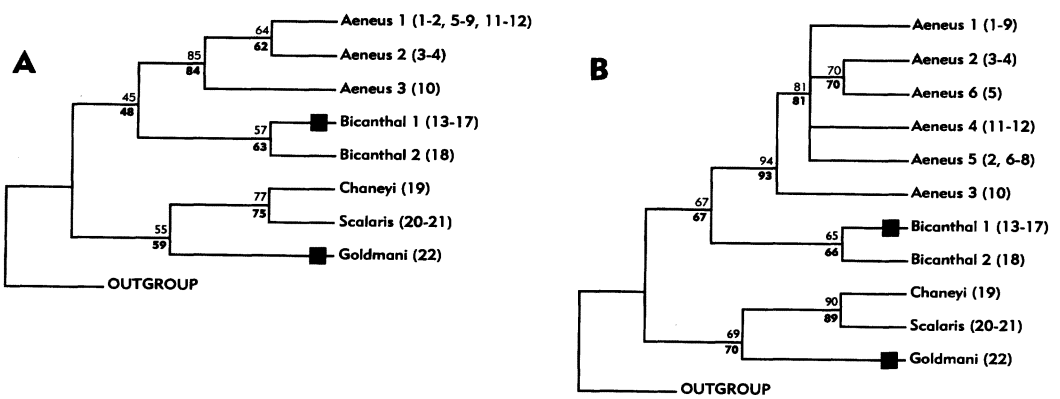

FIG. 3.—Maximum parsimony trees obtained from analysis of (A) the conservative (Table 4) and (B) the expanded data matrix (Table 5). The tree derived from the small data set is 25 steps in length, with a CI = 0.893, RI = 0.880, and RC = 0.786. The consensus tree obtained from the large data matrix is 64 steps with CI = 0.936, RI = 0.944, and RC = 0.884. The black rectangles on the trees indicate viviparous OTU's.

TABLE 5.—Data matrix for the 11 basal units diagnosed by a modified version of the secondary evaluation of Murphy (1993). The samples included in each unit are given in the text, and the characters are coded the same as in Table 4 with the following additions: M = Pep-D (PAP); N = Pnp-A; O = αMan-A; P = Pgm-A; and Q = G3pdh-A[1]. Outgroups are identified by *, and in each character column, electromorphs are identified by those present in each population, followed by the state used in the PAUP analyses (A, B, etc.; see Table 6 for definitions of each character state); missing data are identified by "?".

Terminal unit	Character states																			
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
AENEUS1	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	BC	AA	AB	AC	AB	O	2	A
	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(H)	(A)	(E)	(F)	(E)	(M)	(M)	(M)
AENEUS2	AA	AA	AA	AA	BB	AA	AA	AA	AA	AA	AA	AA	CC	AA	BB	AB	AC	O	2	A
	(A)	(A)	(A)	(A)	(B)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(C)	(A)	(B)	(E)	(F)	(M)	(M)	(M)
AENEUS3	AA	AA	AA	AA	AA	BB	AA	AA	AA	AA	AA	AA	BB	BB	AB	AB	AB	O	2	A
	(A)	(A)	(A)	(A)	(A)	(B)	(A)	(A)	(A)	(A)	(A)	(A)	(B)	(B)	(E)	(E)	(E)	(M)	(M)	(M)
AENEUS4	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	BB	AA	AB	AC	AA	O	2	A
	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(B)	(A)	(E)	(F)	(A)	(M)	(M)	(M)
AENEUS5	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	CC	AA	AB	AC	AA	O	2	A
	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(C)	(A)	(E)	(F)	(A)	(M)	(M)	(M)
AENEUS6	AA	AA	AA	AA	AB	AA	AA	AA	AA	AA	AA	AA	CC	AA	BB	ABC	AA	O	2	A
	(A)	(A)	(A)	(A)	(E)	(A)	(A)	(A)	(A)	(A)	(A)	(A)	(C)	(A)	(B)	(J)	(A)	(M)	(M)	(M)
BICANTHAL1	BB	AA	AA	AA	AA	BB	AA	AA	AA	BB	AA	AA	ABC	BCD	AB	AA	AB	V	4	B
	(B)	(A)	(A)	(A)	(A)	(B)	(A)	(A)	(A)	(B)	(A)	(A)	(J)	(K)	(E)	(A)	(E)	(N)	(N)	(N)
BICANTHAL2	BB	AA	AA	AA	AA	BB	AA	AA	AA	BB	AA	AA	ABC	BB	AB	AA	AA	O	4	B
	(B)	(A)	(A)	(A)	(A)	(B)	(A)	(A)	(A)	(B)	(A)	(A)	(J)	(B)	(E)	(A)	(A)	(M)	(N)	(N)
CHANEYI	BB	BB	AA	BB	AA	BB	BB	AA	AA	AA	AA	AA	DE	BC	AB	AA	AA	O	2	C
	(B)	(B)	(A)	(B)	(A)	(B)	(B)	(A)	(A)	(A)	(A)	(A)	(I)	(H)	(E)	(A)	(A)	(M)	(M)	(O)
SCALARIS	BB	BB	AA	BB	AA	BB	BB	AA	AA	AA	AA	AA	AB	BC	AB	AA	AA	O	2	B
	(B)	(B)	(A)	(B)	(A)	(B)	(B)	(A)	(A)	(A)	(A)	(A)	(E)	(H)	(E)	(A)	(A)	(M)	(M)	(N)
GOLDMANI	BB	CC	—	BB	AA	BB	BB	AA	AA	AA	—	—	DD	BB	AB	AA	AA	V	4	B
	(B)	(C)	(?)	(B)	(A)	(B)	(B)	(A)	(A)	(A)	(?)	(?)	(D)	(B)	(E)	(A)	(A)	(N)	(N)	(N)
VARIABILIS *	CC	CC	CC	CC	BB	BB	AA	BB	BB	DD	BB	CC	AB	AE	BB	CC	AA	O	4	D
	(C)	(C)	(C)	(C)	(B)	(B)	(A)	(B)	(B)	(D)	(B)	(C)	(E)	(G)	(B)	(C)	(A)	(M)	(N)	(P)
PARVUS *	CC	DD	—	CC	BB	CC	CC	BB	BB	DD	BB	DD	AC	—	BB	AA	AA	O	4	B
	(C)	(D)	(?)	(C)	(B)	(C)	(C)	(B)	(B)	(D)	(B)	(D)	(F)	(?)	(B)	(A)	(A)	(M)	(N)	(N)

TABLE 6.—Step matrix used for PAUP analyses with the expanded data set. Character state definitions are: A = presence of allele A only; B = allele B only; C = allele C only; D = allele D only; E = alleles A and B; F = alleles A and C; G = alleles A and E; H = alleles B and C; I = alleles D and E; J = alleles A, B, and C; K = alleles B, C, and D; M = state "A" for morphological and parity characters; N = state "B" for morphological and parity characters; O = state "C" for morphological and parity characters; P = state "D" for morphological and parity characters.

	Character states														
	A	B	C	D	E	F	G	H	I	J	K	M	N	O	P
[A]	0	2	2	2	1	1	1	3	3	2	4	0	0	0	0
[B]	2	0	2	2	1	3	3	1	3	2	2	0	0	0	0
[C]	2	2	0	2	3	1	3	1	3	2	2	0	0	0	0
[D]	2	2	2	0	3	3	3	3	1	4	2	0	0	0	0
[E]	1	1	3	3	0	2	2	2	4	1	3	0	0	0	0
[F]	1	3	1	3	2	0	2	2	4	1	3	0	0	0	0
[G]	1	3	3	3	2	2	0	4	2	3	5	0	0	0	0
[H]	3	1	1	3	2	2	4	0	4	1	1	0	0	0	0
[I]	3	3	3	1	4	4	2	4	0	5	3	0	0	0	0
[J]	2	2	2	4	1	1	3	1	5	0	2	0	0	0	0
[K]	4	2	2	2	3	3	5	1	3	2	0	0	0	0	0
[M]	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
[N]	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
[O]	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
[P]	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0

species. They described the morphological differences among *S. aeneus aeneus*, *S. a. subniger*, and *S. bicanthalis* as follows: *S. a. aeneus* and *S. a. subniger* have single canthals whereas *S. bicanthalis* has two canthals on each side of the head; *S. a. aeneus* has no throat bars, *S. a. subniger* has throat bars that are diffuse, totally limited to the throat, and/or basically transverse or reticular, whereas *S. bicanthalis* has throat bars that are sharply defined, extensive, and longitudinal; and that *S. a. aeneus* and *S. a. subniger* are oviparous, whereas *S. bicanthalis* is viviparous. *Sceloporus chaneyi* was described by Liner and Dixon (1992) on the basis of, among other things, the absence of blue belly patches in males.

Our conservative grouping of samples uses only monomorphic loci showing fixed differences between populations. The second grouping includes polymorphic characters, so some of these are "traits" according to Davis and Nixon (1992), but we suggest that they are valid "characters" if they are concordant with other diagnostic markers because they can be "trapped" in lineages that are not exchanging genes and therefore are likely on separate evolutionary trajectories (Avise and Ball, 1990; Kluge, 1990). We prefer to emphasize this concordance aspect of (presumably) unlinked genetic and/or morphological markers, rather than requiring absolute fixation of single markers. By these criteria, all populations of *S. a. aeneus* (localities 1–12) are diagnosably separate from all populations of *S. bicanthalis* (localities 13–18) on the basis of fixed differences at Ck-A and M-Aat-A (columns A and J, respectively, in Table 4). All populations of *S. a. aeneus* except the Españita population (locality 10) are also diagnosably separate from all populations of *S. bicanthalis* on the basis of a fixed difference at M-Acoh-A (column F of Table 4); at this locus, the Españita population of *S. a. aeneus* shares the same fixed allele as all populations of *S. bicanthalis*.

Although *S. bicanthalis* has been considered a subspecies of *S. aeneus* (Smith and Hall, 1974; Thomas and Dixon, 1976), it is differentiated from *S. a. aeneus* by the above nuclear gene markers, as well as by two morphological differences. First, with few exceptions, all populations of *S. a. aeneus* have two canthal scales (one on each side of the head) while all populations of *S. bicanthalis* have four (two on each side of the head). Second, they differ in

male belly/throat patterns; *S. a. aeneus* has a solid pattern and *S. bicanthalis* has a barred pattern. Guillette and Smith (1985) and Smith et al. (1993) argued that parity modes and number of canthals could distinguish between *S. a. aeneus* and *S. bicanthalis* with 100% resolution, but we found this not to be the case. Though the canthal scale number proved a reliable indicator in nearly all cases (a few individuals of *S. bicanthalis* were found with canthal scale patterns of 2-1 or 1-1 instead of the 2-2 expected for the taxon), parity mode did not. One population of *S. bicanthalis* appears to be entirely oviparous (locality 18) while another shows within-population reproductive bimodality (locality 14). However, the grouping of samples defined by the fixed allozyme differences in Ck-A and M-Aat-A is identical to that defined by these two morphological characters, and on the basis of this level of concordance, we conclude that there are two different species in what is currently recognized as *S. aeneus*. One of these includes all populations of *S. a. aeneus* (localities 1–12), and the second includes all populations of *S. bicanthalis* (localities 13–18). Note that this diagnosis defines *S. bicanthalis* in such a manner as to include both oviparous and viviparous populations (Table 1).

The fixed difference at M-Acoh-A separates the Españita population of *S. a. aeneus* (locality 10, AENEUS 3) from all other populations of *S. a. aeneus* (summarized under AENEUS 2 and AENEUS 1: Fig. 3A), indicating that it may be on a different evolutionary trajectory. Another fixed difference (the duplication at G3pdh-A^2) separates the group AENEUS 2 (localities 3 and 4) from the groups AENEUS 1 and AENEUS 3 within the samples of *S. aeneus*, indicating a possible independent trajectory for these populations. In both cases, the diagnostic apomorphies appear to be fixed (within the limits of our sampling design), but in the absence of support from other characters, we consider these differences simply as indicative of population subdivision within *S. aeneus*. A strict application of the phylogenetic species concept (PSC: Cracraft, 1989; Davis and Nixon, 1992; Vrana and Wheeler, 1992) would require that both of these populations be considered separate species, but we see two problems with this approach. The first is a possible problem of circularity, if recovery of phylogenetic history is used to organize terminal taxa, then it should not also be used to define the terminal taxa to be organized via identification of derived character states for their diagnosis (Mallet, 1995). In other words, the use of phylogenetic methods for identification of derived character states for diagnosis of taxa, which are then used as the terminal units of the phylogenetic analysis, is circular because it attempts to define the items to be discovered by the discovery process (Frost and Kluge, 1995: 284).

A second problem is that such applications reduce speciation simply to the equivalent of the fixation of a uniquely derived trait (Davis and Nixon, 1992), and all species defined by the PSC will of necessity be monotypic throughout their ranges for many characters of potential evolutionary interest (with the trivial exception of Mendelian polymorphisms that characterize virtually all natural populations). In the present case, we could define the populations of BICANTHAL1 (localities 13–17) and BICANTHAL2 (locality 18) as separate species, because they can be diagnosed by fixed differences in parity mode. This certainly indicates some isolation, but we think the case is more compelling that all of these populations can be separated from all others on the bases of several shared differences at both molecular and morphological markers. Further, if this conservative definition is accepted, then *S. bicanthalis* as a species becomes extremely interesting because it is reproductively bimodal, and we can look for evidence of adaptation to different local environments within the species. This kind of character fixation can be established within a species due to local selection pressures in spite of moderately strong gene flow (Endler, 1977), and unless we are prepared to argue that this is a rare or extremely ephemeral part of the evolution-

ary process, then defining species by strict use of the PSC assures that these patterns are never discovered. They will be defined out of existence by an over-reductionist application of the PCS. Evolutionary independence of a lineage assures eventual concordance among different classes of characters as these coalesce over time within a reproductively "closed system" (Moore, 1995), and the conservative approach advocated by Avise and Ball (1990) permits recognition of additional biotic diversity within species, but without oversplitting that may result from an uncritical application of the PSC. We recognize that this approach cannot address the issue of "how many concordant characters are enough", but this is a problem common to many other species concepts, and by itself does not, in our opinion, diminish the return in increased understanding, derived from diagnosis of species based on patterns of congruence among different markers. This will be especially important as more studies are based on multiple data sets, because diagnosis of species based on an overly strict use of the PSC may differ for different types of data (Avise and Ball, 1990; Mallet, 1995). These issues are more complex than we have dealt with here, but we suggest that species diagnosis based on two or more presumably independent characters will significantly decrease the probability of naming temporarily isolated parts of single species. We recognize that there is no way at present to know with certainty "how much divergence" is enough to cross the species "threshold", and that any method will fail on occasion (see discussions in Frost and Kluge, 1995; Graybeal, 1995; O'Hara, 1993).

At a deeper level of divergence, the northern clade of *S. chaneyi* (locality 19), *S. goldmani* (locality 22), and *S. scalaris* (localities 20 and 21) are distinguished from the *S. aeneus-S. bicanthalis* (localities 1–18) clade on the basis of fixed differences at Ak-A, Pk-A, and Mpi-A (columns B, D, and G, respectively, in Table 4). *Sceloporus goldmani* is fixed for a third unique allele at Ak-A. In the more conservative of the two data sets, the two populations of *S. scalaris samcolemani* (localities 20 and 21), which form the SCALARIS group, are clearly distinct from *S. chaneyi* (locality 19), only on the basis of the male belly patterns. Males of *S. scalaris* are characterized by blue coloration with bars while the males of *S. chaneyi* have all-white venters identical to females (Liner and Dixon, 1992). However, in the expanded data set, these taxa are also separated on the basis of differences in the Pep-D locus (column M); *S. chaneyi* is characterized by possession of a unique allele ("e", not fixed: Table 5) while the two populations of *S. scalaris* segregate for two alleles shared with the populations of *S. aeneus* and *S. bicanthalis* (Table 5). The Pep-D(e) allele in *S. chaneyi* is thus concordant with the all-white male venter, and we recognize this taxon as a full species.

In summary, we recognize the following as full species in the *scalaris* complex: *S. scalaris, S. goldmani, S. chaneyi, S. aeneus* (which would include all populations listed as *S. aeneus aeneus*), and *S. bicanthalis* (which would include all populations listed as *S. aeneus bicanthalis*). Smith et al. (1993) have recently argued for the validity of *S. aeneus subniger* as a distinct subspecies on the basis of the black-barred or mottled chin/throat pattern in both sexes (the pigment is more dispersed in *S. a. aeneus*, and never barred or mottled). Based on the range map presented by Smith et al. (their Fig. 2), several of our samples of *S. aeneus* (localities 1, 8, 9, and 12) represent *S. a. subniger*. While we did not quantify patterns of throat color beyond the general scores given in Tables 4 and 5, our genetic data show that these populations are conspecific with the samples from within the range of *S. a. aeneus*, as mapped by Smith et al. (localities 2–7, and 10). Note that we cannot comment on the status of the subspecies of *S. scalaris* not included in this study.

Origins of Viviparity

According to Guillette et al. (1980), the all-viviparous groups of the genus *Sceloporus* are the *S. formosus, S. grammicus*, and *S. torquatus* groups, while the *S. sca-*

laris group is the only one to show both reproductive modes. The species diagnoses given above show *S. bicanthalis* and *S. goldmani* to be viviparous (albeit the first is bimodal) while all others, including the newly described *S. chaneyi*, are oviparous. Because of the consistent placement of *S. bicanthalis* and *S. goldmani* on tree topologies, at least two origins of viviparity within this complex are inferred. This conclusion must be considered tentative, however, because bootstrap proportions are low for both of these clades in the smaller data set (Fig. 3A), even though they approach the 70% proportion in the expanded data set (Fig. 3B).

An alternative to a double origin of viviparity is a single origin of viviparity with a later reversion to oviparity in some clades. If this were the case, based on the tree topologies resolved in this study, the origin of viviparity would have occurred basally and would have included the whole ingroup. A total of three reversions to oviparity would then be needed, one for the CHANEYI-SCALARIS clade, one for the AENEUS clade (which would include all AENEUS groups), and one for the BICANTHAL2 group. This would be a total of four steps needed (one origin of viviparity plus three reversions to oviparity), versus the two needed for the origins of viviparity in the groups GOLDMANI and BICANTHAL1. Thus, a double origin of viviparity is more parsimonious than a single origin followed by three reversals to oviparity.

As a further test, we re-ran both data sets on PAUP, but with the two viviparous groups (GOLDMANI and BICANTHAL1) constrained to form a monophyletic unit. For the more conservative data set, this produced three most parsimonious trees of 27 steps, as compared to the 25-step tree that was produced without the constraint. For the enlarged data set, eight most parsimonious trees of 70 steps were produced, as compared to eight trees of 64 steps obtained without the constraint. For both data sets, shortest trees could not be shown to be significantly more parsimonious than the constraint trees, when tested by the nonparametric method recommended by Templeton (1983; also see Larson, 1994). We recognize that bootstrap proportions may not be the best method for demonstrating strong support for tree structure (these issues are reviewed by Sanderson, 1995), and the relatively small number of phylogenetically informative characters uncovered in this study imposes further limitations on our ability to present a robust hypothesis. Despite these limitations, the "2 origin" hypothesis for the evolution of viviparity in the *S. scalaris* complex is the slightly preferred over the alternatives, and molecular studies currently in progress should provide a sufficient number of new characters to discriminate among these.

There appear to be certain factors that lead to viviparity in reptiles. These include concurrent eggshell reduction (possibly by a simple loss of shell glands: Guillette, 1987) and increased periods of egg retention, as well as the formation of some kind of placenta, perhaps at first one simply for gas and water exchange (Guillette, 1993). In comparisons between *S. aeneus* and *S. bicanthalis*, Guillette (1991) found reductions in egg shell thicknesses and number of uterine glands in *S. bicanthalis*, as well as the presence of a simple chorioallantoic placenta. These same features are present in the European lizard *Lacerta vivipara*, a reproductively bimodal species, and they seem to characterize species exhibiting recently evolved viviparity, reproductive bimodality, or incipient viviparity (Guillette, 1993). Guillette (1993) classified *S. bicanthalis* as a species that has recently evolved viviparity, although like *Lacerta vivipara* it appears to be still in transition.

Guillette (1993) presented a model for the evolution of viviparity in lizards. This model includes environmental factors activating adrenal glands to secrete progesterone, which would lead to egg retention for greater periods of time and could eventually lead to the other factors favoring the transition to viviparity. As part of this transition, Guillette (1993) postulated a series of steps leading to reproductive bimodality within species, possibly even

within populations (depending on environmental factors and individual responses to the environment, and the extent to which these responses have a genetic basis). It appears as though *S. bicanthalis* may be in the midst of undergoing these processes, with many populations having arrived at being fully viviparous, others at more of a prolonged egg retention stage (such as the Nopalillo population, locality 18), and others (such as the Las Vigas population, locality 14) that are at a point where both occur. These populations will be especially important in future studies of the proximate mechanisms described by Guillette (1993).

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