Zootaxa 1609: 53–68 (2007)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Molecular phylogeny of the *Sceloporus torquatus* species-group (Squamata: Phrynosomatidae)

NORBERTO MARTÍNEZ-MÉNDEZ[1] & FAUSTO R. MÉNDEZ-DE LA CRUZ[2]
Laboratorio de Herpetología, Instituto de Biología, Universidad Nacional Autónoma de México, México D.F., 04510, México.
E-mail: [1]nmm@ibiologia.unam.mx; [2]faustor@ibiologia.unam.mx

Abstract

The genus *Sceloporus* is one of the largest genus of lizards in North and Central America, with 22 species groups. Among these, the *torquatus* group has a notably wide geographic distribution with populations occurring from southern United States to Guatemala. In spite of the taxonomical work done with the group, some problems remain unsolved. We therefore obtained the phylogeny of the *torquatus* group, based on 925 bp of the ribosomal 16S gene, 912 bp of the ribosomal 12S gene, and 893 bp of the ND4 gene, for a total of 54 specimens of 25 taxa. The genes were analyzed, both separately and combined, by means of maximum parsimony and Bayesian inference analyses. The subspecies of *S. serrifer* did not form a monophyletic group. The sequence data refuted the morphological evidence that suggested that *S. s. plioporus* and *S. cyanogenys* are closely related to *S. s. serrifer* and to *S. s. prezygus*. Regardless, these last two were recovered as sister taxa. Moreover, evidence was found that *S. ornatus* does not form a monophyletic group, and that *S. ornatus ornatus* and *S. oberon* are a single species, despite their marked differences in coloration and scutelation. In addition, the non-monophyly of *S. mucronatus* was confirmed and the phylogenetic relationships of its different species were determined. At the same time, the subspecies of *S. dugesii* were recovered as a monophyletic group, refuting the non-monophyly of this taxon suggested in the phylogenetic hypothesis of the entire genus.

Key words: Phrynosomatidae; *Sceloporus*; *torquatus* group; phylogeny; molecular systematics, mtDNA sequences

Resumen

El género *Sceloporus* es uno de los géneros más grande de lacertilios de Norte y Centroamérica, con 22 grupos de especies. Entre estos, el grupo *torquatus* tiene una amplia distribución geográfica, con poblaciones que ocurren desde el sur de Estados Unidos hasta Guatemala. No obstante los trabajos taxonómicos realizados hasta ahora con el grupo, algunos problemas permanecen sin resolver. Por esa razón, obtuvimos la filogenia del grupo *torquatus*, basados en 925 pb del gen ribosomal 16S, 912 pb del gen ribosomal 12S y 893 pb del gen ND4, para un total de 54 especimenes de 25 taxa. Los grupos de datos fueron analizados separadamente y en conjunto, por medio de máxima parsimonia e inferencia bayesiana. Las subspecies de *S. serrifer* no fueron recuperadas formando un grupo monofilético, los datos refutan la evidencia morfológica que sugiere que *S. s. plioporus* y *S. cyanogenys* se realcionan con *S. s. serrifer* y con *S. s. prezygus*, sin embargo estos dos últimos sí son recuperados como taxa hermanos. Asimismo, encontramos evidencia que sugiere que las subspecies de *S. ornatus* no forman un grupo monofilético, y que *S. ornatus ornatus* y *S. oberon* forman parte de una sola especie, a pesar de sus marcadas diferencias en coloración y escutelación. También, se confirmó la no monofilia de *S. mucronatus* y se determinaron las relaciones filogenéticas de sus distintas especies. Al mismo tiempo, las subspecies de *S. dugesii* se recuperaron como un grupo monofilético, lo cual refuta la no monofilia de este taxon como se había sido sugerido en la filogenia previa del género.

Accepted by S. Carranza: 10 Sep. 2007; published: 8 Oct. 2007

Introduction

The genus *Sceloporus* **(**Squamata: Phrynosomatidae) is probably the best represented genus of small lizards in North and Central America, with ca. 70 species distributed from the Northern United States to Panama. Within the genus, 22 groups are distinguished, with approximately 80 species, of which some 30 species are viviparous (Sites *et al*. 1992; Wiens and Reeder 1997).

The *torquatus* group (*sensu* Smith 1938) contains viviparous species widely distributed from the southern United States southward into Guatemala. Most of these species occur in mountainous areas with temperate environments. A few species are distributed in lowlands with tropical or semi-desert environments (Smith 1936; Smith 1939; Sites *et al*. 1992). This group was proposed by Smith (1938), originally with the name of *torquatus* group, but later Smith (1939) proposed that the group should be called the *poinsetti* group, because the name of *torquatus* was at one time a secondary homonymy and under the nomenclatural rules of that time, the suppression of any homonym was considered permanent (Bell *et al.* 2003). Nevertheless different rules were proposed and Smith and Taylor (1950) revived *torquatus* as a group name, but this change was made official until 1961, when the new Code appeared.

The *torquatus* group can be diagnosed by a series of characters, described mainly by Smith (1938; 1939), with exception of some characters described later by Wiens and Reeder (1997): wide separation between xiphisternal ribs (Wiens and Reeder 1997); no contact between frontal and interparietal scales; no contact between frontal and median frontonasal scales; median parietal scale present; a lip below tip of scales (Wiens and Reeder 1997); granular skin between scales (Wiens and Reeder 1997); dorsal, ventral, and lateral scales distinctly differing in size; lateral nuchal scales not well differentiated from dorsal nuchal scales; dorsal scales subequal in size; a distinct dark, light bordered nuchal collar; male belly patch with incomplete dark margin (Wiens and Reeder 1997); female belly patches absents; karyological characters and DNA sequences (Wiens and Reeder 1997).

Since the proposal of the *torquatus* group by Smith (1938), the description of many new species and subspecies continued with traditional morphological characters. Nevertheless, when Wiens and Reeder (1997) proposed the *Sceloporus* phylogeny based on molecular and morphological characters, they detected a strongly supported conflict between DNA and morphological data. The study of Wiens *et al*. (1999), in which molecular data for the majority of the subspecies of *S. jarrovii* Cope in Yarrow were obtained, found that these subspecies were not monophyletic, and suggested a series of nomenclatural changes within which five evolutionary species were proposed. Wiens *et al*. (1999) also proposed that the divergence in coloration is possibly the result of sexual selection and habitat features. In other study carried out by Wiens and Penkrot (2002), concerning the delimitation of species using DNA and morphological characters, they used species of the *torquatus* group for the exemplification of a new protocol, and again a discordance between morphology and DNA was found, where two mtDNA clades were recognized as species that lacked diagnostic morphological characters. They established that in the *torquatus* group there is a particular pattern of morphological variation, in which between-species differentiation is small relative to within-species, the worst combination for morphology-based delimitation. For this reason, the taxonomic status of some species of the *torquatus* group remains uncertain, taking into account that in the studies of Wiens and Reeder (1997) and Wiens *et al*. (1999), no DNA sequence data were available for many taxa.

We undertook a phylogenetic investigation of the *torquatus* group using mtDNA sequence data from all taxa. The results of this study are reported herein.

Materials and methods

Taxon sampling

Samples of liver and muscle tissue were obtained from the 17 taxa not included in previous studies on the

torquatus group, and for which no sequence data existed in DNA sequence data banks. Additional samples included a new record (*S.* sp. 1), a population of *S. bulleri* Boulanger (*S. bulleri* 2 + *S. bulleri* 3), additional *S. cyanogenys* Cope (*S. cyanogenys* 2), *S. minor* Cope and a recently discovered population of *S. torquatus melanogaster* Cope (Hernandez-Gallegos *et al*. 2003) (Fig. 1, Tab. 1). We included sequences generated by Wiens and Reeder (1997) and Wiens *et al*. (1999), which were obtained from GenBank (accession numbers in Table 1).

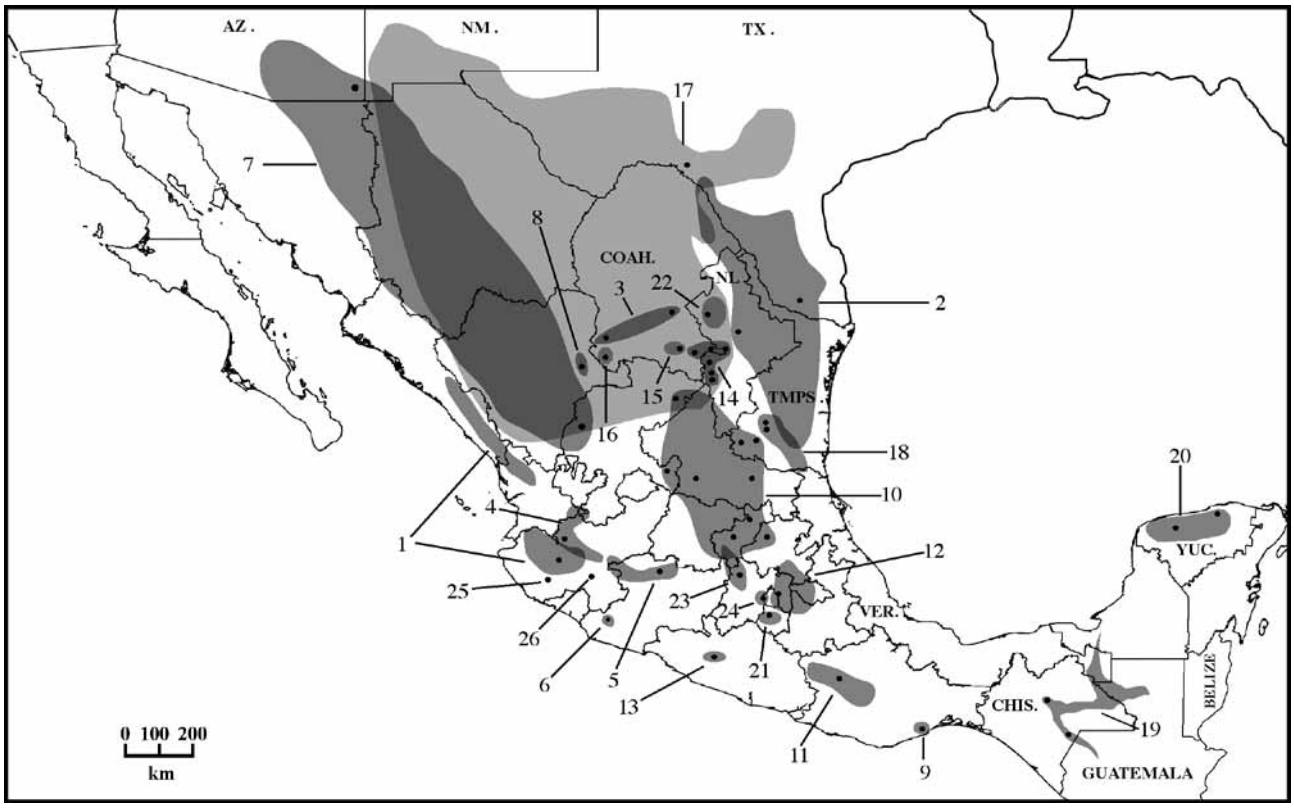

FIGURE 1. Distribution of *Sceloporus torquatus* species-*group* in México, south of United States of America and Guatemala, based on Smith 1938, Wiens *et al.* (1999) and museum data. Dots represents localities sampled for this study and those reported for each specimens included from GenBank. Numbers represents the taxa included in the analyses: 1. *S. bulleri* ; 2. *S. cyanogenys*; 3. *S. cyanostictus*; 4. *S. dugesii dugesii*; 5. *S. d. intermedius*; 6. *S. insignis*; 7. *S. jarrovii*; 8. *S. lineolateralis*; 9. *S. macdougalli*; 10. *S. minor*; 11. *S. mucronatus aureolus*; 12. *S. mucronatus mucronatus*; 13. *S. mucronatus omiltemanus*; 14. *S. oberon*; 15. *S. ornatus caeruleus*; 16. *S. ornatus ornatus*; 17. *S. poinsettii*; 18. *S. serrifer plioporus*; 19. *S. serrifer prezygus*; 20. *S. serrifer serrifer*; 21. *S. sugillatus*; 22. *S. torquatus binocularis*; 23. *S. torquatus melanogaster*; 24. *S. torquatus torquatus*; *Sceloporus* sp. 1; 26. *Sceloporus* sp. 2. The abbreviations means: In United States of America: AZ.= Arizona, NM.= New Mexico, TX.= Texas; In Mexico: CHIS.= Chiapas, COAH.= Coahuila, NL.= Nuevo Leon, TMPS.= Tamaulipas VER.= Veracruz and YUC.= Ycatan.

DNA isolation, PCR amplification and sequencing

MtDNA was isolated from small quantities of liver and muscle (approx. 100 mg) following Fetzer's (1996) extraction protocol with ammonium acetate. The target genes were amplified using the polymerase chain reaction (PCR; Saiki *et al*. 1998). The amplified regions correspond to a fragment of approximately 912 base pairs of the ribosomal 12S (rRNA) gene using the primers tPhe and 12e (Wiens *et al*. 1999); 925 base pairs of the 16S (rRNA) gene using the primers 16SaR-L and 16Sd-H (Reeder 1995) and 893 base pairs of the ND4 gene that additionally included the complete portions of t-RNA-His, t-RNA-Ser and a portion of the t-RNA-Leu, amplified with the primers ND4 and LEU (Arevalo *et al*. 1994; Forstner *et al.* 1995). These genes yielded good results in other studies of *Sceloporus* (Benabib *et al*. 1997; Wiens and Reeder 1997; and Wiens *et al*. 1999).

TABLE 1. Species, localities, voucher specimen number and GanBank accession numbers for specimens evaluated in the *Sceloporus torquatus* species-group. The acronyms follow the nomenclature of Leviton *et al.* (1985) except for MZFC, which corresponds to the Museo de Zoología of the Facultad de Ciencias of the Universidad Nacional Autónoma de México (UNAM); MX, MZFC frozen collection, and IBH, which corresponds to the Colección Nacional de Anfibios y Reptiles of the Instituto de Biología of the UNAM. The numbers and letters after *S. oberon* and *S. minor* correspond to the population and organism code with which they are identified in the study of Wiens *et al*. (1999).

Species	Locality	Voucher	GenBank accesion no.		
			12S	16S	ND4
Sceloporus bulleri 1	México: Jalisco: 1.0 km S Mascota	IBH 18034	DQ525887	DQ525904	DQ525865
Sceloporus bulleri 2	México: Jalisco	MX15-63		EF608027	EF608022
Sceloporus bulleri 3	México: Jalisco	MX15-64		EF608028	EF608023
Sceloporus cyanogenys	United States: Texas: McMullen	LSUMZ 48852	AF15414	AF000876	AF154193
Sceloporus cyanogenys 2	México: Nuevo León: Escobedo: 25.3 km NW Monterrey	IBH 18051	DQ525893	DQ525910	DQ525868
Sceloporus cyanostictus 1a	México: Coahuila: 23.6 km S Monclova	CM 147644	AF154146		AF154194
Sceloporus cyanostictus 1b	México: Coahuila: 1.0 km S San Lorenzo	MZFC 7411b	AF000825	AF000865	AF154195
Sceloporus dugesii dugesii	México: Jalisco: Tapalpa	UTA-R 23955	AF154170	AF000877	AF154190
Sceloporus duguessi intermedius	México: Guanajuato: 2.0 km E Moroleón	IBH 18002	DQ525886	DQ525903	DQ525878
Sceloporus duguessi intermedius 2	México: Guanajuato: 2.0 km E Moroleón	IBH 18004	DQ525889	DQ525906	DQ525866
Sceloporus insignis	México: Michoacán	no voucher	AF000806	AF000846	
Sceloporus jarrovii 11a	México: Zacatecas: 24 km W Fresnillo	CM 147650	AF15173		AF154209
Sceloporus jarrovii 11b	México: Zacatecas: 24 km W Fresnilo	CM 147651	AF15418		AF154210
Sceloporus jarroviii 10	United States: Arizona: Cochise Co., near Portal	LSUMZ 48786	AF154163	AF000881	AF154208
Sceloporus lineolateralis	México: Durango: near Pedricena	MZFC 6650	AF000807	AF000847	AF154211
Sceloporus macdougalli	México: Oaxaca: Rincón Bamba, 35. 2 km SW Tehuantepec	MZFC 7017	AF000809	AF000849	
Sceloporus minor	México: Tamaulipas: 17.7 km SW Ciudad Victoria	IBH 18012	DQ525891	DQ525908	DQ525872
Sceloporus minor 13a	México: Zacatecas: 4.0 km W Concepción del Oro.	MZFC 10703	AF154185		AF154222
Sceloporus minor 14a	México: San Luis Potosí: Colonia Insurgentes, 2.5 km W San Luis Potosí	CM 147653	AF154174		AF154218
Sceloporus minor 15a	México: San Luis Potosí: 14.1 km E Ciudad del Maíz	CM 147630	AF154136		AF154213

to be continued.

TABLE 1. (continued)

Species	Locality	Voucher	GenBank accesion no.		
			12S	16S	ND4
Sceloporus minor 17	México: San Luis Potosí: 22.8 km E Matehuala	CM 147679	AF154148		AF154231
Sceloporus minor 3	México: Queretaro: 4.9 km S Ezequiel Montes	MZFC 10736	AF154138		AF154198
Sceloporus minor 4b	México: Queretaro: 1.0 km S Cadereyta	MZFC 10738	AF154175		AF154200
Sceloporus minor 5	México: Hidalgo: Barranca de los Marmoles W of Jacala	CM 147625	AF154142		AF154201
Sceloporus minor 6a	México: Hidalgo: Puerto de la Zorra, between Cuesta Colorada and Jacala on Hwy 85	CM 147628	AF154143		AF154202
Sceloporus minor 8	México: Tamaulipas: 16.9 km W Ciudad Victoria	MZFC 10666	AF154155		AF154204
Sceloporus mucronatus aureolus	México: Oaxaca: Temazulapan	IBH 18022	DQ525884	DQ525901	DQ525875
Sceloporus mucronatus mucronatus	México: Estado de México: Ajusco Volcano: Ejido Capulín	IBH 18008	DQ525885	DQ525902	DQ525864
Sceloporus mucronatus omiltemanus	México: Guerrero: Omiltemi National Park	UTA-R 24004	L41419	L41469	AF154233
Sceloporus oberon 21 b	México: Nuevo León: 9.0 km E San Roberto	MZFC 8032	AF000826	AF000866	AF154212
Sceloporus oberon 24a	México: Nuevo León: 2.1 km S Santa Clara de Cienega	CM 147675	AF154157		AF154228
Sceloporus oberon 27b	México: Coahuila: N of El Diamante	CM 147674	AF154183		AF154239
Sceloporus oberon 28a	México: Coahuila: 22.3 km E San Antonio de las Alazanas	CM 147641	AF154160		AF154234
Sceloporus oberon 29a	México: Nuevo León: 2.5 km E San Isidro, turnoff for Laguna Sánchez	MZFC 10698	AF154147		AF154236
Sceloporus ornatus caeruleus	México: Coahuila	JAM 652	AF000814	AF000854	AF154240
Sceloporus ornatus ornatus	México: Coahuila: Ojo Caliente N of Ramos Arizpe	IBH 18041	DQ525879	DQ525896	DQ525862
Sceloporus poinsettii	United States: Texas: Val Verde Co.	LSUMZ 48847	AF154176	AF000883	AF154241
Sceloporus serrifer plioporus	México: Tamaulipas: Padilla, 4.5 km NW Ciudad Victoria	IBH 18014	DQ525882	DQ525899	DQ525873
Sceloporus serrifer plioporus 2	México: Tamaulipas: Padilla, 4.5 km NW Ciudad Victoria	IBH 18015	DQ525883	DQ525900	DQ525874
Sceloporus serrifer prezygus	México: Chiapas: 2.5 km NW Teopisca	IBH 18027	DQ525880	DQ525897	DQ525870
Sceloporus serrifer prezygus 2	México: Chiapas: Ixtapa, 26.3 km E San Cristobal de las Casas on Hwy 190	IBH 18095	DQ525881	DQ525898	DQ525875

to be continued.

TABLE 1. (continued)

Species	Locality	Voucher	GenBank accesion no.		
			12S	16S	ND4
Sceloporus serrifer serrifer	México: Yucatan: 13 km N Merida	IBH 18020	DQ525894	DQ525911	DQ525876
Sceloporus serrifer serrifer 2	México: Yucatan: 20 km N Tizimin	IBH 18123	DQ525895	DQ525912	DQ525877
Sceloporus sugillatus 30a	México: Morelos: Lagunas de Zempoala, W of Huitzilac	CM 147623a	AF154187		AF154242
Sceloporus torquatus binocularis	México: Nuevo León	MZFC 8033	AF000827	AF000867	
Sceloporus torquatus melanogaster 1	México: N of Estado de Mexico	UTA-R 24016	AF154179	AF000890	AF154244
Sceloporus torquatus melanogaster 2	México: Estado de México: 2.0 km N Polotitlan	IBH 18006	DQ525892	DQ525909	DQ525863
Sceloporus sp. 1	México: Nayarit: Sierra de Alica: Carretera Huajimin-Tepic	MX14-4	EF608018	EF608026	EF608021
Sceloporus sp. 1	México: Jalisco: Bolaños	MX13-24	EF608016	EF608024	EF608019
Sceloporus sp. 1	México: Jalisco: Carretera Bolaños-Tuxpan de Bolaños	MX13-80	EF608017	EF608025	EF608020
Sceloporus heterolepis	México: Jalisco: Cumbre de los Arrastrados	IBH 18138	DQ525890	DQ525907	DQ525869
Sceloporus grammicus	México: Oaxaca: Sierra de Juárez	UTA-R 23970	L40457	L41464	AF154188

PCR reactions in a Perkin-Elmer 2400 thermocycler had a final volume of 50 µl. The conditions for the PCR reaction for the different genes were: 12S with 45 cycles of 94º C for 30 sec, 53º C for 30 sec, and 72º C for 2 min; 16s with 45 cycles of 94º C for 30 sec, 50º C for 45 sec, and 72º C for 30 sec; and for the ND4, 35 cycles of 94º C for 1 min, 50º C for 1 min, and 72º C for 1 min were performed. The first cycle of each of the amplification reactions included a denaturalization cycle of 94º C for 3 min, and the last cycle was completed with a cycle for final extension (two in the case of ND4) of 72º C for 5 min. The PCR products were purified using the QIA quick purification kit, and the resulting samples were sequenced by means of the automated sequencing service of the UNAM's Instituto de Biología, utilizing an ABI PRISM, 310 Genetic Analyzer (Applied Biosystems) automated sequencer. All DNA sequences obtained were deposited in the GenBank (Accession Nos. DQ525862-DQ525912) and are listed in Table 1.

Sequence alignment

The sequences obtained were compiled and edited in ProSeq 2.91 (Filatov 2002). Sequence alignment was carried out separately for each region, employing Clustal X (Thompson *et al.* 1997), using the default parameters, and, later, manually refined using the secondary structural models for the 12S and 16S (Ortí and Meyer 1987). Consequently, alignment was again made using Clustal X, with apertures and gap extensions of 15:6, 10:5, 6:3 and 3:1. The sequence regions, whose homologies by the nucleotide position were at a variance, in differing penalizations, were considered ambiguous and were not included in the phylogenetic analyses. The ND4 protein-coding genes lacked insertions and deletions (indels) and were aligned by eye. Later, this codifying region was transferred to amino acids in order to check whether stop codons existed that could indicate the presence of pseudogenes. The tRNAs region adjacent to the ND4 was also aligned by eye, and

was later reanalyzed with Clustal X using different gap costs. For the total evidence analysis, the matrices aligned for each region were combined into a new matrix. Different number of terminals for each region were coded as missing data.

Phylogenetic analysis

The phylogenetic analysis of the molecular data used total evidence (Kluge and Wolf 1993). In order to detect possible areas of significant incongruence, the genes were also analyzed independently (Wiens 1998a).

We did not test for the presence of phylogenetic signal. The signal is additive across different matrices and can dominate in a combined analysis in cases where the separate matrices have a very weak signal (Barrett *et al.* 1991; Wenzel and Siddall 1999). Because some of the sequences were obtained from GenBank, the separate matrices did not include the same taxa. Nevertheless, all the sequences were included in the combined analysis to maximize sampling.

Maximum parsimony analyses (MP) were conducted in PAUP version 4.0b10 (Swofford 1998) for the separate and the total evidence data sets. We used a heuristic search with tree bisection and reconnection (TBR) branch swapping and 1000 random sequence addition replicates. Characters were treated as unordered and equally weighted, and gaps were coded as missing data. Branches were collapsed if the maximum length was zero. Clade support was evaluated using nonparametric bootstrap proportions (BSP, Felsenstein 1985) with 1000 pseudoreplicates. BSPs proportions of <70% were considered to indicate poor support (Brandley and De Queiroz 2004). BSPs of =95% were interpreted as representing very strong support and from 70% to 94% moderate support**.**

Modeltest (version 3.07, Posada and Crandall 1998) was used to infer the best-fit model of evolution for the Bayesian inference (BI) analyses for each partition based on the Bayesian Information Criterion (BIC) method. The Hierarchical Ratio Test (hLRTs), although being the most popular method, is not the optimum strategy for choosing substitution models for phylogenies (Sanderson and Kim 2000; Posada and Buckley 2004).

BI analyses (Larget and Simon 1999; Lewis 2001) were performed for 12S, 16S, and ND4 matrices (with four partitions: codons + tRNAs) and for the combined data set with the six previous partitions, using MrBayes 3.0 b4 (Huelsenbeck and Ronquist 2001). Because MrBayes is limited to models with one, two or six base-substitution rate matrices, we used the GTR+I+G model for 12S, 16S and ND4 second and third codon positions instead of TrN+I+G model (best model obtained by Modeltest) because TrN has three parameters. For tRNAs we used the GTR+G model instead of K81uf+G model, because K81uf also has three parameters. For the first position codon in ND4 we used the HYK+G model inferred by Modeltest. In each analysis, four Markov chains were run, beginning with a random tree. The analysis used 2.0×10^6 generations with sampling every 1000 generations. Likelihood scores were graphed against generation time using Tracer v.1. 2.1. (Rambaut and Drummond 2005) to identify stationarity, and thus to determine how many generations must be discarded as burn-in, and whether or not more generations were required to be run. In order to insure that the analyses had found the optimal arrangements, they were performed twice for each data group and the stationarity levels were compared for convergence. When the different analyses reached stationarity and the topologies were congruent, the resultant trees were combined using a majority-rule consensus tree in PAUP ver.4 (Swofford 1998). Congruence for each branch indicated the posterior probability (PP). Using the criterion of α=5%, clades were considered to be significantly supported when PP =95% (Wilcox *et al*. 2002; Reeder 2003).

Choosing the outgroup

In a preliminary analysis, the trees were rooted utilizing sequences of *S. grammicus* Wiegman and *S. megalepidurus* Smith, which are the first and second outgroups of the *torquatus* group (Wiens and Reeder 1997), respectively. However, the furthermost external group contributed less in terms of character states and

rooting information, and introduced errors into the analysis (Lyons-Weiler, *et al*. 1998; Nylander 2001; Sanderson and Shaffer 2002). Therefore, we added one more taxon to the first outgroup (*S. heterolepis* Boulenger), thus breaking the long branch leading to the external group and adding balance to the topology (Swofford and Olsen 1990; Smith 1994).

Results

Sequences

Sequence data from 54 lizards belonging to 25 taxa were assembled. We could not amplify 12S from *S. bulleri* 1 and *S. bulleri* 2. We obtained 912 and 925 bp of the ribosomal genes 12S and 16S respectively, and 709 bp of encoding ND4 plus 184 bp of the adjacent tRNAs. After alignment, a matrix of 2701 characters was obtained, of which 1789 were constant, 304 were variable but not phylogenetically informative, and 599 were potentially phylogenetically informative.

Phylogenetic analyses

Analyses of the separate genes typically resulted in congruent topologies. The relationships are similar for those obtained in the total evidence analyses, with the exception of two incongruent nodes, that were weakly supported (the trees are not shown, but they are available upon request). First, in the analyses of 16S and ND4 (and also in the combined analysis), *S. insignis* Webb was resolved as the sister taxon of a clade formed by (((*S.* sp1 + (S. *t. melanogaster* 1 + S. *t. melanogaster* 2)) + (S. *t. torquatus* Wiegmann + S. *t. binocularis* Dunn)) + ((*S. bulleri* 2 + *S. bulleri* 3) + S. *bulleri* 1)), but with low BSPs (16s and ND4: BSP=57) and high and moderate PPs (16s: PP=100; ND4: PP=94). Alternatively, 12S recovered *S. insignis* as the sister taxon of a clade formed by ((*S. j. jarrovii* 11a + *S. j. jarrovii* 11b) + (*S. jarrovii* 10 + *S. lineolateralis* Smith)) with a weak support (BSP<50, PP=58). Second, *S. ornatus caeruleus* Smith was in a polytomy in the analyses of 16S and ND4, but 12S (like in the combined analysis) recovered it as the sister species of a clade formed by (((*S. cyanogenys* 1, 2, 96) + (*S. plioporus* Smith, 1 + *S. plioporus* 2)) + (*S. j. cyanostictus* Axtell and Axtell, 1a + *S. j. cyanostictus* 1b)) with a weak and strong support (BSP<50, PP=98).

The MP of the combined data found 30 most parsimonious trees (MPTs: length=2254, CI=0.524, RI=0.733) and the strict consensus tree is shown in Figure 2. For the BI of the combined data, the first 2000 generations were discarded as the burn-in. The strict consensus of the MPTs and the Bayesian majority-rule probability tree of 18001 trees were congruent in their relationships, although MP recovered *S. o. caeruleus*, one population of *S. oberon* Smith and Brown (*S. oberon* 21b) and one population of S. *minor* (S. *minor* 13a) as a polytomy. The better resolved BI tree is our preferred phylogenetic hypothesis and is presented in Figure 3 along with PP and BSPs support above and below the branches, respectively. This hypothesis (Fig. 3) shows two strongly supported basal clades, A and B (BSP=100 and PP=100). Clade A includes the subspecies of *S. torquatus* plus *S. bulleri*, *S. insignis*, *S.* sp. 1, *S. linoelateralis* and *S. jarrovii*. whereas Clade B includes the remaining species.

Clade A has two strongly supported subclades (BSP=100, PP=100). In one subclade *S. lineolateralis* was resolved within populations of *S. jarrovii* and this association was strongly supported (BSP=100, PP=100). In the second subclade, *S. insignis* was the sister taxon to all other species (BSP=52, PP=99). The next node of this subclade resolved the populations of *S. bulleri* clade ((*S. bulleri* 1 + (*S. bulleri* 2 + *S. bulleri* 3)) with strong support (BSP=100, PP=100). *Sceloporus* sp. 1 was resolved within the subspecies of *S. torquatus* as ((*S.* sp. 1, *S. t. melanogaster*) + (*S. t. torquatus, S. t. binocularis*)) with moderate and strong support (BSP=72, PP=100). *Sceloporus torquatus* subespecies were the sister group of *S. bulleri* (BSP=95, PP=100).

Within Clade B, Clade C was strongly supported (BSP=100, PP=95). *Sceloporus mucronatus aureolus* Smith was the sister of (*S. m. omiltemanus* Günter + *S. macdougalli* Smith and Bumzahem) and this clade

received moderate support (BSP=67, PP=95). Surprisingly, nominate *S. m. mucronatus* Cope was resolved with strong support (BSP=95, PP=100) in Clade G as the sister taxon of (*S. suguillatus* Smith + *S. poinsettii* Baird and Girard). Therefore, the subspecies of *S. mucronatus* did not form a monophyletic group.

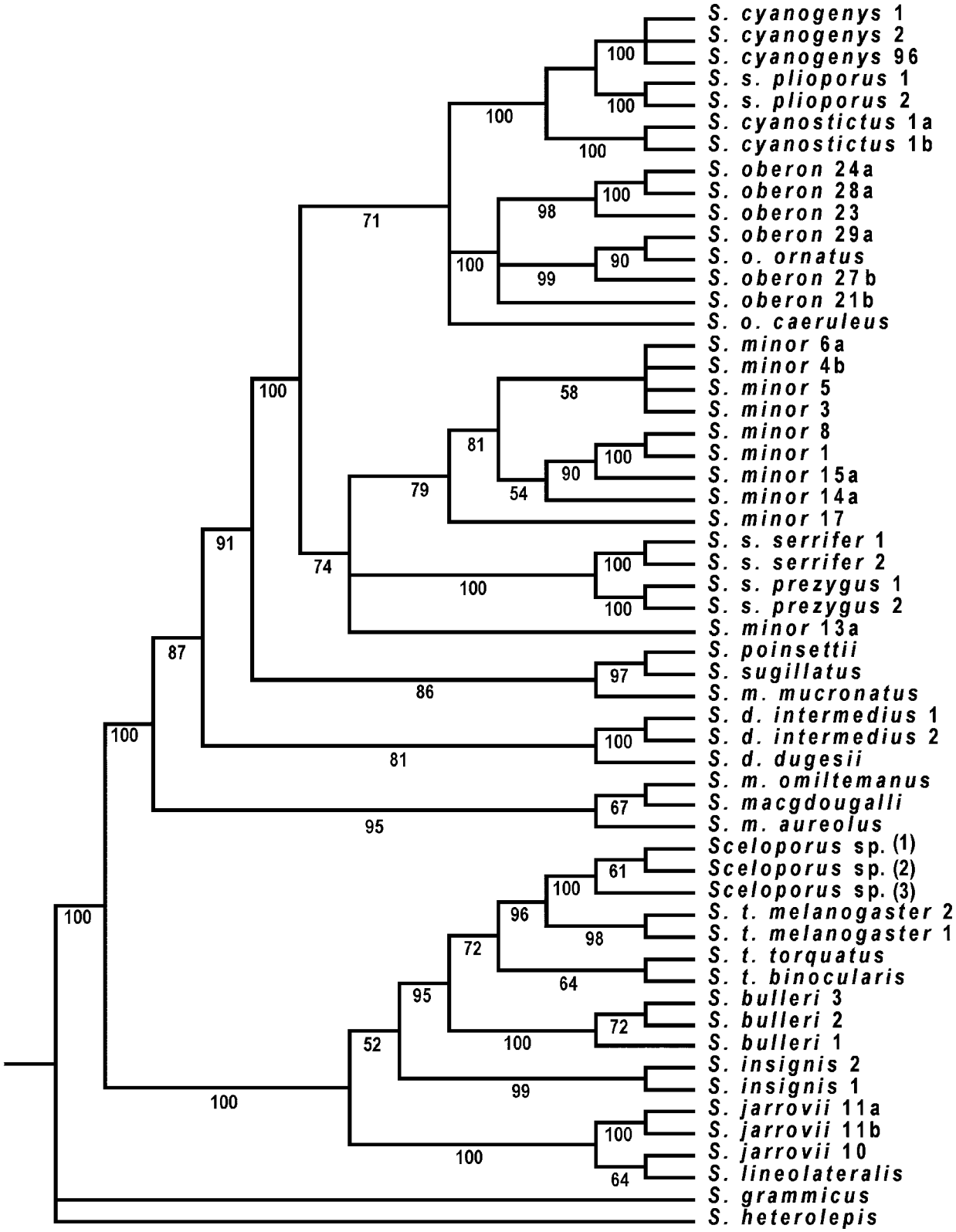

FIGURE 2. Srict consensus of 30 trees from the parsimony analysis based on 12S 16S and ND4 mtDNA sequences (length=2254, CI=0.524, RI=0.733). Bootstrap proportions > 50 % are indicated above the branches.

Clade D contains Clade E as the sister group of Clade F. In Clade E, the monophyly of *S. dugessi* Bocourt is well supported (BSP=81, PP=100). This result differed from that of Wiens and Reeder (1997) who, with weak support, placed *S. d. dugesii* as a sister taxon of *S. poinsettii*.

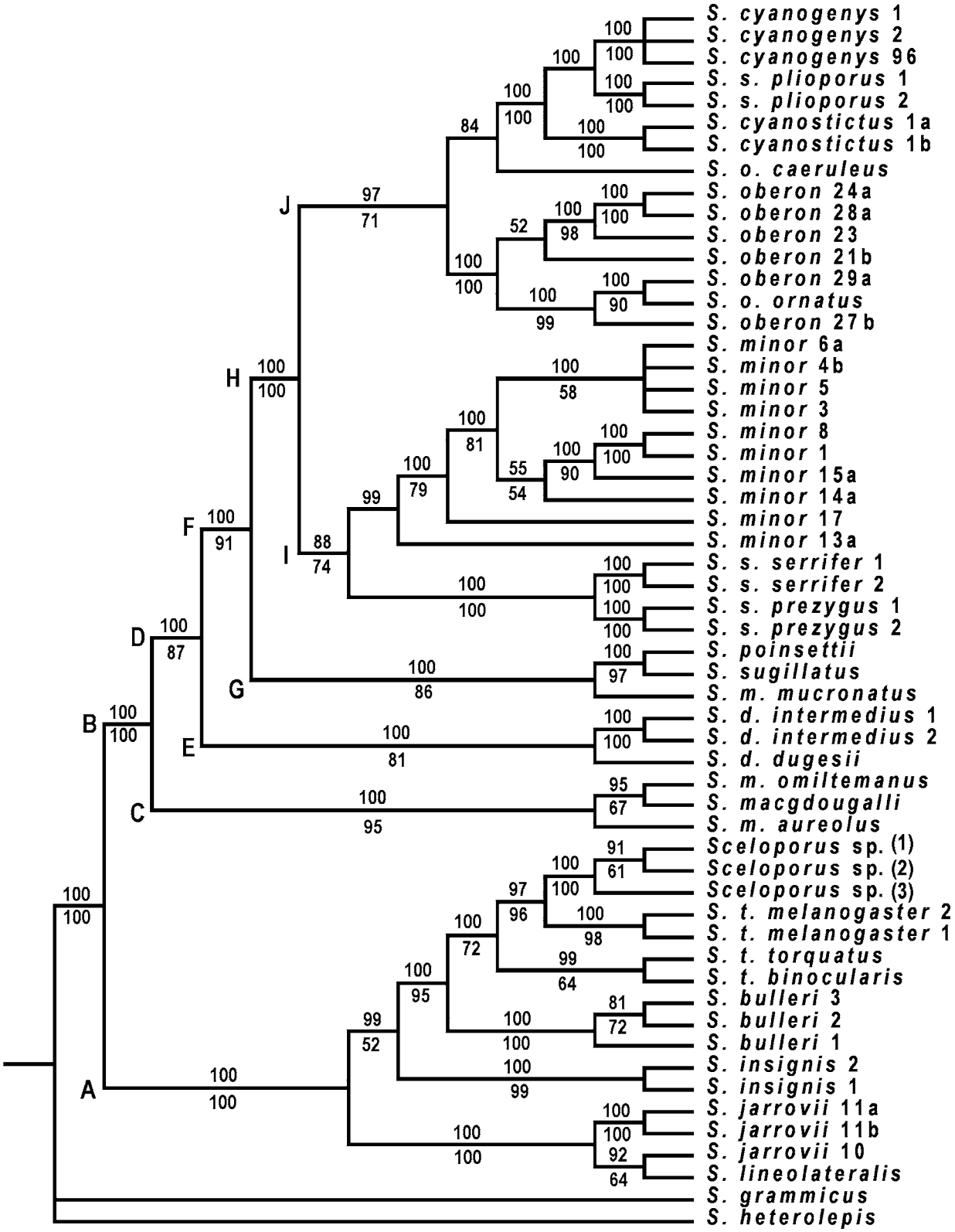

FIGURE 3. Bayesian inference tree based on 12S 16S and ND4 mtDNA sequences. Posterior probabilities > 50% and boostrap proportions > 50 % (from the parsimony analysis) are indicated above and below the branches, respectively.

Clade F had two primary groups, clades G and H, and in turn, Clade H contained clades I and J. Clade I (BSP=74, PP=88) consisted of two subspecies of *S. serrifer* Cope plus *S. minor*; *S. s. serrifer* was the sister to *S. s. prezygus* Smith (BSP=100, PP=100) and together they formed the sister group of *S. minor* (Fig. 3). However, the subspecies of *S. serrifer* were not recovered as a monophyletic group because *S. s. plioporus* was resolved as the sister taxon of *S. cyanogenys* in Clade J (BSP<50, PP=100), an arrangement that agreed with the morphological analysis of Olson (1987).

Incidences of non-monophyly occurred in Clade J. *Sceloporus ornatus ornatus* Baird, branched off from within *S. oberon* and *S. o. caeruleus* was the sister group of *S. cyanostictus*, *S. s. plioporus,* and *S. cyanogenys*. The phylogenetic relationships of *S. cyanogenys*, *S. cyanostictus*, *S. oberon* and *S. minor* are in discordance with the analysis of Wiens *et al*. (1999). We recovered moderate and strong support (BSP=71, PP=97) for the placement of *S. oberon* as sister taxon of *S. cyanogenys*, *S. cyanostictus*, and *S. plioporus*. In contrast, Wiens *et al*. (1999) reported a weakly supported subclade where *S. minor* and *S. oberon* were the sister group of *S. cyanogenys* and *S. cyanostictus*.

TABLE 2. Data partitions, the best models of sequence evolution according to the BIC method and the number of characters of each partition used in the Bayesian inference analysis.

Partition	Model	Number of characters in partition
12S	TrN+I+G	912
16S	TrN+I+G	925
ND4 1st codon	HKY+G	237
ND4 2nd codon	TrN+I+G	236
ND4 3rd codon	TrN+G	236
tRNAs	K81uf+G	184

TABLE 3. Values of the parameters, estimated using the BIC method of Bayesian Inference for the different data groups.

	Substitution rates						Ti/tv ratio	Site rates		Nucleotide frecuencies			
	A<–>C	A<–>G	A<–>T	C<–>G	C<–>T	G<–>T		I	Ã	A	C	G	T
12S	1.0000	5.9702	1.0000	1.0000	9.3163	1.0000	-	0.3641	0.4946	0.3778	0.2361	0.1649	0.2212
16S	1.0000	2.7657	1.0000	1.0000	6.1090	1.0000	-	0.4981	0.5931	0.3735	0.2414	0.1658	0.2194
1stcodon	-	-	-	-	-	-	4.6456	-	0.3055	0.3425	0.2571	0.1717	0.2287
2ndcodon	1.0000	19.4007	1.0000	1.0000	1.3595	1.0000	-	0.5900	0.3189	0.1632	0.2936	0.1454	0.3978
3rdcodon	1.0000	32.0663	1.0000	1.0000	10.6605	1.0000	-	-	2.5339	0.4534	0.3046	0.0478	0.1942
tRNAs	1.0000	2.9227	0.1462	0.1462	2.9227	1.0000	-	-	0.4739	0.3709	0.1958	0.1575	0.2758

Discussion

In this study, significantly and moderately supported relationships were obtained for all species and subspecies of the *torquatus* group. In general, the relationships agreed with those of Wiens *et al.* (1999), although some of the relationships recovered by Wiens and Reeder (1997) differed. Unlike Wiens and Reeder (1997), the monophyly of the subspecies of *S. torquatus* and their relationships with *S. bulleri* and *S. insignis* were strongly supported. *S.* sp. 1 from Jalisco was the sister taxon of *S. t. melanogaster.* Similarly, *S. lineolateralis* was resolved as the sister taxon of *S. jarrovi*, as suggested by Sites *et al*. (1992).

The non-monophyly of *S. mucronatus* was corroborated according to Wiens and Reeder (1997) and *S. m. mucronatus* was supported as being the sister taxon of (*S. sugillatus* + *S. poinsettii*) (BSP=86, PP=100). *Sceloporus m. aureolus* was the sister taxon of (*S. macdougalli* + *S. m. omiltemanus*) (BSP=67, PP=95). In contrast, Wiens and Reeder (1997) reported that *S. macdougalli* was the sister taxon of (*S. m. aureolus* + *S. m. omiltemanus*), albeit with weak support. We found support for the monophyly of *S. dugesii* (BSP=81, PP=100), a relationship that also differs from the analysis of Wiens and Reeder (1997). They resolved *S. d. dugesii* as the sister taxon of *S. poinsettii*, and *S. d. intermedius* as the sister taxon to all other species of the *torquatus* group.

In the study of Wiens and Reeder (1997), *S. s. serrifer*, *S. s. prezygus*, and *S. cyanogenys*, were not found to be sister taxa. However, Wiens and Reeder treated that result with caution, given the low branch support. Similarly, our hypothesis (Fig 3) did not resolve these taxa as being a monophyletic assemblage. This finding contrasts with the morphological evidence of Olson (1987), who proposed that *S. cyanogenys* was a subspecies of *S. serrifer*.

Olson (1987) associated *S. s. plioporus* (not included by Wiens and Reeder 1997) with *S. cyanogenys*. In our study, *S. serrifer plioporus* was the sister taxon of *S. cyanogenys* and this association received strong support (BSP=100, PP=100). This association also has geographical support. Whereas both *S. s. serrifer* and *S. s. prezygus* occur in southeastern Mexico, *S. s. plioporus* principally inhabits southern Tamaulipas and a small portion of northern Veracruz (Fig. 1). This is south of the distribution of *S. cyanogenys*. Olson's results (1987) as well as ours show that *S. s. plioporus* forms the southern part of a morphological cline of *S. cyanogenys*, and should be considered as the same species. A single morphological characteristic typically differentiates *S. s. plioporus* from *S. cyanogenys*. In *S. s. plioporus*, the supraocular scales are complete and separated from the parietals by a row of intervening small scales. Alternatively, in *S. cyanogenys*, the supraocular scales are divided and in contact with the parietal scales. Within populations of *S. s. plioporus* in Tamaulipas, both morphological conditions exist. The percentage of individuals with divided supraocular scales increases northwardly. Similarly, in some individuals, the supraoculars contact with the parietals, and in others they do not. The percentage of individuals that have supraoculars contacting the parietals diminishes northwardly. Unfortunately, we could not locate any population of *S. serrifer* from Veracruz (Smith 1939; Stuart 1970 and Olson, 1987). A large percentage of Veracruz has suffered deforestation and been subjected to other types of ecological modification. For that reason, we cannot genetically determine whether these populations are more closely associated with *S. cyanogenys* or with *S. serrifer* of southeastern Mexico.

Wiens and Reeder (1997) resolved the two subspecies of *S. ornatus* as sister taxa. However, no molecular data were available for *S. o. ornatus* and the association was weakly supported. In contrast, the two subspecies were not recovered as sister taxa in our study. *Sceloporus o. ornatus* occurs in Coahuila, and is geographically close to populations of *S. oberon* (Fig. 1). Although possible, we do not believe that our results are the consequence of a recent invasion or introgression of the maternal genotype of *S. oberon* into *S. o. ornatus*. If migration was involved, then we would expect *S. o. ornatus* to be more closely related to the geographically closest population, that of *S. oberon* 27 from Coahuila (see Figure 1 and Table 1). However, *S. o. ornatus* appeared as the sister group of the geographically furthermost population from Nuevo León (*S. oberon* 29). Moreover, these taxa occur in very different environments. Whereas *S. oberon* occurs in oak woodlands, *S. o. ornatus* lives at lower altitude in desert regions. While *S. oberon* exhibits dark colors on its back, *S. o. ornatus* is yellow and light blue. With respect to the dorsal scales, *S. oberon* has relatively large scales, averaging 37.5 around the body, but *S. o. ornatus* averages 55, smaller scales. Our tree leaves three possible options to consider: 1) *S. oberon* and *S. o. ornatus* form a single species; 2) *S. oberon* contains at least three cryptic species; or 3) the non-monophyly owes to incomplete lineage sorting. An evaluation of highly variable nuclear genes could differentiate between these possibilities. However, for the time being, we prefer the first option and consider the taxa to be conspecific. The phylogenetic relationships of *S. o. caeruleus* are still not satisfactorily resolved, and we believe that more detailed studies are necessary.

The extensive variation in coloration between individuals in the *torquatus* group may reflect sexual selection (Wiens *et al*. 1999). Regardless, environmental characteristics might also play a very important role, particularly in the number and size of the dorsal scales, given that scales are involved in thermoregulation and humidity exchange (Soulé and Kerfoot 1972; Fox 1975).

Taxonomy of the *torquatus* group

In order to obtain a taxonomy that reflects phylogenetic history, a number of taxonomic changes are necessary. The following modifications are proposed:

1) *Sceloporus mucronatus* should be treated as a monotypic species. The subspecies *S. mucronatus mucronatus* should not be recognized.

2) The subspecies *Sceloporus mucronatus aureolus* should be elevated to full species status as *Sceloporus aureolus* [new combination].

3) The subspecies *Sceloporus m. omiltemanus* should be elevated to full species status *as S. omiltemanus* [new combination].

In this study, we showed molecular evidence for the non-monophyly of *S. mucronatus* subspecies, which indicates a discordance between morphological and mtDNA species limits. The main differences between *S. mucronatus* subspecies have traditionally been identified as some patterns on the coloration, the number of dorsal scales and femoral pores (Smith 1939). In *S. m. mucronatus* dorsal scales are 27 to 30 with 11 to 17 femoral pores on each side; in *S. m. omiltemanus* dorsal scales are 30 to 38 with 12 to 16 femoral pores, and in *S. m. aureolus* dorsal scales are 32 to 36 with 12 to 16 femoral pores. Nevertheless, due to wide morphological overlapping between species, no consistent diagnostic characters have been observed.

4) *Sceloporus oberon* should be synonymized into *Sceloporus ornatus. Sceloporus ornatus* Baird, 1859 has priority over *S. oberon* (S. *jarrovii oberon* Smith and Brown, 1941). Although recognition of subspecies has become controversial, *S. ornatus ornatus* could continue to be recognized. If so, then populations presently known as *S. oberon* should be referred to as *S. ornatus oberon* [new combination]. We recognize that this arrangement results in a paraphyletic taxonomy for the subspecies.

5) *Sceloporus ornatus caeruleus* should be elevated to full species status *as S. caeruleus* [new combination].

As in *S. mucronatus*, we observed discordances between morphology and mtDNA data. According to the molecular phylogeny of Wiens *et al*. (1999) *S. jarrovii oberon* and some northern populations of *S. j. minor* are synonymized in *S. oberon*, despite the differences in coloration of these two taxa. Wiens *et al*. (1999) suggested that the differences in dorsal coloration in the populations of *S. oberon* may reflect sexual selection. Furthermore, in our study we also found that *S. o. ornatus* and *S. oberon* conforms an evolutionary species, despite the differences in coloration and scutelation. The populations of *S. oberon* have between 34 to 46 dorsal scales, whereas *S. o. ornatus* have between 55 to 63 dorsal scales with a complex coloration pattern (Smith 1939). The differences in the number of dorsal scales may be due to habitat, as was pointed out in a previous paragraph. Habitat influence may explain the morphological similarities between *S. o. ornatus* and *S. o. caeruleus* which has a high number of dorsal scales (47 to 53) and also occurs in semi-desert habitats, but without a close phylogenetic relationship.

6) *Sceloporus serrifer plioporus* Smith, 1939 from southern Tamaulipas, should be synonymized into *S. cyanogenys* Cope, 1885. The taxonomic status of populations in Veracruz remains uncertain. The original morphological difference between putative populations of *S. s. plioporus* and *S. cyanogenys*, was the divided supraoculars scales in the latter (Smith 1939). However, on closer inspection, these differences are not supported (Olson, 1987) because the percentage of individuals with divided supraoculars scales increases northwardly.

7) *Sceloporus dugesii* should be recognized as being monotypic, instead of having two subspecies *S. d. dugesii* and *S. d. intermedius*. Despite Wiens and Reeder (1997) found some weakly supported morphological

differences between *S. d. dugesii* and *S. d. intermedius*. The main diagnostic character between these two taxa, the presence of head scales microscopically rugose in *S. d. dugesii* (Smith, 1939), is not a fixed character (see morphological matrix in the study of Wienes and Reeder 1997), and it could be chosen on a small sample size basis.

8) *Sceloporus lineolateralis* Smith, 1936 should be synonymized into *Sceloporus jarrovii* Cope, *in* Yarrow, 1875, but potentially recognized as the subspecies *S. jarrovii lineolateralis* [new combination]. Unfortunately *S. j. jarrovii* lacks fixed diagnostic morphological characters (Wiens and Penkrot 2002). The characters early identified by Smith (1939) like diagnostic of *S. j. jarrovii* (e. g., the first canthal seldom forced above canthal ridge by contact of second canthal and subnasal, prefrontals in contact, color pattern etc.), exhibit some intraespecific variation even in other populations. Some authors have similarly reported that *S. lineolateralis* and *S. j. jarrovii* intergrade with each other based on morphological characters (Webb and Hensley 1959; Chrapliwy 1964; Wiens *et al.* 1999). The previous studies along with our molecular results indicate the conspecificity between *S. lineolateralis* and *S. j. jarrovii*.

Acknowledgements

We thank Robert W. Murphy and anonymous reviewers for helpful advice and comments on the manuscript; M. en C. Laura Márquez and the Laboratorio de Biología Molecular at Instituto de Biología, Universidad Nacional Autonoma de Mexico (UNAM) for providing facilities and helping with the laboratory work; and Posgrado en Ciencias Biológicas (UNAM). We also thank Drs. Oscar Flores-Villela (UNAM-MZFC) and Jonathan A. Campbell (University of Texas at Arlington) for providing tissues of *Sceloporus* sp. and *S. bulleri* (2 and 3). Funding for this study was provided by a Ph.D. Scholarship from Consejo Nacional de Ciencia y Tecnología (CONACyT) and from Dirección General de Asuntos del Personal Académico (Project IN213405).

References

Arévalo, E., Davis, S.K. & Sites, J.W., Jr. (1994) Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of *Sceloporus grammicus* complex (Phrynosomatidae) in central México. *Systematic Biology*, 43, 387–481.

Baird, S.F. (1859) Description of new genera and species of North American lizards in the museum of the Smithsonian Institution. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 10, 253–256.

Bell, E.L., Smith, H.M., & Chizar, D. (2003) An Annoted list of the species-group names applied to the lizard genus *Sceloporus*. *Acta Zoologica Mexicana*, n.s., 103–174.

Barrett, M., Donoghue, M.J., & Sober, E. (1991) Against consensus. *Systematic Zoology*, 40, 486–493.

Benabib, M., Kjer, K.M. & Sites, J.W., Jr. (1997) Mitochondrial DNA sequence-based phylogeny and the evolution of viviparity in the *Sceloporus scalaris* group (Reptilia: Squamata). *Evolution*, 51, 1262–1275.

Brandley, M. C. & De Queiroz, K. (2004) Phylogeny, ecomorphological evolution, and historical biogeography of the *Anolis cristatellus* series. *Herpetological Monographs*, 18, 90–126.

Cope, E. D. (1875) Check list of North American Batrachia and Reptilia with a systematic list of the higher groups and an essay on geographic distribution based on the specimens in United States National Museum. *Bulletin of United States Natural Museum*, 1, 1–104.

Cope, E. D. (1885) A contribution to the herpetology of Mexico. I. The collection of the Comisión Científica. IV. Cozumel Island. VI. A synopsis of the Mexican species of the genus *Sceloporus*. Wieg. *Proceedings of American Philosophical Society*, 22, 379–404.

Chrapliwy, P. S. (1964) Taxonomy and distribution of *jarrovii* complex of lizards of the *torquatus* group, genus *Sceloporus*. Ph.D. dissertation. University of Illinois, Urban, IL.

Dugès, A. A. D. (1877) Una nueva especie de saurio. *La Naturaleza*, 4, 29–34.

Felsenstein, J. (1985) Confidents limits on phylogenies: an approach using bootstrap. *Evolution*, 39, 783–781.

Fetzner, J.W. Jr. (1999) Extracting High-Quality DNA from shed reptile skins: A simplified method. *Biotechniques*, 26,

1052–1054.
Filatov D.A. (2002) ProSeq: A software for preparation and evolutionary analysis of DNA sequence data sets. *Molecular Ecology Notes*, 2, 621–624.
Forstner, M.R., Davis, S. K. & Arévalo, E. (1995) Support for the hypothesis of anguimorph ancestry for the suborder Serpentes from phylogenetic analysis of mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 4, 93–102.
Fox, S. F. (1975) Natural selection on morphological phenotypes of the lizard *Uta stansburiana*. *Evolution*, 29, 95–107.
Hernández-Gallegos, O., Rodríguez-Romero, F. & Casas-Andreu, G. (2003) *Sceloporus torquatus melanogaster. Herpetological Review*, 34, 385.
Huelsenbeck, J. P. & Ronquist, F. (2001) MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17, 754–755.
Kluge, A. G. & Wolf, A. J. (1993) Cladistics: What´s in a word?. *Cladistics*, 9, 183–199.
Larget, B. & Simon, D. L. (1999) Markov chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic tress. *Molecular Biology and Evolution*, 16, 750–759.
Larsen, K.R. & Tanner, W. W. (1974) Numeric analysis of the lizard genus *Sceloporus* with special reference to cranial osteology. *Great Basin Naturalist*, 35, 1–20.
Larsen, K.R. & Tanner, W. W. (1975) Evolution of the sceloporine lizards (Iguanidae). *Great Basin Naturalist*, 35, 1–20.
Lee, J. C. (1996) *The Amphibians and Reptiles of the Yucatan Peninsula*. Cornell University Press, E.U.
Lee, J. C. (2000) *A Field Guide to the Amphibians and Reptiles of the Maya World, the Lowlands of México, Northern Guatemala, and Belize*. Cornell University Press, Ithaca, New York, 402 pp.
Leviton, A. E., Gibbs, R. H., Heal, E. & Dawson, C. E. (1985) Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia*, 1985, 802–832.
Lewis, P.O. (2001) Phylogenetics systematics turns over a new leaf. *Trends in Ecology and Evolution*, 16, 30–37.
Lyons-Weiler, J., Hoelzer, G. A. & Tausch, R. J. (1998) Optimal outgroup analysis. *Biological Journal of the Linnean Society*, 64, 493–511.
Martin, P. S. (1952) A new subspecies of the iguanid lizard *Sceloporus serrifer* from Tamaulipas, Mexico. *Occasional Papers of the Museum of Zoology University of Michigan*, 534, 1–7.
Nylander, J. A. A. (2001) Taxon sampling in phylogenetic analysis: Problems and strategies reviewed. Introductory Research Essay No. 1. Department of Systematic Zoology, Evolutionary Biology Centre, Uppsala University.
Olson , R. E. (1987) Taxonomic revision of the lizards *Sceloporus serrifer* and *cyanogenys* of the Gulf Coastal Plain. *Bulletin of the Maryland Herpetological Society*, 23, 158–167.
Ortí, G. & Meyer, A. (1997) The radiation of characiform fishes and the limits of resolution of mitochondrial ribosomal DNA sequences. *Systematic Biology*, 46, 75–100.
Posada, D. & Buckley, T. R. (2004) Model selection and model averaging in phylogenetics: advantages of Akaike Information Criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology*, 53, 793–808.
Posada, D., & Crandall, K. A. (1998) Modeltest: Testing the model of DNA substitution. *Bioinformatics*, 14, 817–818.
Rambaut, A., & Drummond, A. (2005) Tracer v1.2.1 2003- MCMC Trace File Analyser University of Oxford. Available from http://evolve.zoo.ox.ac.uk/beast/
Reeder, T.W. (1995) Phylogenetic relationship among phrynosomatid lizards as inferred from mitochondrial ribosomal DNA sequences: substitutional bias and information content of transitions relative to transversions. *Molecular Phylogenetics and Evolution*, 4, 203–222.
Reeder, T.W. (2003) A phylogeny of the Australian *Sphenomorphus* group (Scincidae: Squamata) and the phylogenetic placement of the crocodile skinks (Tribolonotus): Bayesian approaches to assessing congruence and obtaining confidence in maximum likelihood inferred relationships. *Molecular Phylogenetics and Evolution*, 27, 384–397.
Saiki, R.K., Gelfand, D.H., Stoffel, S., Scharf, S.J., Higuchi, R., Horn, G.T., Mullis, K.B. & Erlich, H.A. (1998) Primer-directed enzymatic amplification of DNA with a thermostable DNA polymerase. *Science*, 239, 487–491.
Sanderson, M. J. & Kim, J. (2000) Parametric phylogenetics?. *Systematic Biology*, 49, 817–829.
Sanderson, M. J. & H. B. Shaffer. 2002. Troubleshooting molecular phylogenetic analyses. *Annual Review of Ecology and Systematics*, 33, 49–72.
Sites, J. W., Jr., Archie, J. W., Cole, Ch. J. & Flores-Villela, O. (1992) A review of phylogenetic hypotheses for lizards of the genus *Sceloporus* (Phrynosomatidae): Implications for ecological and evolutionary studies. *Bulletin of the American Museum of Natural History*, 213, 1–110.
Smith, A. B. (1994) Rooting molecular trees: problems and strategies. *Biological Journal of the Linnean Society*, 51, 279–292.
Smith, H. M. (1936) Description of new species of lizards of the genus *Sceloporus* from Mexico. *Proceedings of the Biological Society of Washington*, 49, 87–96.
Smith, H. M. (1938) The lizard of the *torquatus* group of the genus *Sceloporus* Wiegmann 1828. *University of Kansas, Scientific Bulletin*, 24, 539–693.
Smith, H. M. (1939) The Mexican and Central American lizards of the genus *Sceloporus*. *Field Museum of Natural His-*

tory, Publications in Zoology Series, 26,1–397.
Smith, H. M. & Brown, B. C. (1941) A new subspecies of *Sceloporus jarrovii* from Mexico. *Zoological Series of the Field Museum of* N*atural History*, 24, 253–257.
Smith, H. M. & Taylor, E. H. (1950) An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. *Bulletin of United States Natural Museum*, 199, 1–253.
Soulé, M. & Kerfoot, C. (1972) On the climatic determination of scale size in a lizard. *Systematic Zoology*, 21, 97–105.
Stuart, L. C. (1970) A brief review of the races of *Sceloporus serrifer* Cope with especial reference to *Sceloporus serrifer prezygus*. *Herpetologica* 26, 141–149.
Swofford, D. L. (1998) "PAUP": Phylogenetic Analysis Using Parsimony (And other Methods), version 4. Sinauer, Sunderland, MA.
Swofford, D. L. & Olsen, G. J. (1990) Phylogeny reconstruction. *In*: Hillis, D. M. & Moritz, C. (Eds.). *Molecular Systematics*. Sunderland, Mass. Sinauer Press, pp. 411–501.
Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. & Higgins, D.G. (1997) The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, 24, 4876–4882.
Webb, R. G. & Hensely (1959) Notes on reptiles from the Mexican state of Durango. Publications of the Museum, Michigan State University. Biological series,1, 252–258.
Wenzel, J. W. & Sidall M. E. (1999) Noise. *Cladistics*, 15, 51–64.
Wiens, J. J. (1998a) Combining data sets with different phylogenetic histories. *Systematic Biology*, 47, 568–581.
Wiens, J. J., & Penkrot, T. A. (2002) Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). *Systematic Biology*, 51, 69–91.
Wiens, J. J., Reeder, T.W. & Nieto-Montes de Oca, A. (1999) Molecular phylogenetics and evolution of sexual dichromatism among populations of the Yarrow´s spiny lizard (*Sceloporus jarrovii*). *Evolution*, 53, 1884–1897.
Wiens, J. J., & Reeder, T.W. (1997) Phylogeny of spiny lizards (*Sceloporus*) based on molecular and morphological evidence. *Herpetological Monographs*, 11, 1–101.
Wilcox, T.P., Zwickl, D.J., Heath, T.A. & Hillis, D.M. (2002) Phylogenetic relationships of the dwarf boas and comparison of Bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution*, 25, 361–371.