

## MOLECULAR STUDIES ON THE GENUS *EUMECES* WIEGMANN, 1834: PHYLOGENETIC RELATIONSHIPS AND TAXONOMIC IMPLICATIONS

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(with three text-figures)

**ABSTRACT.**— After the taxonomic status of the genus *Eumeces* Wiegmann, 1834 had been neglected for more than half a century, a recent publication split *Eumeces* into four genera. Based on a molecular data set, we provide evidence suggesting that the recently named taxonomic units represent monophyletic radiations. Since some of the previously proposed names for the genera violate the rules of the International Code of Zoological Nomenclature (ICZN), the nomenclatural situation is clarified and new names are proposed. The genus *Neoseps* Stejneger, 1910 is synonymised with *Pariocela* Fitzinger, 1843.

**KEY WORDS.**— *Eumeces*, *Eurylepis*, *Mesoscincus*, *Neoseps*, *Novoeumeces*, *Scincopus*, *Scincus*, mtDNA, phylogeny, nomenclature.

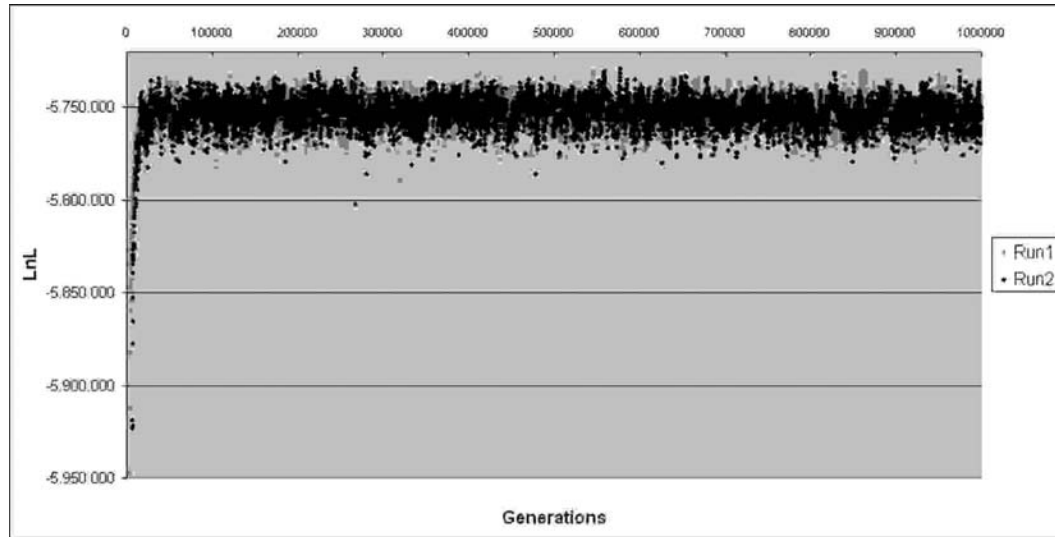
### INTRODUCTION

Until recently, the genus *Eumeces* Wiegmann, 1834 was one of the most speciose scincid genera known, with about 50 species recognized (Taylor, 1935; Eiselt, 1940; Mertens, 1946; Lieb, 1985; Hikida and Motokawa, 1999), being surpassed only by *Sphenomorphus* Fitzinger, 1843, *Mabuya* Fitzinger, 1826, *Ctenotus* Storr, 1964, *Lerista*, Bell, 1833 and *Emoia*, Gray, 1845. Many of the larger skink genera have been regarded as repositories (e.g., *Lygosoma* Hardwicke and Gray, 1827) or have been identified as non-monophyletic groups (e.g., *Mabuya*, *Sphenomorphus*) with the consequence that most large scincid genera have been subject to attempts to split them into smaller taxonomic groups. Only recently have attempts been convincingly proposed (e.g., *Mabuya*; comp. Mausfeld et al., 2002) or are currently being reviewed (e.g., *Sphenomorphus*).

The first comprehensive revision of the genus *Eumeces* was carried out by Taylor (1935). On the basis of shared colour patterns and scalation

features he differentiated no less than 50 species (and 14 subspecies) in 15 species-groups within *Eumeces*, which he assigned to three major groups (group I consisting of the *schneiderii*-, *schwartzei*- and *taeniolatus* species-groups; a monotypic group II with only *E. longirostris* included; and group III consisting of all other eleven species-groups sensu Taylor, 1935). But still he had “no intention in mind of considering them of the status of genera or subgenera” (Taylor, 1935: 36), even though the species of the genus *Eumeces* are not only widely distributed (occurring throughout large parts of the Holarctic region) thus indicating possible barriers for a continuous gene flow, but they also display a considerable amount of morphological and ecological diversity (e.g., Taylor, 1935; Fitch, 1955; Bobrov, 1993; Kato and Ota, 1994; Hosono and Hikida, 1999; Griffith et al., 2000; Lazell and Ota, 2000).

Several generic names have been proposed for various subgroups within *Eumeces*, but only two serious attempts have been made to split the



**FIGURE 1:** The log probability of the observed combined 16S and 12S DNA sequences through time for both of the chains run in this study. Each chain started from a different random tree. The samples taken from the first 100,000 generations were discarded as the burn-in for the chain, and inferences are based on samples from the remaining parts of the chain.

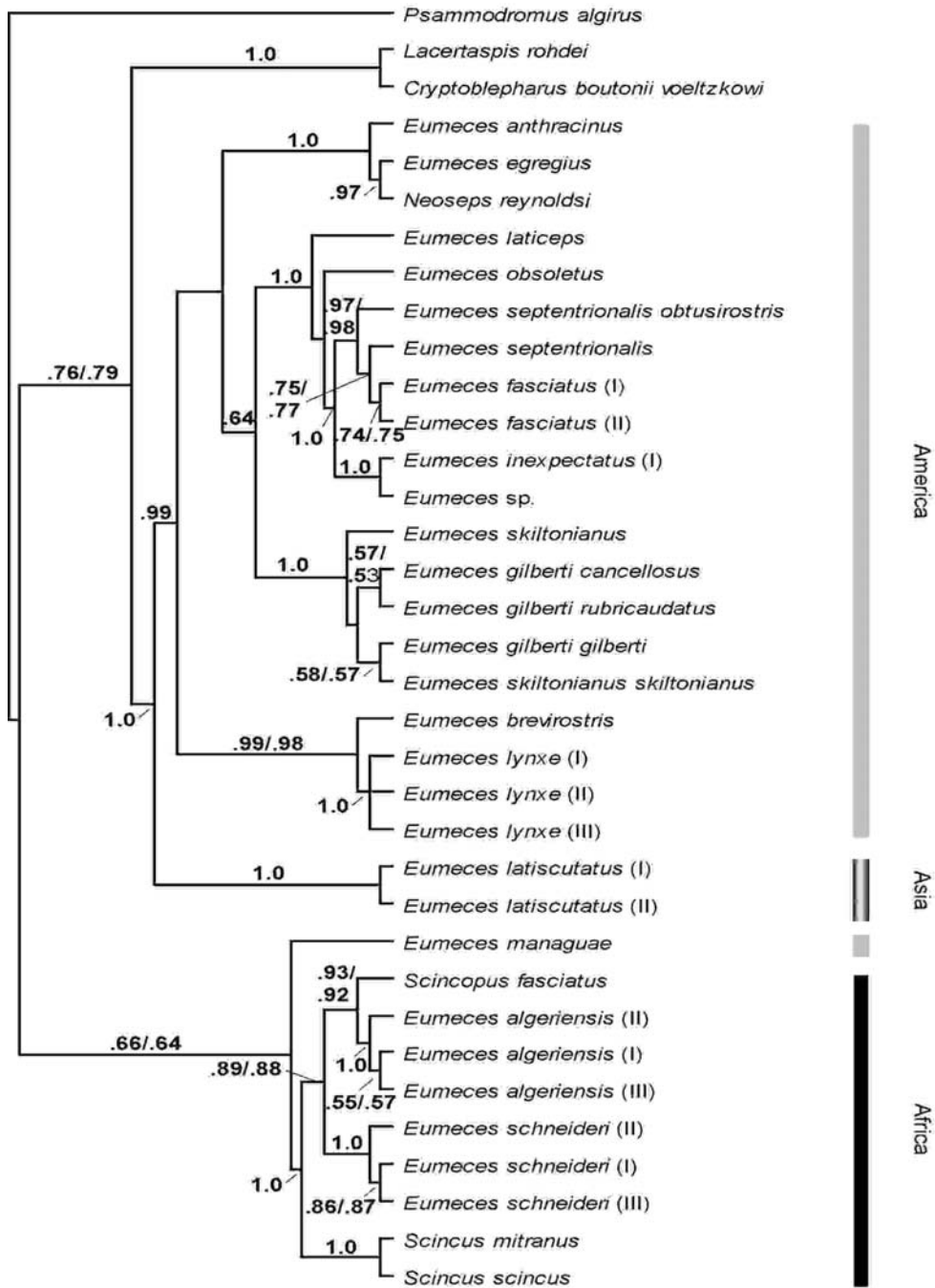
genus. One was carried out just before the revision of Taylor (1935) by Dunn (1933), who placed two Central American species (*E. managuae* and *E. schwartzei*) and the Southwest Asian species *E. taeniolatus* (as well as *E. scutatus*, now considered a synonym of *taeniolatus*) in a separate genus, *Eurylepis* Blyth, 1854. This view was subsequently rejected by Taylor (1935) who regarded the genus *Eumeces* as a natural, monophyletic group (“The likelihood that further generic or subgeneric divisions of the genus will ever be considered for species now known is extremely remote. [...] I feel quite certain that any breaking up of the present group here treated as a generic entity is unwise, since, if begun, it would necessitate the erection and recognition of several genera, four of which (including *quadrilineatus*, *egregius*, *taeniolatus*, *lynxe*) would be monotypic and would in no measure have the same generic significance as even the genera (subgenera) formed from the genus “*Lygosoma*” as used by Boulenger”; Taylor, 1935: 37).

Taylor (1935) also placed the species of *Eumeces* occurring in West Asia, Cyprus and Africa (comp. Mertens, 1920, 1924, 1946; Göçmen et al., 2002) in the *schneideri*-group, then comprising six species and one subspecies.

At present, however, most authorities consider the *schneideri*-group to be composed of only two species with five subspecies [*E. s. schneideri* (Daudin, 1802); *E. s. pavimentatus* (Geoffroy-Saint-Hillaire, 1827); *E. s. princeps* (Eichwald, 1839); *E. s. zarudnyi* Nikolsky, 1899; *E. s. blythianus* (Anderson, 1871); *E. a. algeriensis* (Peters, 1864); *E. a. meridionalis* Domergue, 1901]. The type species of the genus *Eumeces* (*E. (s.) pavimentatus*) is included in the *schneideri*-group.

Two closely related genera, *Scincopus*, Peters, 1864 and *Scincus*, Laurenti, 1768, are known to be partly sympatric with the species of the *schneideri*-group. Arnold and Leviton (1977) thought of them to be descendants of *E. schneideri*, but their exact phylogenetic relationships with respect to each other and to *Eumeces* remain unresolved.

The three proposed subgroups of Taylor (1935) have undergone rather different subsequent treatments (e.g., Eiselt, 1940; Mertens, 1920, 1924; Lieb, 1985; Kato et al., 1994; Hikida and Motokawa, 1999; Richmond and Reeder, 2002) and are now regarded as representing four different groups with taxonomic hierarchies that differ substantially from those of the groups proposed by Taylor. While groups II and III (sensu



**FIGURE 2:** Cladogram of the maximum-likelihood tree based on 928 bp of the combined mitochondrial 16S and 12S ribosomal RNA gene sequences. Values (bold) at the nodes are Bayesian posterior probabilities (values below 0.5 not shown).

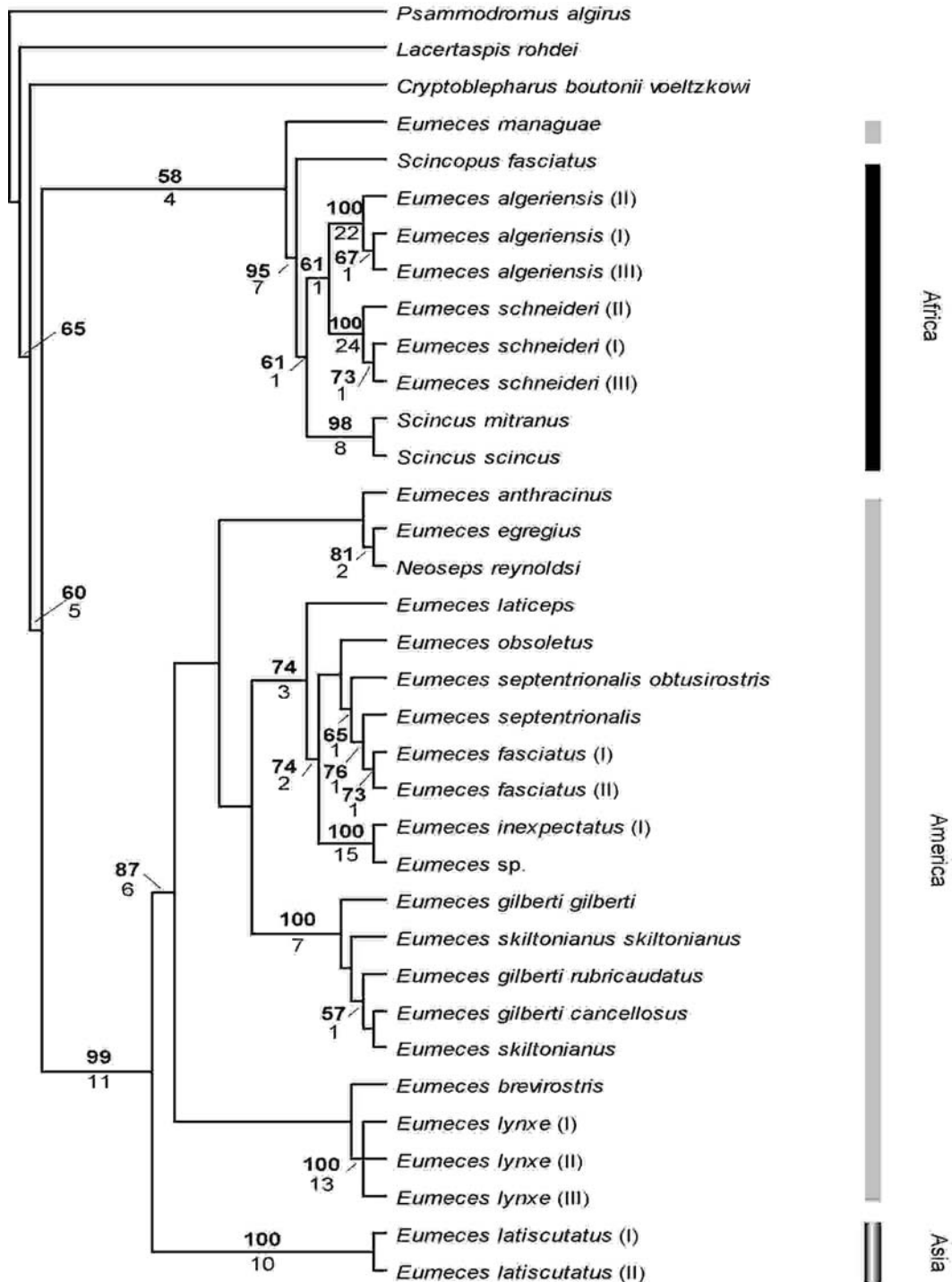


FIGURE 3: Cladogram of the maximum-parsimony tree based on 928 bp of the combined mitochondrial 16S and 12S ribosomal RNA gene sequences. Upper (bold) values at the nodes are bootstrap values in percent (2000 replicates with 100 random additions; values below 50 % not shown); lower values are Bremer decay indices.

Taylor, 1935) have been pooled to form the so-called *Pariocela* section (sensu Fitzinger, 1843), group I has been split into three independent sections, which are considered to be of equal taxonomic rank as the *Pariocela* section.

The *Eumeces taeniolatus*-group consists of only two species (*E. poonaensis* Sharma, 1970 and *E. taeniolatus*, [Blyth, 1854]), which have a rather limited distribution area in Pakistan, Afghanistan and the bordering countries (Boulenger, 1890; Taylor, 1935; Haas, 1957; Sharma, 1970; Szcherbak, 1990; Leviton et al., 1992; Griffith et al., 2000).

The *Eumeces schwartzei*-group is now considered to comprise three species (*E. altamirani* Dugès, 1891; *E. managuae* Dunn, 1933; and *E. schwartzei* Fischer, 1884), and is only known from Central America (Dugès, 1891; Taylor, 1935, 1936, 1956; Smith and Taylor, 1950; Cruz et al., 1979; McCoy et al., 1986).

The most recent attempt to split *Eumeces* has been in the framework of a morphological re-analysis of the genus by Griffith et al. (2000). On the basis of a rather small morphological character matrix (which includes several characters with an underlying ecological basis or which are based on highly labile features like colour) they proposed the most radical taxonomic changes for the genus yet. They recognized the four groups mentioned above, and raised them all to a generic status. As these authors intended to keep the name *Eumeces* for the North American *Pariocela* section of the genus, they have filed a petition with the ICZN to designate *Lacerta fasciata* Linnaeus 1758 as type species of *Eumeces*, which would preserve the genus name *Eumeces* for the *Pariocela* section (Murphy et al., submitted). They argue that this way the majority of species (which is correct) and the "vast majority of literature" (which is far from being correct) could be kept connected to the name *Eumeces*. Following their line of thought, they propose a new generic name "*Novoeumeces*" for the *schneideri* species-group, revalidate the name *Eurylepis*, Blyth, 1854 for the *taeniolatus* species-group, and propose the new generic name *Mesoscincus* for the *schwartzei* species-group. This last step

was necessary, since the generic name *Platypholis* proposed by Dugès (1891), is preoccupied by *Platypholis* Boulenger 1890 (a gekkonid genus), and is therefore unavailable. Additionally, based on only two skull characters, they regarded the *Pariocela* species-group as the most basal group of all skinks worldwide, and thus they described a new subfamily, *Eumecinae*, for this assemblage.

The present analysis uses molecular sequence data to reanalyze the phylogenetic relationships, to answer questions regarding the monophyly of the proposed genera and the proposed new subfamily *Eumecinae*, and to extend our knowledge of the placement of the different genera with respect to the closely related genera *Scincopus* and *Scincus*.

#### MATERIAL AND METHODS

Thirty-five combined, 16S and 12S, sequences (Table 1) comprised 1016 bp (lengths referring to the aligned sequences including gaps) were obtained. Five short sections (together 88 bp) (71 bp from the original 16S data set and 17 bp from the 12S data set) were too variable to be reliably aligned, and were excluded from the analyses, resulting in a total of 928 bp which were used in the analyses. For the likelihood calculations, an additional 32 sites (positions containing gaps) were excluded. *Psammodromus algirus* (Lacertidae), *Lacertaspis rohdei* and *Cryptoblepharus boutonii voeltzkowi* (Scincidae: Lygosominae) were used as outgroup taxa.

DNA was extracted from the tissue samples using QuiAmp tissue extraction kits (Quiagen). The primers 16sar-L (light chain; 5' - CGC CTG TTT ATC AAA AAC AT - 3') and 16sbr-H (heavy chain; 5' - CCG GTC TGA ACT CAG ATC ACG T - 3') of Palumbi et al. (1991) were used to amplify a section of the mitochondrial 16S ribosomal RNA gene. PCR cycling procedure was as follows; an initial denaturation step of 90 s at 94°C followed by 33 cycles of denaturation for 45 s at 94°C, primer annealing for 45 s at 55°C and extension for 90 s at 72°C. Additionally, a section of the mitochondrial 12S ribosomal RNA gene was amplified using the primers 12SA-L (light chain; 5' - AAA CTG

**TABLE 1:** List of voucher specimens for each species included in the present study, with their respective localities, collection numbers and accession numbers (12S, 16S). Abbreviations: ZFMK for Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany; LSUMZ for Louisiana State University, Museum of Zoology, Louisiana, USA; and CAS for California Academy of Sciences, San Francisco, USA.

Species	Locality	Collection number	Accession number
<i>Eumeces algeriensis</i> (I)	North Africa	ZFMK 72254	AY308344 / AY308195
<i>Eumeces algeriensis</i> (II)	Tafraoute, Morocco	voucher not collected	AY308345 / AY308196
<i>Eumeces algeriensis</i> (III)	Tiznit, Morocco	GenBank	AF054526 / AF054540
<i>Eumeces algeriensis</i> (IV)	Africa	GenBank	EAY14451 / -
<i>Eumeces anthracinus</i>	Natchitoches Parish: Lonleaf Vista, USA	LSUMZ H-2881	AY308346 / AY308197
<i>Eumeces brevisrostris</i>	Tamaulipas, Mexico	LSUMZ H-14817	AY308347 / AY308198
<i>Eumeces egregius</i>	USA	GenBank	AB016606 / AB016606
<i>Eumeces fasciatus</i> (I)	Mississippi, Covington Co., USA	CAS 207212	AY308348 / AY308199
<i>Eumeces fasciatus</i> (II)	USA	voucher not collected	AY308349 / AY308200
<i>Eumeces gilberti cancellosus</i>	California, Alameda Co., USA	CAS 208654	AY308350 / AY308201
<i>Eumeces gilberti gilberti</i>	California, Fresno Co., USA	CAS 208719	AY308351 / AY308202
<i>Eumeces gilberti rubricaudatus</i>	California, Kern Co., USA	CAS 205791	AY308352 / AY308203
<i>Eumeces inexpectatus</i> (I)	Georgia, Liberty Co., USA	voucher not collected	AY308353 / AY308204
<i>Eumeces inexpectatus</i> (II)	USA	GenBank	- / MTEINX16S
<i>Eumeces laticeps</i>	Florida, Washington Co., USA	CAS 203093	AY308354 / AY308205
<i>Eumeces laticutatus</i> (I)	Japan	ZFMK 70469	AY308355 / AY308206
<i>Eumeces laticutatus</i> (II)	Kyoto City, Japan	GenBank	AB028770 / AB028781
<i>Eumeces lynxe</i> (I)	Hidalgo, Mexico	LSUMZ H-14969	AY308356 / AY308207
<i>Eumeces lynxe</i> (II)	Hidalgo, Mexico	LSUMZ H-14970	AY308357 / AY308208
<i>Eumeces lynxe</i> (III)	Veracruz, Mexico	LSUMZ H-14980	AY308358 / AY308209
<i>Eumeces managuae</i>	Guanacaste, Costa Rica	ZFMK 57771	AY308433 / AY308281
<i>Eumeces obsoletus</i>	USA	ZFMK 77248	AF548781 / AF549169
<i>Eumeces schneideri</i> (I)	North Africa	ZFMK 77812	AY308361 / AY308212
<i>Eumeces schneideri</i> (II)	Egypt	ZFMK 77478	AY308362 / AY308213
<i>Eumeces schneideri</i> (III)	West Africa	GenBank	AB028800 / AB028812
<i>Eumeces septentrionalis</i>	Wisconsin, USA	LSUMZ H-1231	AY308363 / AY308214
<i>Eumeces septentrionalis obtusirostris</i>	Kansas, Sumner Co., USA	GenBank	AY046420 / AY046462
<i>Eumeces skiltonianus</i>	Nevada, Washoe Co., USA	CAS 202952	AY308364 / AY308215

<i>Eumeces skiltonianus skiltonianus</i>	California: Riverside Co.: Diamond Valley, USA	CAS 200629	AY308365 / AY308216
<i>Eumeces</i> sp.	Florida, Broward Co., USA	CAS 208643	AY308366 / AY308217
<i>Neoseps reynoldsi</i>	Florida, USA	voucher not collected	AY308360 / AY308211
<i>Scincopus fasciatus</i>	ca. 30 km NW Rosso, Mauritania	ZFMK, uncatalogued	AY308453 / AY308302
<i>Scincus mitranus</i>	Al Ain, United Arab Emirates	BMNH, uncatalogued	AY308454 / AY308303
<i>Scincus scincus</i>	Israel	ZFMK 72239	AY308455 / AY308304
<i>Cryptoblepharus boutonii voeltzkowi</i>	St. Augustin, Madagascar	voucher not collected	AY308336 / AY308187
<i>Lacertaspis rohdei</i>	Mt. Nlonako, Cameroon	ZFMK 75382	AY308386 / AY308236
<i>Psammotromus algirus</i>	Tanger, Cap Spartel, Morocco	GenBank	AF206588 / AF206588

GGA TTA GAT ACC CCA CTA T - 3') and 12SB-H (heavy chain; 5' - GAG GGT GAC GGG CGG TGT GT - 3') of Kocher et al. (1989). Cycling procedure was as follows: 35 cycles of denaturation 45 s at 94°C, primer annealing for 60 s at 50°C and extension for 120 s at 74°C (12S). PCR products were purified using Qiaquick purification kits (Qiagen). Sequences were obtained using an automatic sequencer (ABI 377). Sequences have been submitted to Genbank; for accession numbers compare Table 1.

Sequences were aligned using ClustalX (Thompson et al., 1997; default parameters). The alignment was subsequently adjusted manually using the program BioEdit (Hall, 1999). To determine the statistical validity of combining the 16S and 12S data sets for phylogenetic analyses, we performed the partition homogeneity (PH) test. We used PAUP\*4.0b10 (Swofford, 2002) to generate a null-distribution of length differences using 1000 same-sized, randomly generated partitions from the original data with replacement.

Prior to phylogenetic reconstruction, we tested for homogeneity of base frequencies among taxa using the  $\chi^2$  test as implemented in PAUP\*4.0b10 (which ignores correlation due to phylogenetic structure): (1) over all sites, (2) over parsimony-informative sites only, (3) without constant sites (parsimony-uninformative and constant sites will mislead the  $\chi^2$  test; Misof et al., 2001). All phylogenetic reconstructions were conducted with the combined data set of the 16S and 12S gene fragments.

We performed maximum parsimony (MP), maximum likelihood (ML) and Bayesian reconstructions. For ML and Bayesian analysis parameters of the model were estimated from the data set using Modeltest 3.0 (Posada and Crandall, 1998) and MrModeltest 1.1b (Nylander, 2002), respectively.

As ML bootstrap calculations are extremely time-consuming and a recent simulation study suggested Bayesian posterior probabilities represent much closer estimates of true clade probabilities, we used Bayesian analysis to estimate posterior probabilities for the phylogenetic relationships inferred in the ML analyses. Clades with PP  $\geq$  95% were considered strongly (significantly) supported.

Additionally, we used bootstrap analyses with 2000 pseudoreplicates for MP and Bremer Decay Indices (BDI) to evaluate the relative branch support in phylogenetic analysis. For the MP analysis, we used the "heuristic search" with the "random addition" option of PAUP\* (Swofford, 2002) with 10 replicates, using the TBR (tree bisection-reconnection) branch swapping option.

All Bayesian (Rannala and Yang, 1996; Larget and Simon, 1999; Mau et al., 1999; Li et al., 2000; Huelsenbeck et al., 2001) analyses were performed with MrBayes, version 3.0b4

(Huelsenbeck and Ronquist, 2001), which approximates the posterior probabilities (PP) of trees. We ran two MCMC analyses for  $10^6$  generations each. The initial 100,000 (10%) trees were disregarded as “burn-in” (Fig. 1). We consider probabilities of 95% or greater to be significantly supported. The exact parameters used for the Bayesian analyses followed those described in detail by Reeder (2003) and Table 2.

### RESULTS

Of the 1016 characters from the combined 16S and 12S rRNA genes 449 sites were variable and 241 were parsimony-informative. The matrix for

**TABLE 2:** Combined 16S + 12S. Parameter estimates of the substitution model (GTR + I + G), sampled after the burn-in phase of the chain. The columns indicate the parameter, mean and 95% credible interval for the parameter. The parameters are TL, the tree length;  $r_{ij}$ , rate of substitution between nucleotides  $i$  and  $j$  measured relative to the rate between G and T ( $\rho_{GT}=1$ );  $\pi_i$ , base frequencies;  $\alpha$ , gamma shape parameter for among-site variation; and *Pinvar.*, proportion of invariable sites. Upper values in each pair correspond to the 1. run; lower values correspond to the 2. run.

Parameter	Mean	95% Credity Interval
TL	2.144995 2.155316	(1.831000, 2.520000) (1.816000, 2.575000)
$r_{GT}$	1.000000 1.000000	1.000000, 1.000000 1.000000, 1.000000
$r_{CT}$	28.056685 28.219089	(13.532508, 63.873212) (12.689248, 59.780160)
$r_{CG}$	1.126511 1.132002	(0.288083, 2.815524) (0.363334, 2.875285)
$r_{AT}$	2.695892 2.694440	(1.167896, 6.388330) (1.060047, 5.957160)
$r_{AG}$	13.601788 13.652822	(6.285310, 29.632246) (6.100779, 28.483158)
$r_{AC}$	4.278407 4.291890	(1.873923, 9.979367) (1.846635, 9.467517)
$\pi_A$	0.331984 0.332206	(0.305361, 0.358863) (0.305480, 0.359952)
$\pi_C$	0.255699 0.255511	(0.231757, 0.279378) (0.232286, 0.280094)
$\pi_G$	0.188326 0.188072	(0.165085, 0.211881) (0.165570, 0.212244)
$\pi_T$	0.223991 0.224210	(0.201785, 0.247360) (0.202472, 0.247175)
$\alpha$	0.637758 0.631050	(0.363735, 1.000408) (0.353439, 0.982877)
<i>Pinvar.</i>	0.406778 0.404888	(0.250790, 0.507954) (0.239500, 0.506734)

the uncorrected p-distances for all nucleotide sites is presented in Table 3.

In the data set, a phylogenetic signal is clearly present (g1 = -0.7194, p = 0.01; 12S: -0.6033, p = 0.01; 16S: -0.7928, p = 0.01). When all characters were included, we found no significant deviation from the homogeneity of base frequencies among taxa ( $\chi^2 = 22.8058$ , p = 1.0000, df = 102). The same was true without constant sites ( $\chi^2 = 57.8606$ , p = 0.9999, df = 102) and for the parsimony-informative sites only ( $\chi^2 = 77.3902$ , p = 0.9669, df = 102).

The heuristic search of the MP analysis produced 20 equally most-parsimonious trees (tree length = 905; CI = 0.434; RI = 0.692; RC = 0.301). The MP strict consensus tree with bootstrap support is shown in Fig. 3, the optimal ML tree and the MrBayes tree are shown in Fig. 2. The comparison between the different likelihood scores for each model showed that the GTR + I +  $\Gamma$  model (Yang, 1994) was determined to be the optimal model for the combined data set. This model incorporates unequal base frequencies [ $\pi(A) = 0.32720$ ,  $\pi(T) = 0.22170$ ,  $\pi(C) = 0.25520$ ,  $\pi(G) = 0.19590$ ], a proportion of invariable sites ( $I = 0.4916$ ), and a gamma distribution shape parameter ( $\alpha = 0.6688$ ). The optimal ML tree had a log-likelihood of  $-\ln L = 5708.25$ .

The partition homogeneity test failed to detect significant incongruence between the two data sets ( $P = 1 - (869/1000) = 0.131$ ), suggesting that the two mtDNA fragments could be combined.

All phylogenetic methodologies used agree in the resulting general topology. In the trees resulting from the combined data sets, two major monophyletic groups can be detected, which are both strongly supported. The first clade (called the African clade from here onwards) includes all African *Eumeces* species as well as the genera *Scincopus* and *Scincus* (MP: 95 / PP: 1.0 / BDI: 7). In the MP analysis *Scincopus fasciatus* is placed as the most basal taxon, although with low bootstrap support (MP: 61 / BDI: 1). In the Bayesian analyses this species is found as sister species to the *Eumeces algeriensis* cluster, with rather strong support (PP: .92|.93). The two included *Scincus* species are sister species in all analyses with very strong support (MP: 98 / PP:



1.0 / BDI: 8) and are placed either basal to a clade containing all included vouchers of *Eumeces algeriensis* and *E. schneideri* (MP: 61 / BDI: 1) or basal to the remaining species of the African clade (PP: .89|.88) each with low bootstrap support. The several included voucher specimens for each of the latter two species are grouped together and both are strongly supported [(MP: 100 / PP: 1.0 / BDI: 22) and (MP: 100 / PP: 1.0 / BDI: 24), respectively].

*Eumeces managuae* is the sister-group to the African clade in both the MP and the ML analyses, though with very low bootstrap support (MP: 58 / PP: .66|.64 / BDI: 4).

The second major clade contains the Asian and all American members of *Eumeces* and *Neoseps reynoldsi*. *Eumeces laticutatus* is the sister-group to the American subclade in all trees with strong bootstrap support (MP: 87 / PP: .99 / BDI: 6). The American subclade is further subdivided into several smaller monophyletic terminal groups. Nonetheless, all analyses show at least three strongly supported clades within this polytomy: the first consists of all included (sub-)species of *E. skiltonianus* and *E. gilberti* (MP: 100 / PP: 1.0 / BDI: 7); the second includes *E. laticeps*, *E. obsoletus*, *E. septentrionalis*, *E. fasciatus*, *E. inexpectatus* and *Eumeces* sp. (MP: 74 / PP: 1.0 / BDI: 3); and the third contains just two species (*E. egregius* and *Neoseps reynoldsi*), and surprisingly, shows strong support for a close relationship of these two taxa (MP: 81 / PP: .97 / BDI: 2). Additionally, the Bayesian analysis gives very strong evidence for a fourth clade, which contains the Mexican *Eumeces* species, *E. brevirostris* and *E. lynxe* (PP: .99|.98), though none of the other search algorithms give any bootstrap support for this grouping.

#### DISCUSSION

The systematic relationships of the species of the genus *Eumeces* have been mostly neglected since the major revision of Taylor (1935). Perhaps the apparent stability implied by such a comprehensive work and the self-confidence with which Taylor (1935) argued in his monumental review, tempted subsequent researchers

to only examine the group structure within this large genus, since the general integrity of *Eumeces* seemed to be out of question for most researchers.

This arrangement was long kept despite several compelling findings, which reveal clear differences between zoogeographically independent groupings (especially between African and American species-groups). These differences were primarily based on analyses of chromosomes numbers in the different groups. While a large number of studies showed that all species of the American *Pariocela* section have  $2n = 26$  chromosomes (e.g., Deweese and Wright, 1970; Wu, 1983; Capriglione, 1987; Guo and Dong, 1988; Kato et al., 1998), several papers showed that all African species of the genus *Eumeces* are unique in having a constant  $2n = 32$  chromosomes (Gorman, 1973; Kupriyanova, 1973; DeSmet, 1981; Kupriyanova, 1986; Erementschenko et al., 1992; Caputo et al., 1993, 1994; Hassan, 1996). The *E. taeniolatus* group also could be differentiated from either group, being unique in having  $2n = 28$  chromosomes (Ivanov and Bogdanov, 1975; Kupriyanova, 1986; Erementschenko et al., 1992).

Taxonomic nomenclature should reflect genealogical associations, and given the non-monophyletic position of the different subgroups of *Eumeces* revealed by previous analyses, a revision of the genus *Eumeces* is long overdue. As all molecular analyses clearly support the independent origin of several groups (see below), a taxonomic recognition of these groups as full valid genera is recommended.

Despite the comparatively low number of the characters used in the morphological analyses of Griffith et al. (2000), the phylogenetic independence of three of their proposed four groups (no member of the *E. taeniolatus* species-group could be included in the present analysis) is supported in all molecular analyses. This is somewhat surprising since a close examination of the characters used to discriminate the species-groups in the Griffith et al. (2000) paper reveals several characters that are ecologically labile (e.g., the general colour pattern, the number and shape of the ear lobules, the scale thick-

TABLE 3: Summary of the uncorrected p-distances for the combined 16S and 12S data sets.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 <i>Psammiodromus algirus</i>	-														
2 <i>Panaspis rohdei</i>	0.1853	-													
3 <i>Cryptoblepharus boutonii voeltzkowi</i>	0.1969	0.1362	-												
4 <i>Eumeces algeriensis (I)</i>	0.1858	0.1531	0.1512	-											
5 <i>Eumeces algeriensis (II)</i>	0.1902	0.1558	0.1527	0.0037	-										
6 <i>Eumeces algeriensis (III)</i>	0.1939	0.1600	0.1567	0.0128	0.0146	-									
7 <i>Eumeces anthracinus</i>	0.1845	0.1405	0.1516	0.1330	0.1362	0.1390	-								
8 <i>Eumeces brevirostris</i>	0.1915	0.1345	0.1515	0.1424	0.1483	0.1507	0.0726	-							
9 <i>Eumeces egypticus</i>	0.1812	0.1602	0.1493	0.1391	0.1410	0.1468	0.0650	0.0824	-						
10 <i>Eumeces fasciatus (I)</i>	0.1848	0.1352	0.1474	0.1419	0.1465	0.1463	0.0711	0.0649	0.0781	-					
11 <i>Eumeces fasciatus (II)</i>	0.1840	0.1410	0.1479	0.1442	0.1469	0.1458	0.0744	0.0685	0.0787	0.0024	-				
12 <i>Eumeces gilberti cancellosus</i>	0.1721	0.1327	0.1399	0.1414	0.1460	0.1471	0.0675	0.0625	0.0708	0.0532	0.0570	-			
13 <i>Eumeces gilberti gilberti</i>	0.1773	0.1373	0.1364	0.1426	0.1473	0.1474	0.0731	0.0692	0.0766	0.0624	0.0664	0.0222	-		
14 <i>Eumeces gilberti rubricaudatus</i>	0.1732	0.1315	0.1375	0.1426	0.1473	0.1484	0.0664	0.0614	0.0696	0.0521	0.0559	0.0055	0.0189	-	
15 <i>Eumeces inexpectatus (I)</i>	0.1868	0.1481	0.1498	0.1373	0.1422	0.1433	0.0794	0.0698	0.0829	0.0451	0.0460	0.0582	0.0640	0.0558	-
16 <i>Eumeces laticeps</i>	0.1867	0.1347	0.1362	0.1470	0.1493	0.1543	0.0675	0.0658	0.0719	0.0433	0.0453	0.0543	0.0598	0.0532	0.0616
17 <i>Eumeces laticaudatus (I)</i>	0.1897	0.1489	0.1461	0.1437	0.1329	0.1384	0.1114	0.0963	0.1059	0.1040	0.1061	0.1014	0.0993	0.0981	0.1034
18 <i>Eumeces laticaudatus (II)</i>	0.1877	0.1431	0.1374	0.1411	0.1384	0.1369	0.0969	0.0796	0.0993	0.0800	0.0782	0.0785	0.0826	0.0746	0.0959
19 <i>Eumeces lynx (I)</i>	0.1747	0.1294	0.1423	0.1343	0.1387	0.1418	0.0520	0.0537	0.0754	0.0578	0.0605	0.0610	0.0665	0.0576	0.0724
20 <i>Eumeces lynx (II)</i>	0.1760	0.1316	0.1435	0.1343	0.1387	0.1418	0.0520	0.0537	0.0754	0.0578	0.0605	0.0632	0.0687	0.0599	0.0724
21 <i>Eumeces lynx (III)</i>	0.1749	0.1309	0.1423	0.1332	0.1375	0.1405	0.0546	0.0537	0.0755	0.0559	0.0581	0.0635	0.0691	0.0602	0.0724
22 <i>Eumeces managatae</i>	0.1672	0.1372	0.1358	0.1198	0.1228	0.1231	0.1024	0.1188	0.1205	0.1152	0.1189	0.0980	0.1003	0.0958	0.1123
23 <i>Eumeces obsoletus</i>	0.1939	0.1435	0.1523	0.1398	0.1413	0.1452	0.0824	0.0718	0.0847	0.0411	0.0420	0.0706	0.0766	0.0683	0.0533
24 <i>Eumeces schneideri (I)</i>	0.1803	0.1527	0.1502	0.0873	0.0888	0.0976	0.1316	0.1351	0.1280	0.1344	0.1360	0.1280	0.1269	0.1256	0.1381
25 <i>Eumeces schneideri (II)</i>	0.1731	0.1443	0.1449	0.0839	0.0860	0.0964	0.1216	0.1259	0.1203	0.1245	0.1300	0.1183	0.1172	0.1160	0.1328
26 <i>Eumeces schneideri (III)</i>	0.1822	0.1560	0.1543	0.0905	0.0909	0.0972	0.1347	0.1386	0.1309	0.1378	0.1387	0.1315	0.1304	0.1292	0.1417
27 <i>Eumeces septentrionalis</i>	0.1843	0.1360	0.1470	0.1412	0.1458	0.1456	0.0687	0.0670	0.0766	0.0067	0.0071	0.0555	0.0622	0.0522	0.0486
28 <i>Eumeces septentrionalis obtusirostris</i>	0.1827	0.1373	0.1365	0.1225	0.1246	0.1312	0.0741	0.0644	0.0645	0.0182	0.0169	0.0491	0.0577	0.0491	0.0494
29 <i>Eumeces skiltonianus</i>	0.1805	0.1326	0.1363	0.1402	0.1448	0.1457	0.0631	0.0636	0.0684	0.0566	0.0605	0.0121	0.0255	0.0132	0.0618
30 <i>Eumeces skiltonianus skiltonianus</i>	0.1775	0.1365	0.1356	0.1358	0.1403	0.1421	0.0688	0.0638	0.0697	0.0548	0.0572	0.0200	0.0245	0.0167	0.0620



ness and the general shape of the head are all different in the *E. schneideri*-group). These characters could therefore easily be of convergent origin (and in case they have no heritable components, they would be phylogenetically uninformative). Nonetheless, even if the character matrix of Griffith et al. (2000) should be regarded with utmost caution, its general results regarding the different major species-groups are proven valid by our molecular data, and therefore making taxonomic consequences highly warranted.

Of the four independent genera proposed Griffith et al. (2000), only the revived genus *Eurylepis* could not be confirmed in our molecular analyses. Still, regarding its unique number of chromosomes and the many morphological differences (e.g., Taylor, 1935), a preliminary assignment of this species-group to a distinct genus seems justified. Future molecular studies, which include sequence data of its members, should corroborate this arrangement.

The newly erected genus *Mesoscincus* Griffith, Ngo and Murphy, 2000 (*schwartzzei*, *altamirani*, *managuae*) was only represented by an individual of the last species in our analysis. As this species is not grouped with the American subgroup (as one might have expected from a zoogeographical perspective) and it appears as sister taxon to the African clade (with only low bootstrap support) in the cladograms this is a clear indication of its generic distinction. While Taylor (1935) thought this species-group to be closely related to the Asiatic forms, the results of the molecular analyses indicate a closer relationship to the African species. An analysis with a more comprehensive taxon sampling may reveal differing affinities, and we presently cannot judge the validity of such a relationship.

Although the type species of *Eumeces*, *E. pavimentatus*, is part of the African radiation of the genus, Griffith et al. (2000) ignored this fact and installed the subfamily *Eumecinae* (which incorporated all species of the *Pariocela* section), which they thought to be the most basal of all Scincinae. Implying a dispersalist hypothesis, this would imply that all known species of skinks originated in North America. Regarding the low

number of synapomorphies for this subfamily, and the fact that one of the two used characters is the general shape of the head (which is, of course, strongly ecologically influenced; but compare discussion below), this is a rather daring approach.

They additionally tried to suppress the correct nomenclatural situation by applying to the ICZN to designate *Lacerta fasciata* Linnaeus, 1758 as the type species of *Eumeces* (Murphy et al., submitted). That way, they would be able to keep the name *Eumeces* for the species of the *Pariocela* section, while giving a new generic name, *Novoeumeces*, to the former *E. schneideri* species-group. Because a polarity decision of the used molecular data cannot be made unambiguously, the recovered topologies can neither confirm nor refute the validity of such a subfamily. The positioning of the two non-*Eumeces* *scincines* varies throughout the different molecular analyses, partly supporting (Fig. 3) the proposed subfamily but also refuting it (Fig. 2).

However, even if the subfamily *Eumecinae* represents a true monophyletic group, Griffith et al.'s (2000) justification to "preserve the genus for most of the species [...] and the vast majority [of] literature", expresses only a "personal preference" of these authors and does not represent any taxonomical problem, which is of concern for the ICZN. While in the Code all kinds of exceptional taxonomic situations are presented (ICZN, 1999), the situation discussed above is not related to any of them. Therefore the name *Novoeumeces* Griffith, Ngo and Murphy, 2000 must be considered an objective junior synonym of *Eumeces* Wiegmann, 1834 (comp. also Bauer et al., 2003: 269). From the results discussed above, the name *Eumeces* must be restricted to the African *E. schneideri* species-group of *Eumeces* sensu lato, while the North American and the remaining Asian species must be renamed. Since this whole group has always been referred to as the *Pariocela* species-group and to avoid further taxonomic confusion, a designated type species for the group should be chosen so that this name can be elevated to genus rank.

The close relationships of the species of the genera *Scincopus* and *Scincus* with respect to

*Eumeces* sensu stricto (see above) is corroborated by the respective genetic distances (Table 3). While among the specimens of *E. algeriensis* (0.3-1.3%) and *E. schneideri* (0.0-0.1%) respectively, only low to very low differences are present, there is a strong interspecific differentiation between the two (8.4-9.1%). As the intergeneric differences of both species to *Scincopus* (10.0-10.4% and 10.1-10.7%, respectively) and even more to the two species of *Scincus* examined (8.8-9.6% and 7.3-8.6%, respectively) are at the same level as the intrageneric differences, the taxonomic status of both *Scincopus* and *Scincus* as independent genera appears questionable.

Within the *Pariocela* section, the analysis shows that "*E.*" *egregius* and *Neoseps reynoldsi* are sister species. The genetic differentiation between the two species (5%), both of which are endemic to Florida, is at the same general level as between the other species of the section, and therefore *N. reynoldsi* is a specialized member of the *Pariocela* section of *Eumeces* sensu lato, which has developed a distinct morphology (Schmidt, 1955) as a consequence of its burrowing mode of living. This is another striking example, that ecologically variable morphological characters should only be used in any phylogenetic analysis if they are interpreted with the utmost caution. As a consequence, the name *Neoseps* Stejneger, 1910 must be synonymised. If the name *Pariocela* Fitzinger, 1843 should be retained for the group, *Neoseps* would become its objective junior synonym (see also Telford, 1959; Richmond and Reeder, 2002).

Despite the incompleteness of the taxon sampling, the recovered topologies support some of the proposed subgroups within the *Pariocela* section. The *laticeps* species-group (*laticeps*, *inexpectatus*, *fasciatus*) as already defined by Taylor (1935) is part of a well supported clade, which also includes the species of the *obsoletus*- and *anthracinus* species-groups (*obsoletus*, *septentrionalis*, *obtusirostris*). This former group is supposed to be closely related to some Asian species (Taylor, 1935), which cannot be confirmed here due to the lack of Asiatic voucher species. "*Eumeces*" *anthracinus* itself is not part

of this group, since it is consistently placed outside the latter clade, and is mostly recovered as sister species to "*E.*" *egregius*.

Lieb (1985) regarded "*E.*" *laticutatus* as a member of the *laticeps* species-group. This arrangement is not confirmed by the present work, since the *laticeps*-group is always placed far from the two specimens of *laticutatus* in the cladograms. Nonetheless, it is interesting to note that the position of the latter species is inconsistent in the different trees. All analyses place *laticutatus* as sister-group to the *Pariocela* species-group. Since a biochemical analysis by Kato et al. (1994) shows *laticutatus* to be deeply embedded in an East Asian radiation, and several studies about the origin of the North American scincid fauna propose an Asian origin for all scincid species, a positioning of *laticutatus* in a basal position to the rest of the *Pariocela* section appears possible.

The included species of the *skiltonianus* species-group (*skiltonianus*, *gilberti*, *rubricaudatus*) form a strongly supported clade. However, the expected clustering of the included species and subspecies of the group is not as expected by the respective taxonomic status given to the different forms, as one would expect true subspecies to be related closest to the respective nominate form. The shown topologies are explained by the observed genetic differences between the included forms. "*Eumeces*" *gilberti rubricaudatus* is more closely related to *s. skiltonianus* (2.0%) than to its nominate species *g. gilberti* (2.2%). A comprehensive genetic analysis by Richmond and Reeder (2002), which included 53 populations of the different morphospecies of the *skiltonianus* species-group, found that the current distribution and morphotypes are the result of an ecological speciation, and that the evolutionary changes in body size are correlated with differences in adult colour pattern. They conclude that body size was likely the target of natural selection and that differences in colour pattern are probably "secondary consequences of evolving large body size". This is a good example that, despite the undisputed usefulness of morphological differences and mitochondrial DNA in taxonomic classifica-

tions, the utmost care must be taken when dealing with recently evolved and closely related parapatric species-groups.

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