

P. Lymberakis<sup>1,\*</sup>,  
N. Poulakakis<sup>1,2</sup>,  
A. Kaliontzopoulou<sup>3,4</sup>,  
E. Valakos<sup>5</sup> & M. Mylonas<sup>1,2</sup>

<sup>1</sup>Natural History Museum of  
Crete, University of Crete,  
Knosou Av., PO Box 2208,  
71409 Irakleio, Greece

<sup>2</sup>Department of Biology,  
University of Crete, Greece

<sup>3</sup>CIBIO/UP, Centro de  
Investigação em Biodiversidade  
e Recursos Genéticos, Campus  
Agrário de Vairão, 4485-661,  
Vairão, Portugal

<sup>4</sup>Herpetologia, Dep. Biologia  
Animal, Fac. Biologia, University  
of Barcelona. Av. Diagonal 645  
08015 Barcelona, Spain

<sup>5</sup>Section of Animal and Human  
Physiology, Department of  
Biology, University of Athens,  
Greece

submitted June 2006

accepted February 2007

## Two new species of *Podarcis* (Squamata; Lacertidae) from Greece

**Abstract** Recently, several works have focused on the lacertid lizards of the genus *Podarcis*, revealing cases of hidden diversity and paraphyly, and offering evidence that suggests the revision of the extant taxonomical arrangements within the genus. Hidden diversity and paraphyly have been shown to exist in the relationships between the Balkan species *P. peloponnesiaca* and *P. erhardii* as well. Here we couple a molecular (mtDNA) dataset with a corresponding morphological one, consisting of morphometric and pholidotic characters, to check for concordance between the two. Phylogenetic analyses reinforced previous suggestions for paraphyly of *P. erhardii* with respect to *P. peloponnesiaca*. We found the variation of certain pholidotic characters concordant with the relationships inferred from partial mtDNA sequences, whereas morphometric characters were not. The latter is possibly due to greater influence of morphometric characters by environmental factors. To avoid the observed paraphyly we proceed with the description of the populations from Crete and the islet of Pori, until now designated as *P. erhardii*, as separate taxa at the species level.

**Key words** *Podarcis cretensis*, *Podarcis lewendis*, new species, phylogeny, morphology, mtDNA, taxonomy

## Introduction

The genus *Podarcis* is comprised of 17 currently recognised species in southern Europe, where they are the predominant reptile group (Harris & Arnold, 1999; Harris & Sa-Sousa, 2002; Sa-Sousa & Harris, 2002). The taxonomy of *Podarcis* is complex and has been continuously revised, largely because the species are morphologically very similar yet exhibit high intraspecific variability (Arnold, 2002).

There is substantial evidence from morphological and genetic data that *Podarcis* is a monophyletic group (Arnold, 1973, 1989; Harris *et al.*, 1998; Fu, 2000; Oliverio *et al.*, 2000). Its closest relative, as derived from morphology, is the Moroccan *Lacerta* (*Teira*) *andreanskyi* (Arnold, 1989).

Recently, several works have focused on *Podarcis*, revealing cases of hidden diversity and paraphyly, and offering evidence that suggest the revision of the extant taxonomical arrangements within the genus (Castilla *et al.*, 1998; Sá-Sousa *et al.*, 2000; Harris & Sá-Sousa, 2001, 2002; Poulakakis *et al.*, 2003, 2005).

Phylogenetic relationships between *P. erhardii* and *P. peloponnesiaca* have been long demonstrated (Arnold, 1973; Mayer, 1986). Recent publications on the phylogenetic relationships of Greek species of *Podarcis* based on partial mtDNA sequences (Poulakakis *et al.*, 2003, 2005) revealed that *P. erhardii* is paraphyletic with respect to *P. peloponnesiaca*.

Little attention has been paid to the methods and data used to recognise and delimit species (Wiens, 1999) and the problem becomes particularly apparent when the meagre literature on the methodology of species delimitation is contrasted with the extensive body of work on the theory and methods of phylogenetic analysis (Wiens & Penkrot, 2002).

The latter authors propose a method for delimiting species by evaluating the consensus of groupings as inferred by morphological and molecular datasets. Here we follow Wiens and Penkrot (2002), comparing the two types of datasets between *P. erhardii* and *P. peloponnesiaca* populations in order to reach solid phylogenetic and taxonomic conclusions concerning the two taxa in question.

## Materials and methods

### Phylogenetic analysis based on partial mtDNA sequences

We compared partial mitochondrial *cyt b* gene (412 bp) of 144 specimens (102 *P. erhardii*, 11 *P. peloponnesiaca* and 31 *P. muralis*). Specimens of *P. erhardii* include 22 out of the 28 described subspecies plus three populations for which there is no available subspecific designation. The geographical distribution of the populations analysed is presented in Fig. 1. For details on species, subspecies, specimens used and localities, see Appendix 1, which is available as 'Supplementary

\*Corresponding author. Email: lyberis@nhmc.uoc.gr

data' on Cambridge Journals Online: which is available as "Supplementary data" on Cambridge Journals Online: [http://www.journals.cup.org/abstract\\_S1477200008002727](http://www.journals.cup.org/abstract_S1477200008002727).

The six *P. erhardii* subspecies not represented in the analyses, are distributed in islets of the Cyclades archipelago. Until future collections are made we consider these populations to be closely related to the haplotypes of the 11 subspecies from Cyclades studied here.

Total genomic DNA was extracted from 93 specimens of *Podarcis* using the protocol of Poulakakis *et al.* (2003). Double-stranded PCR was used to amplify a ~400 bp of the mitochondrial DNA *cyt b* gene using universal primers (L14724 and H15175; Palumbi, 1996). The PCR cycle program comprised an initial denaturation at 94 °C for 5 min, followed by 35 cycles of 1 min at 94 °C, 1 min at 47 °C, and 1 min at 72 °C. The cycling was ended with 10 min sequence extension at 72 °C. All specimens were sequenced directly from the PCR products using the primers mentioned above on an ABI 377 automated sequencer. Sequences for both strands were determined. GenBank accession numbers for the sequences obtained are: AY896054-146. Sequences were aligned using the ClustalX program package (Thompson *et al.*, 1997). The MEGA computer package (v.2, Kumar *et al.*, 2001) was used to determine the number and type of nucleotide substitutions in pairwise comparisons of sequences, to measure the degree of divergence between sequences and to identify the unique sequences for phylogenetic analysis. Analyses for phylogenetic inference were conducted using two methods: maximum likelihood (ML) and Bayesian inference (BI). For phylogenetic analysis, a data set of 144 *cyt b* sequences were used including the 43 sequences (AF486191-233) of Poulakakis *et al.* (2003), 1 sequence of *P. peloponnesiaca* (AF133452): Harris and Arnold (1999), and 7 sequences of *P. muralis* (AF248007, AF080278, AY234155, AY194855, AY185096, AY374256, AY585686).

For ML analysis (Felsenstein, 1981), the best-fit model of DNA substitution and the parameter estimates used for tree construction were chosen by performing hierarchical likelihood-ratio tests (Huelsenbeck & Crandall, 1997) in Modeltest (v.3.06; Posada & Crandall, 1998). Likelihood-ratio tests indicated that the GTR model+I+G (Rodriguez *et al.*, 1990), with  $-\ln L = 4823.2788$ , had the lowest likelihood score and showed a significantly better fit than the other, less complicated models. Heuristic ML searches were performed with 10 replicates of random sequence addition and TBR branch swapping (PAUP 4.0b10a; Swofford, 2002). Since a ML tree search with such a complex model would be computationally excessive, we employed only 100 iterations (Felsenstein, 1985).

BI was performed with the software MrBayes (v3.0B; Huelsenbeck & Ronquist, 2001) using the GTR model of substitution with rate heterogeneity set to a gamma distribution, hence applying the fewest possible number of constraints to the dataset. The analysis was run with four chains for  $10^7$  generations and the current tree was saved to file every 100 generations. This generated an output of  $10^5$  trees. The  $-\ln L$  stabilised after approximately  $10^5$  generations and the first  $10^4$  trees (10% 'burn-in' in Bayesian terms, chain had not become stationary) were discarded as a conservative measure to

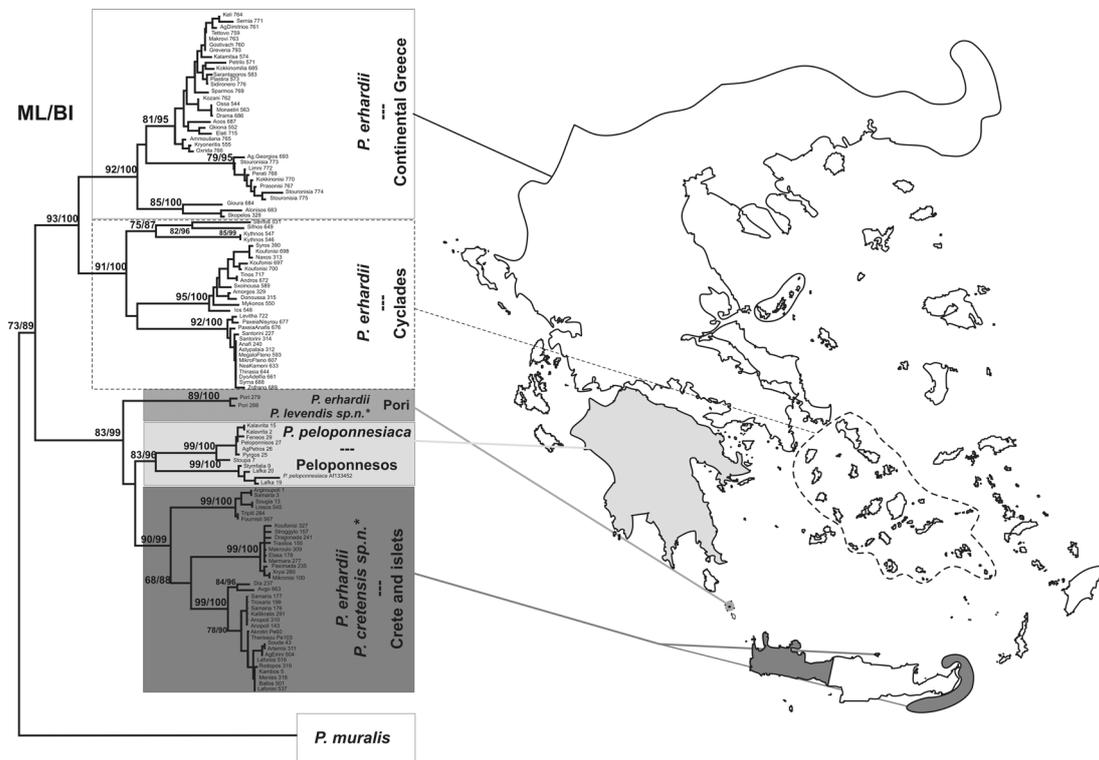
avoid the possibility of including random, sub-optimal trees. The percentage of samples recovering any particular clade in a Bayesian analysis represents that clade's posterior probability (Huelsenbeck & Ronquist, 2001). We used one of the methods of Leaché & Reeder (2002) to assure that our analyses were not trapped on local optima. In particular, the posterior probabilities for individual clades obtained from separate analyses (4 runs) were compared for congruence (Huelsenbeck & Imennov, 2002), given the possibility that two analyses could appear to converge on the same ln-likelihood value, while actually supporting incongruent phylogenetic trees.

## Morphological data

We examined 12 biometric characters: snout-vent length (SVL), trunk length (TRL, defined as the closest distance between anterior and posterior limbs), tail length (TL) only for animals with entire, not regenerated tails, pileus length (PL), pileus width (PW), head height (HH), eye-snout distance (ESD) defined as the distance from the tip of the snout to the border between the 2nd and 3rd supraoculars, mouth opening (MO) measured from the tip of the snout to the posterior border of the last supralabial scale, femur length (FL), tibia length (TBL), tarsus length (TAL) and 4th toe length (4TL) from the base of the heel to the tip of the 4th toe (including the nail). In addition to linear biometric, we recorded 6 pholidotic (meristic) characters as well: the number of femoral pores (FPN), subdigital lamellae of the 4th toe (SLN), temporal scales (TEMP), supraciliary granules (SCGN), gular scales (GSN) and collar scales (CSN). All bilateral characters were recorded on the right side of the lizard body when possible and all measurements were taken following the suggestions of Pérez-Mellado and Gosá (1988) on the biometry and pholidosis of the Lacertidae and the descriptions of characters in Kaliontzopoulou *et al.* (2007). Only adult animals were included in the analysis of linear biometric data, whereas for pholidosis immature were also included since scalation does not change throughout the lizard's life (Carretero & Llorente, 1993). All characters were measured using a digital calliper to the closest 0.1 mm.

For all analyses, specimens of *Podarcis* were pooled in four groups according to their phylogenetic relationships as inferred by the partial mtDNA sequence analyses (Fig. 1).

Biometric variables were all normally distributed (Anderson-Darling test,  $P > 0.1$ ) and were thus examined using parametric statistics. However, most of the pholidotic variables significantly deviated from normality (Anderson-Darling test,  $P < 0.05$ ), non-parametric statistics were therefore applied. Univariate comparisons of the biometric variables revealed that a marked sexual dimorphism existed in all groups for most of the characters studied. Males and females from Crete were significantly different for all characters (Student's *t*-test,  $P < 0.05$ ), except for trunk length (TRL, Student's *t*-test,  $P = 0.17$ ). For the rest of the groups, males and females differed significantly for all the characters studied (Student's *t*-test,  $P < 0.05$ ), except for SVL, TL and TRL (Student's *t*-test,  $P > 0.1$  in all cases). Therefore, consequent comparisons of biometric variables were performed separately for each sex. We conducted univariate comparisons in order to examine the



**Figure 1** Maximum likelihood (ML) tree under the GTR+I+G model of evolution rooted with *P. muralis*. Numbers above branches indicate bootstrap values greater than 50% based on 100 iterations (ML) and posterior probabilities (BI) respectively. Asterisks indicate proposed new taxonomy.

differences between the different groups for the characters studied. Further, we applied multivariate analysis techniques to test if groupings of populations corroborate the results of the molecular analyses. Finally, we conducted a discriminant analysis in order to identify those characters that could be useful for species diagnosis.

For the construction of a morphology-based tree we followed Wiens and Penkrot (2002) creating step matrices based on frequencies (mean values of characters) for each of the four groups plus *P. muralis* as an outgroup. The characters we used are: GSN, known as a diagnostic character between *P. muralis* and *P. erhardii* (Gruber, 1987), but largely overlapping within *P. erhardii* and *P. peloponnesiaca*, SCGN, TEMP, SVL, FPN and SLN.

### Taxonomical approach

We consider two possible solutions for avoiding the paraphyly described above: either (A) join all the populations of the clade containing *P. peloponnesiaca*, and *P. erhardii* populations from Crete and Pori, under the same name (i.e. *P. peloponnesiaca*) and describe them as a separate taxon distinct from *P. erhardii* populations from Cyclades and mainland Greece; or (B) raise *P. erhardii* populations from Crete and Pori to species level as new taxa.

There are more possible solutions to the observed paraphyly, but we reject them as less parsimonious and lacking substantial evidence (e.g. the solution to sink *P. peloponnesiaca* as a synonym of *P. erhardii*). Because the populations in question (i.e. in Crete, Peloponnesos and Pori) are allopatric,

we cannot take taxonomical decisions based on the biological species concept.

We thus evaluated the two solutions in accordance with the reasoning of Good and Wake (1993) as well as that of Wiens (2004), i.e. putting forth the evolutionary species concept. We followed Wiens and Penkrot (2002), who predict (and further on demonstrate the validity of their prediction) that given enough time, distinct species should: (1) have exclusive DNA haplotype phylogenies relative to other species, (2) have one or more diagnostic morphological characters (either fixed or at high frequency), and (3) form strongly supported clades of populations based on morphology, adding that the strongest evidence for distinct species would be concordance between the different approaches.

## Results

### Phylogenetic analysis based on partial mtDNA sequences

The analysis of sequences from 144 individuals revealed 120 unique haplotypes of *Podarcis*. The lengths of these sequences ranged from 390 to 415 bp. No deletions or insertions were detected.

Tree length distribution, determined from random sampling of  $10^6$  unweighted trees, was significantly skewed to the left ( $g_1 = -0.471$ ), suggesting a strong phylogenetic signal in the data ( $P < 0.01$ ; Hillis & Huelsenbeck, 1992). Maximum likelihood analysis under the GTR+I+G model resulted in a

topology with  $\ln L = -4775.2358$  (Fig. 1). For the Bayesian inference method, which is consistent with the likelihood one, identical topologies were recovered for each of the 4 runs with the full dataset, although posterior probabilities for some of the nodes differed slightly between each of the Bayesian runs. The mean  $-\ln$  likelihood of these trees was  $-4761.4578$ .

All phylogenetic analyses of the partial mtDNA sequence data showed that the haplotypes of *P. erhardii* are not exclusive. *Podarcis erhardii* appears in two separate clades. The first corresponds geographically to mainland Greece and the Aegean islands (in clear frames in Fig. 1) and the second to the populations from the island of Crete and its satellite islets (darkly shaded in Fig. 1). The latter appears as a sister group to the clade, which includes *P. peloponnesiaca* and *P. erhardii* from the islet of Pori (lighter shades in Fig. 1). In terms of phylogenetic relationships, *P. erhardii* from Crete appears to be related to *P. erhardii* from the islet of Pori and *P. peloponnesiaca*, even though their exact position on the tree is not definite according to the statistical results (low bootstrap values). It is clear from the above analysis that the phylogenetic affiliations produced from the molecular data do not agree with the species and subspecies groupings of the extant classification of our sampled populations.

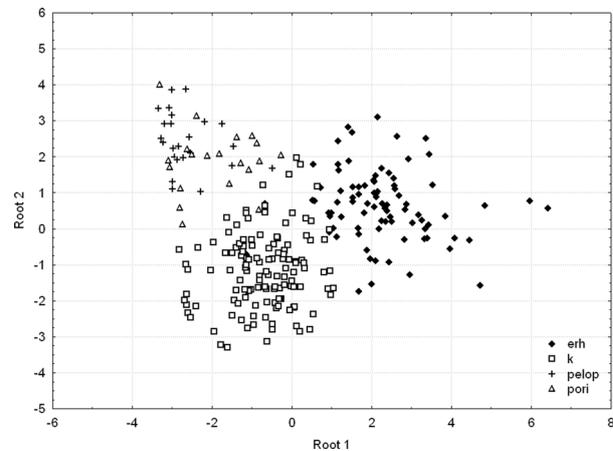
### Morphological data

Univariate comparisons of biometric characters revealed significant differences between animals of the same sex among different groups for all the characters studied (Tables 1 and 2). It is important to note that variation in SVL coincided in the two sexes and revealed an interesting pattern: animals from Pori presented no significant differences in SVL from those of *P. peloponnesiaca*, but differed significantly from all other groups. Thus, the animals studied may be assigned to two groups according to their SVL: a group of ‘bigger’ animals including *P. peloponnesiaca* and animals from the islet of Pori and a group of ‘smaller’ animals including Cretan populations and the rest of *P. erhardii*.

Pholidotic characters showed a different pattern of variation. Sexual differences were scarce, although significant in some cases. For example, some of the groups (Cretan populations and the rest of *P. erhardii* populations) show significant differences between the sexes in number of femoral pores. This is interesting, but not surprising since sexual dimorphism in size and aspect of femoral pores is known to be a common trait in various lizard families (Cole, 1966). Sexual dimorphism patterns are presented in Table 3.

Due to the fact that sexual dimorphism was not prominent for most groups and since our objective was to test the groups’ consistency, multivariate comparisons were conducted pooling the two sexes. The Kruskal–Wallis ANOVAs among the groups revealed significant differences for all characters ( $P < 0.01$ ) except for CSN ( $P = 0.397$ ). Among these characters some, such as SCGN, presented important differences between the groups, and could be useful for their discrimination.

Results from discriminant analysis using the biometric variables were not congruent with the phylogenetic grouping of the different populations. The discriminant analysis con-



**Figure 2** Canonical analysis scatterplot based on the pholidotic variables. erh. = *P. erhardii* from continental Greece and Cyclades, k. = Crete, pelop. = *P. peloponnesiaca*, pori. = Pori.

ducted using pholidotic characters resulted in a highly correct classification of individuals (95.35%), corroborating the results inferred from mtDNA analysis (Table 4, Figure 2). All the pholidotic characters studied except for CSN were important for discrimination among groups and entered in the discriminant functions.

Morphological characters used for species diagnoses are shown in Fig. 3 a–d. Results from the construction of a morphology-based tree are presented in Fig. 4. We initiated the construction of the tree using these characters (i.e. SCGN, TEMP, SVL) and continued repeating the same procedure adding a new character at a time. Analyses were performed using PAUP v4.0b10a (Swofford, 2002). Confidence in the nodes was assessed by 1000 bootstrap replicates (Felsenstein, 1985).

The separation of the taxa, when constructing the tree based on SCGN, TEMP and SVL, is in accordance with the respective clades of the phylogenetic analyses inferred by mtDNA. Bootstrap values decrease rapidly with the addition of other morphological characters, which largely overlap within the taxa in question. The topology of the tree is entirely rearranged when more than two homoplastic characters are included.

The only ambiguous point concerns the topology of the clade containing the populations of *P. peloponnesiaca*, and those from Crete and Pori. The morphology-based tree may result from the effect of mean SVL similarity of *P. peloponnesiaca* with the population from the islet of Pori. The cyt *b*-based tree has low bootstrap support ( $< 50%$ , thus not presented) for the topology of the same clade.

### Taxonomy

The monophyly of the clade containing populations from Peloponnesos, Crete and Pori is strongly supported by molecular (Poulakakis *et al.*, 2003, 2005, present study) and morphological data (less than 7 and discontinuous Supraciliary Granules, SCGN, Fig. 3a). Consequently there is a need to rearrange the taxonomic status of the populations within this group.

		SVL	TL	TRL	PL	PW	HH	ESD	MO	FL	TBL	TAL	4TL
<i>P. 'erhardii'</i> (Crete)	Male	59.4 ± 0.6 (63)	101.3 ± 2.1 (26)	28.7 ± 0.3 (63)	14.3 ± 0.1 (63)	9.1 ± 0.1 (63)	7.0 ± 0.1 (63)	5.7 ± 0.07 (63)	10.9 ± 0.1 (63)	10.3 ± 0.1 (63)	9.3 ± 0.1 (63)	4.6 ± 0.1 (63)	9.6 ± 0.1 (63)
		50.4–71.5	84.6–117.1	23.3–34.4	11.8–17.3	6.6–11.3	5.1–9.8	4.6–7.0	8.0–14.0	8.7–12.9	7.5–10.9	3.80–5.90	6.5–11.0
	Female	55.5 ± 0.6 (46)	80.2 ± 3.4 (17)	29.5 ± 0.4 (46)	11.96 ± 0.1 (46)	7.49 ± 0.1 (46)	5.8 ± 0.14 (46)	4.9 ± 0.06 (46)	9.6 ± 0.16 (46)	8.5 ± 0.12 (46)	7.76 ± 0.1 (46)	3.9 ± 0.09 (46)	8.16 ± 0.1 (46)
		45.6–64.0	50.2–106.5	23.2–33.9	10.4–14.6	5.9–8.7	3.8–9.3	4.0–5.8	7.0–12.9	7.0–10.7	6.4–9.0	3.0–5.6	6.5–10.4
	<i>t</i> -value	4.46	5.49	-1.37	12.37	8.33	5.95	8.89	5.27	10.18	10.56	7.63	8.26
	<i>d.f.</i>	107	41	107	107	107	107	107	107	107	107	107	107
<i>P</i>	2.01E-05	2.27E-06	0.173	2.39E-22	2.98E-13	3.38E-08	1.64E-14	7.10E-07	1.98E-17	2.78E-18	1.03E-11	4.27E-13	
<i>P. 'erhardii'</i> (Pori)	Male	74.0 ± 0.99 (8)	126.8 ± 4.99 (7)	37.04 ± 0.9 (8)	17.75 ± 0.13 (8)	9.21 ± 0.5 (8)	9.16 ± 0.23 (8)	7.4 ± 0.1 (8)	14.75 ± 0.3 (8)	13.55 ± 0.32 (8)	12.35 ± 0.16 (8)	6.35 ± 0.15 (8)	13.6 ± 0.27 (8)
		69.1–77.6	110.0–151.0	32.3–39.6	17.2–18.2	8.0–12.5	8.20–10.00	7.0–7.75	13.2–15.8	12.5–15.0	11.7–12.9	5.6–7.0	12.2–14.5
	Female	71.5 ± 1.46 (10)	118.13 ± 2.9 (6)	39.05 ± 1.2 (10)	15.24 ± 0.3 (10)	7.58 ± 0.2 (10)	7.6 ± 0.1 (10)	6.5 ± 0.1 (10)	12.2 ± 0.2 (10)	10.86 ± 0.3 (10)	10.2 ± 0.1 (10)	5.6 ± 0.16 (10)	11.99 ± 0.3 (10)
		62.1–77.6	113.0–132.0	31.0–44.2	13.9–17.4	6.8–8.9	7.1–8.1	6.1–6.9	10.9–13.6	9.4–12.3	9.9–10.6	4.9–6.5	9.5–13.0
	<i>t</i> -value	1.37	1.43	-1.25	7.40	3.11	6.46	8.12	6.98	6.60	12.45	1.37	1.43
	<i>d.f.</i>	16	11	16	16	16	16	16	16	16	16	16	11
<i>P</i>	0.188	0.180	0.228	1.50E-06	6.73E-03	7.88E-06	4.59E-07	3.13E-06	6.14E-06	1.21E-09	0.188	0.180	
<i>P. erhardii</i> (Cyclades and Continental Greece)	Male	58.97 ± 0.88 (36)	96.54 ± 3.16 (28)	27.98 ± 0.5 (36)	14.63 ± 0.20 (35)	9.41 ± 0.16 (35)	7.48 ± 0.1 (34)	6.0 ± 0.08 (35)	12.23 ± 0.21 (35)	10.7 ± 0.2 (36)	9.72 ± 0.15 (35)	5.20 ± 0.11 (36)	11.04 ± 0.20 (36)
		50.7–70.6	58.6–130.0	23.1–33.4	12.5–17.0	6.6–11.3	5.6–8.9	4.9–7.3	10.1–14.2	8.8–13.4	8.0–12.1	3.8–6.9	7.9–13.5
	Female	56.81 ± 1.04 (30)	103.5 ± 2.91 (20)	29.14 ± 0.7 (30)	12.62 ± 0.18 (30)	7.87 ± 0.16 (30)	6.26 ± 0.1 (30)	5.38 ± 0.1 (30)	10.49 ± 0.2 (30)	9.45 ± 0.24 (30)	8.42 ± 0.17 (30)	4.53 ± 0.10 (30)	9.66 ± 0.21 (30)
		49.2–75.2	77.5–135.5	21.7–37.2	11.2–15.0	6.3–10.1	5.3–7.7	4.8–6.7	8.7–13.2	6.7–12.0	6.3–11.2	3.7–5.9	7.9–12.2
	<i>t</i> -value	1.60	-1.55	-1.47	7.48	6.67	7.05	5.69	4.86	6.29	4.08	5.59	4.62
	<i>d.f.</i>	64	46	64	63	63	62	63	63	64	63	64	64
<i>P</i>	0.115	0.127	0.146	2.93E-10	7.49E-09	1.75E-09	3.50E-07	3.40E-08	1.28E-04	5.27E-07	1.91E-05	1.46E-05	
<i>P. peloponnesiaca</i> (Peloponnisos)	Male	70.6 ± 1.75 (12)	125.4 ± 3.53 (6)	33.4 ± 1.34 (12)	17.32 ± 0.39 (12)	10.58 ± 0.3 (12)	9.25 ± 0.3 (12)	7.4 ± 0.14 (12)	15.05 ± 0.3 (12)	13.43 ± 0.5 (12)	11.4 ± 0.3 (12)	5.9 ± 0.1 (12)	13.17 ± 0.25 (12)
		57.4–77.3	113.0–135.8	25.7–40.2	14.40–19.10	8.9–12.2	7.2–11.0	6.5–8.1	12.6–16.3	10.0–16.8	9.7–13.4	5.2–6.6	12.0–14.3
	Female	71.5 ± 2.03 (11)	121.7 ± 7.06 (5)	36.22 ± 1.1 (11)	15.05 ± 0.3 (11)	9.03 ± 0.42 (11)	8.2 ± 0.25 (11)	6.52 ± 0.2 (11)	13.40 ± 0.3 (11)	11.35 ± 0.2 (11)	10.35 ± 0.3 (11)	5.4 ± 0.15 (11)	12.2 ± 0.34 (11)
		59.5–82.0	105.2–145.3	29.0–42.5	13.3–16.9	7.0–11.0	6.9–9.3	5.2–7.6	11.8–14.9	10.2–12.4	8.3–11.4	4.7–6.2	10.0–13.8
	<i>t</i> -value	-0.34	0.50	-1.59	4.45	2.97	2.56	3.64	3.85	3.52	2.69	2.36	2.35
	<i>d.f.</i>	21	9	21	21	21	21	21	21	21	21	21	21
<i>P</i>	0.736	0.631	0.127	2.24E-04	7.23E-03	1.83E-02	1.53E-03	9.24E-04	2.01E-03	1.38E-02	2.83E-02	2.84E-02	

**Table 1** Descriptive statistics and Students' *t*-test comparisons between the sexes for the biometric characters in the four groups examined. The first line represents Mean ± SE (N) and the second the range. See Materials and methods for variables' abbreviations.

	Males		Females	
	F	P	F	P
SVL	37.34	1.11E-16	54.36	0.00
TL	14.344	3.15E-07	21.287	1.14E-08
TRL	27.499	1.76E-13	33.982	6.44E-15
PL	44.36	0.00	57.20	0.00
PW	5.801	1.00E-03	9.113	2.39E-05
HH	23.952	4.52E-12	35.865	1.67E-15
ESD	56.37	0.00	61.58	0.00
MO	46.824	0.00	51.832	0.00
FL	43.028	0.00	31.273	4.55E-14
TBL	50.50	0.00	50.328	0.00
TAL	41.089	0.00	42.397	0.00
4TL	78.586	0.00	70.315	0.00

**Table 2** Results of the univariate ANOVAs conducted among the four groups for the biometric variables in the two sexes. See Materials and methods for variables' abbreviations. Degrees of freedom df = 3 for all comparisons.

The prerequisites of Wiens and Penkrot (2002) for delimiting species are satisfied in the case of the three populations of this group. Specifically, for the condition ‘... given enough time’, there is a consensus among scientists for the estimated 5

My time span of separation of these populations (Meulenkamp, 1985; Schüle, 1993).

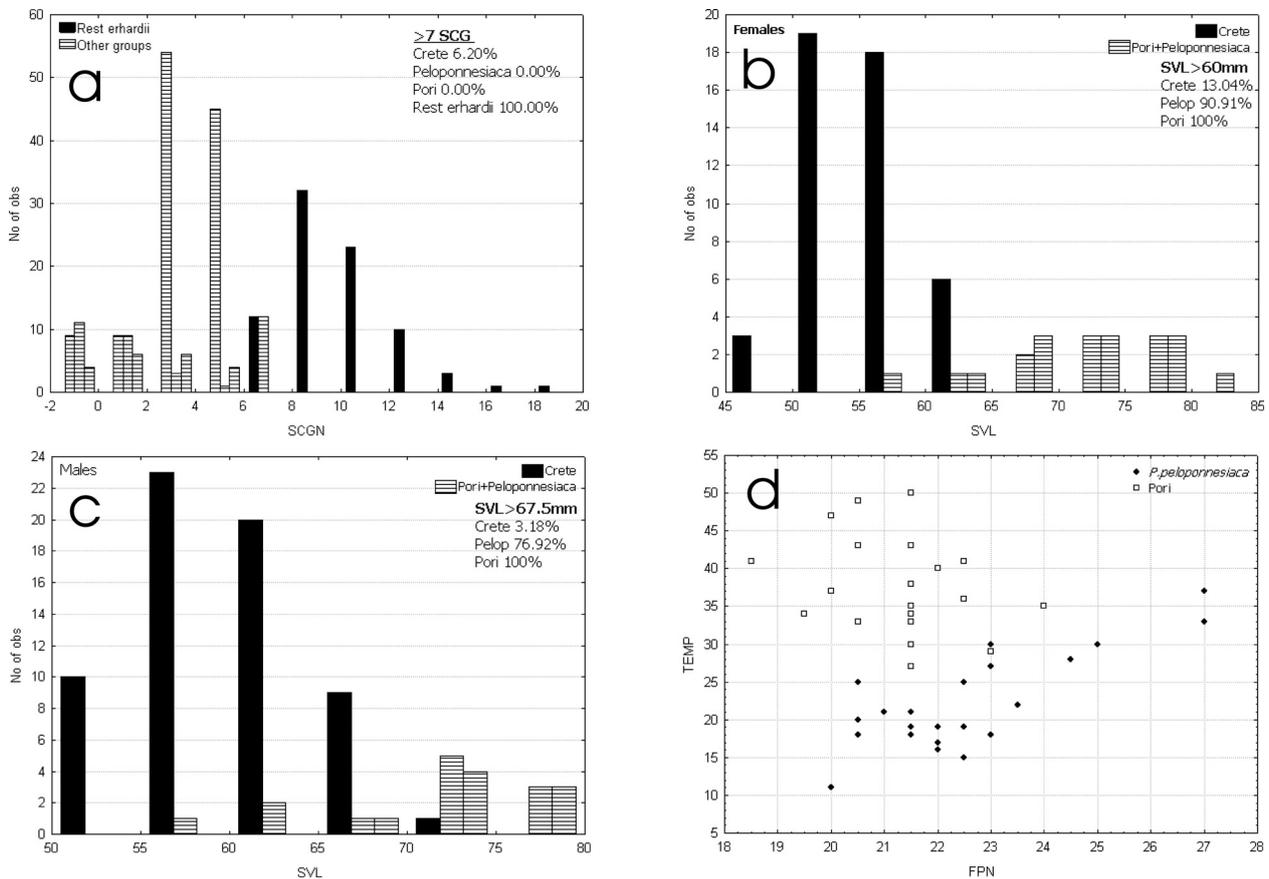
Solid evidence for the satisfaction of the first criterion is provided in the latter works and here. Moreover, indirect molecular data (Harris, 2002; compare with Table 5) reinforce the distinction among the three populations.

The second criterion concerning one or more diagnostic morphological characters is also satisfied as shown by the analysis on morphological characters. Adult female lizards of Peloponnesos and Pori have SVL > 60 mm (95.24% of individuals studied), while 86.96% of females from Crete are smaller than 60 mm (Fig. 3b). Adult males of the first group have SVL > 67.5 mm (85.72% of individuals studied), while 96.83% of males from Crete are smaller than that (Fig. 3c).

Lizards from Pori differ from *P. peloponnesiaca* in the number of femoral pores and temporal scales (Table 3). Combining these two characters, the two populations can be distinguished since lizards from Pori have more temporal scales and fewer femoral pores than those of *P. peloponnesiaca* (Fig. 3d).

Finally the clades based on morphology are strongly supported and in agreement with the respective molecular ones (Fig. 4, Fig. 1). This concordance provides further support to the biogeographical scenario which Poulakakis *et al.* (2003) proposed.

Seeing the above, we reject the first solution for raising the paraphyly observed and following the second solution we describe a new species from the islet of Pori and



**Figure 3** Diagnostic characters for the four groups studied. See Materials and methods for variables' abbreviations.

		FPN	SLN	TEMP	SCGN	GSN	CSN
<i>P. 'erhardii'</i> (Crete)	Male	19.2 ± 0.18 (63)	25.97 ± 0.26 (63)	52.70 ± 1.54 (63)	4.07 ± 0.23 (63)	30.81 ± 0.28 (63)	10.29 ± 0.14 (63)
		15.5–22.5	19–30	28–92	0–7.5	26–35	8–13
	Female	18.39 ± 0.23 (46)	25.20 ± 0.27 (46)	47.17 ± 1.66 (46)	3.85 ± 0.26 (46)	29.98 ± 0.37 (46)	9.80 ± 0.11 (46)
		16–22	21–31	29–83	0–7.5	25–36	8–11
	<i>z</i>	–2.660	–2.310	–2.555	–0.801	–1.951	–2.396
	<i>P</i>	7.82E-03	2.09E-02	1.06E-02	0.423	0.510	1.66E-02
<i>P. 'erhardii'</i> (Pori)	Male	21.88 ± 0.43 (8)	31.13 ± 0.55 (8)	38.88 ± 2.88 (8)	2.38 ± 0.74 (8)	29.25 ± 0.48 (8)	10.50 ± 0.27 (8)
		20–24	30–34	29–50	0–5.5	28–32	10–12
	Female	20.85 ± 0.4 (10)	29.4 ± 0.34 (10)	38.40 ± 1.38 (10)	2.35 ± 0.56 (10)	27.6 ± 0.45 (10)	10.50 ± 0.34 (10)
		18.5–22.5	27–31	33–47	0–4.5	26–31	9–12
	<i>z</i>	–1.377	–2.399	0.000	0.000	–2.399	0.044
	<i>P</i>	0.168	1.64E-02	1.00	1.00	1.64E-02	0.965
<i>P. erhardii</i> (Cyclades and Continental Greece)	Male	21.99 ± 0.30 (35)	28.49 ± 0.34 (35)	61.63 ± 3.17 (35)	10.84 ± 0.51 (35)	29.51 ± 0.55 (35)	10.29 ± 0.22 (35)
		19.5–26.5	25–33	31–106	3–18.5	24–38	8–13
	Female	20.85 ± 0.25 (30)	27.63 ± 0.33 (30)	58.40 ± 3.86 (30)	10.28 ±	29.27 ± 0.52 (30)	10.00 ± 0.19 (30)
		18–23.5	24–31	27–114	0.38 (30) 7.5–15	23–35	8–12
	<i>z</i>	–2.395	–1.632	–0.796	–1.369	–0.243	–0.809
	<i>P</i>	1.66E-02	0.103	0.426	0.171	0.808	0.418
<i>P. peloponnesiaca</i> (Peloponnisos)	Male	23.19 ± 0.60 (13)	28.31 ± 0.31 (13)	23.92 ± 2.13 (13)	0.81 ± 0.38 (13)	28.77 ± 0.80 (13)	10.23 ± 0.32 (13)
		20–27	27–30	13–28	0–4.5	24–34	9–12
	Female	21.68 ± 0.32 (11)	27.91 ± 0.39 (11)	20.27 ± 1.04 (11)	0.95 ± 0.33 (11)	27.82 ± 0.67 (11)	10.55 ± 0.28 (11)
		20.5–23.5	26–30	15–27	0–3	24–31	9–12
	<i>z</i>	–1.825	–0.695	–1.101	0.492	–0.608	0.840
	<i>P</i>	0.07	0.49	0.27	0.62	0.54	0.40

**Table 3** Descriptive statistics and Mann–Whitney *U* test comparisons between the sexes for the pholidotic characters in the four groups examined. The first line represents mean ± SE (N) and the second the range. See Materials and methods for variables' abbreviations.

**Discriminant Function Analysis Summary**  
**Wilks' Lambda: 0.08638 approx.  $F(15,690) = 65.749, P < 0.0001$**

	Wilks' Lambda	Partial Lambda	F-remove (3.25)	P level	Toler.	1-Toler. (R-Sqr.)
FPN	0.130	0.664	42.1	4.71E-22	0.847	0.153
SLN	0.109	0.793	21.8	1.50E-12	0.915	0.085
TEMP	0.097	0.888	10.5	1.66E-06	0.874	0.126
SCGN	0.250	0.346	157.5	0.00E-01	0.839	0.161
GSN	0.098	0.877	11.7	3.45E-07	0.886	0.114

**Classification functions**

	<i>P. erhardii</i> (P = 0.3295)	Crete (P = 0.50)	<i>P. peloponnesiaca</i> (P = 0.093)	Pori (P = 0.0775)
FPN	4.961	4.223	6.225	5.380
SLN	6.026	5.691	6.353	6.972
TEMP	-0.031	0.018	-0.107	-0.033
SCGN	1.295	-0.164	-1.122	-0.897
GSN	3.202	3.316	2.632	2.668
Constant	-192.064	-163.554	-197.348	-200.633

**Classification Matrix**

	Per cent correct	<i>P. erhardii</i>	Crete	<i>P. peloponnesiaca</i>	Pori
<i>P. erhardii</i> (Cyclades and Continental Greece)	96.471	82	3	0	0
<i>P. 'erhardii'</i> Crete	96.124	5	124	0	0
<i>P. peloponnesiaca</i>	100.000	0	0	24	0
<i>P. 'erhardii'</i> Pori	80.000	0	2	2	16
Total	95.349	87	129	26	16

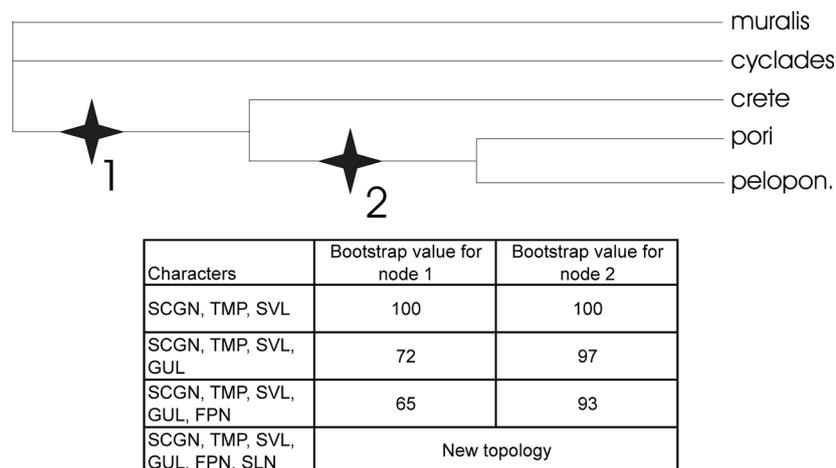
**Table 4** Results of the discriminant analysis conducted with the pholidotic variables. See Materials and methods for variables' abbreviations.

assign full species status to the populations of *Podarcis* from Crete.

***Podarcis cretensis*** (Wettstein, 1952)  
 Crete and satellite islands (Greece), Fig. 5.

**Synonyms**

*Lacerta muralis* subsp. *fusca* (part); (Bedriaga, 1878) (in Boettger, 1888), *Lacerta taurica* var. *maculata* (part); (Bedriaga, 1881), *Lacerta erhardii naxensis* (part); (Werner,



**Figure 4** Maximum Parsimony tree as inferred from morphological characters. See Materials and methods for variables' abbreviations.

Groups	1	2	3	4	5
(1) <i>P. 'erhardii'</i> (Crete)	<b>(3.5)</b>				
(2) <i>P. 'erhardii'</i> (Pori)	9.0	<b>(0.2)</b>			
(3) <i>P. erhardii</i> (Cont. Greece/Cyclades)	14.9	14.2	<b>(3.3)</b>		
(4) <i>P. peloponnesiaca</i>	7.97	7.7	13.6	<b>(3.1)</b>	
(5) <i>P. muralis</i>	15.0	15.75	16.2	17.05	<b>(3.7)</b>

**Table 5** Sequence divergences (%) (Tamura – Nei model) among *Podarcis* populations as grouped in Fig. 1. Values in diagonal represent within clade sequence divergences.



**Figure 5** Young male of *Podarcis cretensis* (sp. nov.) from NW Crete.

1899) (in Wettstein, 1931), *Lacerta erhardii cretensis* (Wettstein, 1952), *Lacerta erhardii leukaorii* (Wettstein, 1952), *Lacerta erhardii elaphonisii* (Wettstein, 1952), *Lacerta erhardii punctigularis* (Wettstein, 1952), *Lacerta erhardii schiebeleri* (Wettstein, 1952), *Lacerta erhardii obscura* (Wettstein, 1952), *Lacerta erhardii rechingeri* (Wettstein, 1952), *Lacerta erhardii werneriana* (Wettstein, 1953).

### Comment

In Wettstein (1952) the description of Cretan populations at the sub-specific level follows the order presented above. Thus the name *cretensis* has priority over the other names which follow in the same publication.

**HOLOTYPE.** One male. NMW (Naturhistorischen Museums in Wien) 8272; O. WETTSTEIN leg., 22. IV. 1942, (Tiedemann *et al.*, 1994).

### Type locality (as in Wettstein 1952)

Kisamo Kastelli, nordwestliches Kreta

**PARATYPES.** NMW 8254: 1–3 Kisamo Kastelli; WETTSTEIN leg., 1942. – NMW 8254:4 Kisamo Kastelli; WETTSTEIN leg., 22.4.1942. – NMW 8254:5 Nerokuru bei Canea, NW Kreta; ATTEMS leg., 5. 5. 1900, ATTEMS don., XI. 1931. – NMW 8254:6 Platanos bei Canea, NW Kreta; ATTEMS leg., 3. 5. 1900, ATTEMS don., 1931. – NMW

8254:7 Nerokuru, S Canea, ca. 200 m; G. SCHIEBEL leg., 29.3.1925. – NMW 8254:8 oberhalb Laki; 25. 4. 1942. – NMW 8254:9 Merades, NW Kreta; G. SCHIEBEL leg., 7. 3. 1925. – NMW 8254:10 Dintorni bei Canea, NW Kreta. – NMW 8254:11 Laki, N-Hang der Leuka-Ori, W-Kreta; WETTSTEIN leg., 10. VI. 1942. – NMW 8254:12 Halbinsel Korikos in Frigana; WETTSTEIN leg., 19. 4. 42. – NMW 8254:13 Zwischen Skines und Rumata, 30 km SW Chania; RECHINGER leg., 29. 5. 1942. – NMW 8254:14 Perivolia, NW Kreta; ATTEMS leg. et don., XI. 1931. – NMW 8254:15 Akrotiri-Hals bei Chania; WETTSTEIN leg., 29. 4. 1942. – NMW 8254:16 Omalos, W-Kreta; ATTEMS leg., 8. 5. 1900, ATTEMS don., XI. 1931. – NMW 8254:17 Kreta; Linnea Nr. 6, 1890. – NMW 8254:18 Omalos-Hochebene; 7. 6. 1942. – NMW 8254:19 Tucla, Suda Bai; REBEL leg., 9. V. 1904, (Tiedemann *et al.*, 1994).

### Differential diagnosis

Differs from *P. erhardii* in few (<7) and discontinuous supra-ciliary granules.

Differs from *P. peloponnesiaca* in smaller SVL (see Table 1) and a combination of pholidotic characters (fewer femoral pores, fewer subdigital lamellae, and more temporal scales, see Table 3).

### Variation

Pholidotic and morphometric variation in Tables 1 and 3.

### Distribution

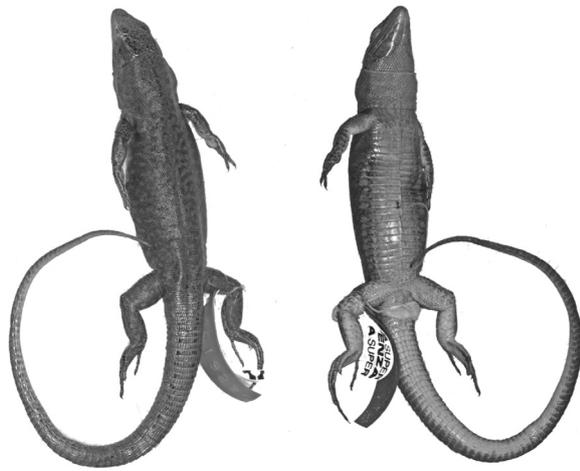
The species is endemic to Crete and its satellite islands. On the island of Crete it is present only on the western part, mostly to the west of a N–S axis ‘cutting’ Crete at the town of Rethymno. In this area it is found from sea level to 2000 m a.s.l. The satellite islets viewed from S–West, to East, to N–West, are: Elaphonisos, Artemis, Gaidouronisi (=Chryssi), Mikronisi (immediately East of Gaidouronisi), Kavalloi (first record for the species), Elasa, Paximada, Dragonada, Prassonisi (immediately North of Dragonada) Avgo (first record for the species), Dia, Karga, Ag. Nikolaos (in the gulf of Souda) and Ag. Theodoroi (=Thodorou).

### Subspecies

The subspecies described by Wettstein (1952, 1953), based mainly on morphometric characters and colour patterns, are not in accordance with the phylogenetic relationships proposed (Poulakakis *et al.* 2003, 2005 and present work). This was expected according to the results presented, which show that morphometric characters do not follow phylogeny. Nevertheless, Wettstein (1952, 1953) thoroughly described extant differences. In the light of the present work, we consider that these differences are due to environmental factors and thus suggest regarding the former subspecies as ecomorphs.

### *Podarcis levendis* new species

Pori and Lagouvardos islets, N of Antikythira, between Crete and Peloponnesos (Greece), (Fig. 6).



**Figure 6** Type specimen of *Podarcis lewendis* (sp. nov.).

### Synonyms

*Podarcis erhardii* in Valakos *et al.* (1995).

**HOLOTYPE.** One male. NHMC 80.3.51.830. Collected on 20.I.1992 by E. Valakos.

### Type locality

Islet Pori, 7.4 km N of the island of Antikythira, between Crete and Peloponnesos and islet Lagouvardos (=Poreti) 3.4 km W–SW of Pori.

**PARATYPES.** NHMC80.3.51.828 ♂; NHMC80.3.51.829 ♀; NHMC80.3.51.831 ♂; NHMC80.3.51.832 ♀; NHMC80.3.51.835 ♂; NHMC80.3.51.836 ♀; NHMC80.3.51.837 ♀; NHMC80.3.51.838 ♀; NHMC80.3.51.839 ♀; NHMC80.3.51.840 ♂; NHMC80.3.51.842 ♀; NHMC80.3.51.843 ♀; Collected by E. Valakos 20.I.1992, from the islet Pori.

NHMC80.3.51.833 ♂; NHMC80.3.51.834 ♀; Collected by M. Mylonas 20.I.1992, from the islet Lagouvardos.

### Differential diagnosis

One of the largest species of the genus along with *P. peloponnesiaca*. Differs from the latter in larger number of temporal scales (Table 3, Fig. 3d). Larger and more robustly built than *P. cretensis* (sp. nov.) and *P. erhardii* (Table 1). Also differs from *P. cretensis* (sp. nov.) in a combination of more femoral pores and subdigital lamellae (Table 3). Finally differs from *P. erhardii* in few (<7) and discontinuous supraciliary granules.

### Description of the holotype

Well preserved alcohol specimen.

Measurements (in mm): Snout Vent length 77.6; Pileus length 18; Pileus width 8.8; Head height 9.6; Trunk length 39.6; Tail length 151; Femur length 14.6; Tibia length 12.8; Tarsus length 7; 4th Toe length 14.

Pholidosis (where relevant L, R): Supraciliary Granules (1,1); Femoral Pores (22,21) Gular scales 30; Temporal scales (42,43); Scales under 4th Toe (22, 31). The low number of scales of the left toe is probably due to an old wound of the animal's left foot, which has resulted in the amputation of the

5th toe. Scales around mid-body 60. Ventrals in transversal rows 24.

Colouration (in alcohol): basic dorsal colour of head, body and legs, dark green with black reticulations. Laterally black reticulation is heavier. Two light stripes begin from the outer, posterior, edges of the Pileus and fade behind the front legs. Tail olive green with two series of black spots, which fade after the first 1/5 of its length. Ventral colour is light green, fading to dirty white-yellow at the hind limbs and tail. First row of ventral scales from each side bicoloured: the half closer to the back light blue and the ventral half the same basic colour with dark green spots.

### Variation

Pholidotic and morphometric variation in Tables 1 and 3.

### Distribution

Only on the islets Pori and Lagouvardos, N of the island of Antikythira, between Crete and Peloponnesos.

### Etymology

In honour of the Leventis Foundation which funded NHMC research trips on the small islets of the Aegean. Moreover, 'Leventis' (pronounced Levéndis, which is the reason for choosing the proposed orthography) is a medieval Greek word derived from Levantes (= East). It is an adjective meaning brave man, as were the sailors of the East Mediterranean. We consider that this relict species, which survived for at least 5 My on two small islets isolated from any similar taxon, qualifies as brave.

### Discussion

The principal question of this work is if within the two basal lineages we may split populations in distinct taxa at the species level. Moreover, the answer to this question, apart from its interest per se, is necessary to avoid the paraphyly of *P. erhardii* with respect to *P. peloponnesiaca*. Changing the taxonomic status of taxa is a task to be carried out with prudence, but in some cases unavoidable (Arnold, 2000). Good and Wake (1993) state that our general goal is to discern genetically cohesive units that are evolutionarily independent and to recognise them taxonomically as species. Our view is that the case of *Podarcis* species discussed here clearly fits this statement.

The wide overlapping of the range of most biometric characters within *P. erhardii*, prevented previous researchers such as Wettstein (1952, 1953, 1957) from deciphering phylogenetic relationships of the taxon based on morphology. Here we show that certain pholidotic characters have geographically consistent intraspecific (hereafter, interspecific) variations (Fig. 4), which are concordant with the phylogenetic relationships inferred by mtDNA (Fig. 1). Pholidotic characters have long been used for taxonomic purposes within reptile taxa, and especially in the lacertids family (Pérez-Mellado & Gosá, 1988; and in many instances in Böhme, 1986). In the case presented, differentiation of certain pholidotic characters is concordant with phylogenesis as inferred from partial mtDNA. Such are the autapomorphic low number of temporal scales for

*P. peloponnesiaca*, the synapomorphic low number of supraciliary granules for *P. cretensis* (sp. nov.), *P. levendis* (sp. nov.) and *P. peloponnesiaca*, or as previously known (Gruber, 1987), low number of gular scales for *P. muralis*.

However, it is not easy to explain the low SCG numbers in *P. peloponnesiaca*, *P. cretensis* (sp. nov.) and *P. levendis* (sp. nov.) from an evolutionary perspective. Do supraciliary granules have an adaptive 'value'? If the answer is positive, why have they remained in equally low numbers in these three taxa, which are found in such different environmental backgrounds? On the other hand, if we suppose that they have no adaptive value, was it entirely by chance that they remained so stable in numbers after 5 My of separate evolutionary history? An answer may be sought by the study of the same trait in similar taxa.

Certain biometric characters examined appear to evolve independently of phylogenesis and seem more influenced by environmental factors. This is in accordance with previous works (Pounds, 1988; Losos, 1990; Carretero & Llorente, 1993; Aerts *et al.*, 2000; Vanhooydonck *et al.*, 2000) where the influence of environmental factors on biometric characters has been demonstrated.

Nevertheless, future studies, overlaying various biometric, ecological or behavioural character states on the proposed phylogeny, may offer powerful inferences about the sequence of changes that probably occurred (Pianka, 2001) and consequently deeper understanding of the history of *Podarcis* in Greece.

## Acknowledgements

We wish to thank J. Moravec and an anonymous referee for observations which greatly improved the original manuscript. We are indebted to G. Mantziou and C. Kassara, for valuable help throughout the preparation of this work and A. Orphanoudakis-Demers for English editing.

## References

- AERTS, P., VAN DAMME, R., VANHOYDONCK, B., ZAAF, A. & HERREL, A. 2000. Lizard locomotion: how morphology meets ecology. *Netherlands Journal of Zoology* **50**, 261–277.
- ARNOLD, E.N. 1973. Relationships of the Palearctic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammotromus* (Reptilia, Lacertidae). *Bulletin of the British Museum of Natural History* **25**, 291–366.
- ARNOLD, E.N. 1989. Towards the phylogeny and biogeography of the Lacertidae. Relationships within an Old-World family of lizards derived from morphology. *Bulletin of the British Museum of Natural History (Zoology)* **55**, 209–257.
- ARNOLD, E.N. 2000. The gender of *Podarcis* and the virtues of stability, a reply to W. Böhme. *Bonner Zoologische Beiträge* **49**, 71–74.
- ARNOLD, E.N. 2002. *A Field Guide to the Reptiles and Amphibians of Britain and Europe*. Collins, London.
- BÖHME, W. 1986. *Handbuch der Reptilien und Amphibien Europas (Band 2/II Echsen (Sauria) III (Lacertidae III. Podarcis)*. Aula-Verlag Wiesbaden, 435 pp.
- CARRETERO, M.A. & LLORENTE, G.A. 1993. Morfometría en una comunidad de lacertidos mediterráneos, y su relación con la ecología. *Historia Animalium* **2**, 77–99.
- CASTILLA, A.M., FERNANDEZ-PEDROSA, V., BACKELJAU, T., GONZALEZ, A., LATORRE, A. & MOYA, A. 1998. Conservation genetics of insular *Podarcis* lizards using partial cytochrome *b* sequences. *Molecular Ecology* **7**, 1407–1411.
- COLE, C.J. 1966. Femoral glands in lizards. A review. *Herpetologica* **22**, 199–206.
- FELSENSTEIN, J. 1981. Evolutionary trees from DNA sequences. A maximum likelihood approach. *Journal of Molecular Evolution* **17**, 368–376.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies. An approach using the bootstrap. *Evolution* **39**, 783–791.
- FU, J. 2000. Toward the phylogeny of the family Lacertidae – Why 4708 base pairs of mtDNA sequences cannot draw the picture. *Biological Journal of the Linnean Society* **71**, 203–217.
- GOOD, D. & WAKE, D. 1993. Systematic studies of the Costa Rican Moss Salamanders, genus *Noiotriton*, with descriptions of three new species. *Herpetological Monographs* **7**, 131–159.
- GRUBER, U. F. 1987. *Podarcis erhardii* (Bedriaga, 1876) – Ägäische Mauereidechse. In: BÖHME, W., Ed., *Handbuch der Reptilien und Amphibien Europas (Band 2/II Echsen (Sauria) III (Lacertidae III. Podarcis)*. Aula-Verlag Wiesbaden, pp. 26–49.
- HARRIS, D.J. 2002. Reassessment of comparative genetic distances in reptiles from the mitochondrial cytochrome *b* gene. *Herpetological Journal* **12**, 85–86.
- HARRIS, D.J. & ARNOLD, E.N. 1999. Relationships of wall lizards, *Podarcis* (Reptilia, Lacertidae) based on mitochondrial DNA sequences. *Copeia* **3**, 749–754.
- HARRIS, D.J., ARNOLD, E.N. & THOMAS, R.H. 1998. Relationships of lacertid lizards (Reptilia; Lacertidae) estimated from mitochondrial DNA sequences and morphology. *Proceedings of the Royal Society, London* **265**, 1939–1948.
- HARRIS, D.J. & SÁ-SOUSA, P. 2001. Species distinction and relationships of the Western Iberian *Podarcis* lizards (Reptilia, Lacertidae) based on morphology and mitochondrial DNA sequences. *Herpetological Journal* **11**, 129–136.
- HARRIS, D.J. & SÁ-SOUSA, P. 2002. Molecular phylogenetics of Iberian wall lizards (*Podarcis*). Is *Podarcis hispanica* a species complex? *Molecular Phylogenetics and Evolution* **23**, 75–81.
- HILLIS, D.M. & HUELSENBECK, J.P. 1992. Signal, noise, and reliability in molecular phylogenetic analysis. *Journal of Heredity* **83**, 189–195.
- HUELSENBECK, J.P. & CRANDALL, K.A. 1997. Phylogeny estimation and hypothesis testing using maximum likelihood. *Annual Review of Ecology and Systematics* **28**, 437–466.
- HUELSENBECK, J.P. & IMENNOV, N.S. 2002. Geographic origin of human mitochondrial DNA. Accommodating phylogenetic uncertainty and model comparison. *Systematic Biology* **51**, 155–165.
- HUELSENBECK, J.P. & RONQUIST, F.P. 2001. MRBAYES. Bayesian inference of phylogenetic trees. *Bioinformatics* **17**, 754–755.
- KALIONTZOPOULOU, A., CARRETERO, M.A. & LLORENTE, G.A. 2007. Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. *Journal of Morphology* **268**, 152–165.
- KUMAR, S., TAMURA, K., JAKOBSEN, I.B. & NEI, M. 2001. MEGA2. Molecular Evolutionary Genetics Analysis software. *Bioinformatics* **17**, 1244–1245.
- LEACHÉ, A.D. & REEDER, T.W. 2002. Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood and Bayesian approaches. *Systematic Biology* **51**, 44–68.
- LOSOS, J.B. 1990. Ecomorphology, performance capability and scaling of West Indian *Anolis* lizards. an evolutionary analysis. *Ecological Monographs* **60**, 369–388.
- MAYER, W. 1986. Protein electrophoretic investigations in *Podarcis erhardii* and *Podarcis peloponnesiaca* (Lacertidae, Sauria). *Biologia Gallo-Hellenica* **12**, 459–462.
- MEULENKAMP, J.E. 1985. Aspects of the Late Cenozoic evolution of the Aegean Region. In: STANLEY, D.J. & WEZEL, F.C., Eds., *Geological Evolution of the Mediterranean Basin*. Springer, New York, pp. 307–321.

- OLIVERIO, M., BOLOGNA, A.M. & MARIOTTINI, P. 2000. Molecular biogeography of the Mediterranean lizards *Podarcis* Wagler, 1830 and *Taira* Gray, 1838 (Reptilia, Lacertidae). *Journal of Biogeography* **27**, 1403–1420.
- PALUMBI, S. 1996. Nucleic Acids II: The Polymerase Chain Reaction. In: HILLIS, D.M., MORITZ, C. & MABLE, B.K., Eds., *Molecular Systematics*. Sinauer, Sunderland, pp. 205–248.
- PÉREZ-MELLADO, V. & GOSÁ, A. 1988. Biometría y folidosis en Lacertidae (Sauria, Reptilia). Algunos aspectos metodológicos. *Revista Española de Herpetología* **3**, 105–119.
- PIANKA, E.R. 2001. The role of phylogenetics in evolutionary ecology. In: LYMBERAKIS, P., VALAKOS, E., PAFILIS, P. & MYLONAS, M., Eds., *Herpetologia Candiana*. SEH, Irakleio, pp. 1–20.
- POSADA, D. & CRANDALL, K.A. 1998. Modeltest. Testing the model of DNA substitution. *Bioinformatics* **14**, 817–818.
- POULAKAKIS, N., LYMBERAKIS, P., ANTONIOU, A., CHALKIA, D., ZOUROS, E., MYLONAS, M. & VALAKOS, E. 2003. Molecular phylogeny and biogeography of the wall-lizard *Podarcis erhardii* (Squamata, Lacertidae). *Molecular Phylogenetics and Evolution* **28**, 38–46.
- POULAKAKIS, N., LYMBERAKIS, P., VALAKOS, E., ZOUROS, E. & MYLONAS, M. 2005. Phylogenetic relationships and biogeography of *Podarcis* species from the Balkan Peninsula, by bayesian and maximum likelihood analyses of mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **37**, 845–857.
- POUNDS, J. A. 1988. Ecomorphology, locomotion, and microhabitat structure patterns in a tropical mainland *Anolis* community. *Ecological Monographs* **58**, 299–320.
- RODRIGUEZ, F., OLIVER, J.F., MARIN, A. & MEDINA, J.R. 1990. The general stochastic model of nucleotide substitutions. *Journal of Theoretical Biology* **142**, 485–501.
- SÁ-SOUSA, P., ALMEIDA, A.P., ROSA, H., VICENTE, L. & CRESPO, E.G. 2000. Genetic and morphological relationships of the Berlenga wall lizard (*Podarcis bocagei berlengensis*, Lacertidae). *Journal of Zoological Systematics and Evolutionary Research* **38**, 95–102.
- SÁ-SOUSA, P. & HARRIS, D.J. 2002. *Podarcis carbonelli* Perez-Mellado, 1981 is a distinct species. *Amphibia-Reptilia* **23**, 459–468.
- SCHÜLE, W. 1993. Mammals, vegetation and the initial human settlement of the Mediterranean islands. A palaeoecological approach. *Journal of Biogeography* **20**, 399–412.
- SWOFFORD, D.L. 2002. PAUP 4.0b10a. *Phylogenetic Analysis using Parsimony (and other Methods)*. Sinauer, Sunderland, MA.
- THOMPSON, J.D., GIBSON, T.J., PLEWNIAC, F., JEANMOUGIN, F. & HIGGINS, D.G. 1997. The ClustalX windows interface flexible strategies for multiple sequence alignment aided by quality analysis tool. *Nucleic Acids Research* **24**, 4876–4882.
- TIEDEMANN, F., HÄUPL, M. & GRILLITSCH, H. 1994. Kataloge der Typen der Herpetologischen Sammlung Teil II. Reptilia. *Katalog der wissenschaftlichen Sammlungen des Naturhistorischen Museum in Wien* **10**, 1–110.
- VALAKOS, E.D., MARAGOU, P. & MYLONAS, M. 1995. Geographical distribution. *Podarcis erhardii*. *Herpetological Review* **26**, 155.
- VANHOYDONCK, B., VAN DAMME, R. & AERTS, P. 2000. Ecomorphological correlates of habitat partitioning in Corsican lacertid lizards. *Functional Ecology* **14**, 358–368.
- WETTSTEIN, O.V. 1952. Dreizehn neue Reptilienrassen von den Ägäischen Inseln. *Anzeiger der Mathematisch-Naturwissenschaftliche Klasse, Österreichische Akademie der Wissenschaften, Wien* **15**, 251–256.
- WETTSTEIN, O.V. 1953. Herpetologia Aegaea. *Sitzungsberichte Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse Wien* **162**, 651–833.
- WETTSTEIN, O.V. 1957. Nachtrag zu meiner Herpetologia Aegaea. *Sitzungsberichte Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse Wien* **166**, 123–164.
- WIENS, J.J. 1999. Polymorphism in systematics and comparative biology. *Annual Review of Ecology and Systematics* **30**, 327–362.
- WIENS, J.J. 2004. What is speciation and how should we study it? *American Naturalist* **163**, 915–923.
- 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.