# Podarcis siculus latastei (Bedriaga, 1879) of the Western Pontine Islands (Italy) raised to the species rank, and a brief taxonomic overview of Podarcis lizards

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**Abstract.** In recent years, great attention has been paid to many *Podarcis* species for which the observed intra-specific variability often revealed species complexes still characterized by an unresolved relationship. When compared to other species, *P. siculus* underwent fewer revisions and the number of species hidden within this taxon may have been, therefore, underestimated. However, recent studies based on genetic and morphological data highlighted a marked differentiation of the populations inhabiting the Western Pontine Archipelago. In the present work we used published genetic data (three mitochondrial and three nuclear gene fragments) from 25 *Podarcis* species to provide a multilocus phylogeny of the genus in order to understand the degree of differentiation of the Western Pontine populations. In addition, we analyzed new morphometric traits (scale counts) of 151 specimens from the main islands of the Pontine Archipelago. The phylogenetic analysis revealed five principal *Podarcis* groups with biogeographic consistency. The genetic distinctiveness of the *Podarcis* populations of the Western Pontine Islands is similar or even more ancient than those observed in numerous other pairs of *Podarcis* sister species. In the light of these evidences we raise the Western Pontine lizards to specific rank; thus they should be referred to as *Podarcis latastei*.

Keywords. Reptilia, Podarcis latastei, Podarcis siculus, insular lizards, Mediterranean.

## INTRODUCTION

The wall lizards belonging to the genus *Podarcis* Wagler, 1830 are among the most speciose vertebrates in Europe, representing one of the most important faunistic elements of the Mediterranean insular biota. Originally, two opposite taxonomic viewpoints ("lumping" and "splitting") were – partly emotionally – discussed in the late 19<sup>th</sup> and early 20<sup>th</sup> centuries. At that time the most prominent representative of the "lumpers" was George A. Boulenger (1859-1937) who joined numerous wall lizards together under the name "*Lacerta muralis*" distinguish-

ing, as some predecessors did, only "varieties" within this species (Boulenger, 1887, 1905, 1913, 1920). His main antagonist, representing the taxonomic "splitter" faction, was Ludwig von Méhely (1862-1953) who considered many of Boulenger's "varieties" to be distinct species (Méhely, 1907, 1909). He wrote: «Like a night-mare, the so-called *muralis* question is burdening the mind of herpetologists» (Méhely, 1907). Despite modern approaches, molecular genetics included, Méhely was closer to the current concept than his more influential contemporary colleague; however, the number of *Podarcis* species is still debated. For example, 21 taxa were recognized as

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valid species by Speybroeck et al. (2010), whereas other authors have suggested 23 (Sindaco et al., 2013; Uetz and Hošek, 2016; but see Psonis et al., 2017). The taxonomic wavering of the genus *Podarcis* is mainly due to the presence of marked intra-specific variability with multiple species complexes characterized by unresolved relationships (Harris and Arnold, 1999; Oliverio et al., 2000; Harris et al., 2005; Lymberakis et al., 2008). Table 1 summarizes this taxonomic/nomenclatural history of the currently recognized *Podarcis* species.

In contrast to the great taxonomic attention paid to numerous Podarcis species, P. siculus has undergone fewer revisions and the number of species hidden within this taxon may have been underestimated. Podarcis siculus (Rafinesque-Schmaltz, 1810) was originally described as Lacerta sicula. However, because of its distribution over a large part of Italy (Sicily, Sardinia and numerous minor islands, islets and rocks) and Dalmatia, several subspecies were described. Some of them were originally assigned to "Lacerta" muralis (more than 90 were listed together with their type localities by Henle and Klaver, 1986). This situation led some authors to hypothesize the presence of a species complex similar to those observed in other *Podarcis* assemblages (Oliverio et al., 1998, 2000; Harris and Sa-Sousa, 2002). More recent studies based on mitochondrial (Podnar et al., 2005) and nuclear (Senczuk et al., 2017) markers have supported the monophyly of P. siculus and revealed surprisingly high genetic divergences between the main constituent evolutionary lineages, most comparable to those observed between many recognized Podarcis species (Harris et al., 2005). In addition, recent studies using molecular markers (mitochondrial and nuclear DNA) and geometric morphometrics have revealed that the populations from the Western Pontine Islands represent an evolutionarily independent unit (Senczuk et al., 2018a, 2018b). The genetic distances of these populations with respect to mainland ones were extraordinary high (p-distances of 7-10% for the mtDNA cytb gene), and the head morphology was clearly distinguishable with respect to the mainland and Sicilian populations (Senczuk et al., 2018a; 2018b).

The Pontine Archipelago is located 40 km off the Tyrrhenian coast and comprises the Western Pontine islands Ponza, Palmarola, Zannone and Gavi, and the Eastern Pontine islands Ventotene and Santo Stefano. From the Pontine Archipelago, the following nominal insular intraspecific taxa have been described: *Lacerta muralis* var. *latastei = Podarcis siculus latastei* (Bedriaga, 1879 a, b) from Ponza; *Lacerta muralis parkeri = Podarcis siculus parkeri* (Mertens, 1926) from Santo Stefano; *Lacerta sicula sancti-stephani = Podarcis siculus sanctistephani* (Mertens, 1926) from Santo Stefano; *Lacerta sicula* 

ventotenensis = Podarcis siculus ventotenensis (Taddei, 1949) from Ventotene; Lacerta sicula pasquinii = Podarcis siculus pasquinii (Lanza, 1952) from Scoglio Cappello near Palmarola; Lacerta sicula patrizii = Podarcis siculus patrizii (Lanza, 1952) from Zannone; Lacerta sicula lanzai = Podarcis siculus lanzai (Mertens, 1967) from Gavi and Lacerta sicula palmarolae = Podarcis siculus palmarolae (Mertens, 1967) from Palmarola (cfr. Lanza and Corti, 1996; Corti et al., 2010).

Podarcis siculus parkeri was synonymized with P. s. sanctistephani (Mertens and Wermuth, 1960; Mertens, 1965), which is believed to have become extinct during the first decades of the last century (1914 at the latest), and replaced by P. s. siculus (Mertens, 1965). Henle and Klaver (1986), reviewing the intraspecific taxa, followed Mertens (1965) in considering P. s. ventotenensis as a synonym of the nominotypical form, and listed P. s. latastei, P. s. lanzai, P. s. pasquinii, P. s. patrizii and P. s. palmarolae as valid subspecies. These five taxa occur in the Western Pontine Islands, which are believed to have been connected to the mainland in the Pleistocene, whereas the Eastern Pontine Islands (Ventotene, Santo Stefano) seem never to have been, being located along the 500 m isobath (Woldstedt, 1958; Mertens, 1965, 1967).

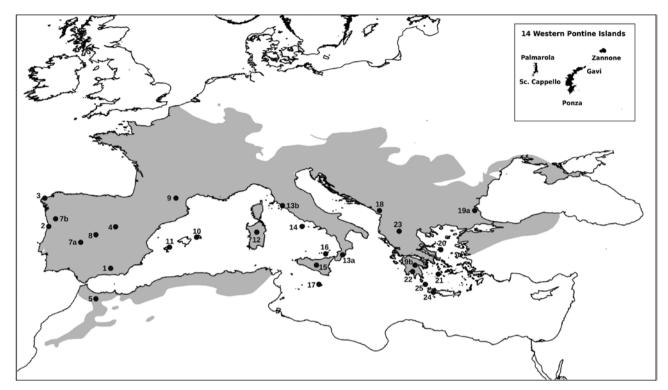
The deep genetic distance recently found between the Eastern and the Western Pontine Islands populations (Senczuk et al., 2018a), geometric morphometrics (Senczuk et al., 2018b), classical morphometric and meristic data, as well as an updated time calibrated multilocus phylogeny of *Podarcis* (Wagler, 1830), all suggest that the Western Pontine lizards deserve their own specific status and should be referred to as *Podarcis latastei* (Bedriaga, 1879), which we characterize and redescribe here.

#### MATERIALS AND METHODS

Molecular phylogenetics

To obtain a robust and time calibrated phylogeny of *Podarcis* as a whole, three mitochondrial (*16s*; *cytb*, and *nd4*) and three nuclear (*mc1r*, *pod15b* and *pod55*) gene fragments from 25 *Podarcis* species, including several subspecies, were retrieved from GenBank (all samples are reported in Fig. 1 and Table 1, localities and accession numbers are reported in Appendix 1, Table A1). Most of the retrieved sequences for each species belong to the same individual, when not possible we selected individuals of close geographic origin. All final consensus alignments were computed for each gene separately using BioEdit 7.2 (Hall, 1999). Coding gene fragments (*cytb*, *nd4* and *mc1r*) were translated into amino acids to assess the lack of stop codons.

For each alignment we used jModelTest v.2.1.3 (Darriba et al., 2012) to assess the best model of nucleotide evolution under the corrected Akaike Information Criterion (AICc). To



**Fig. 1.** Distribution of the genus *Podarcis* and location of the samples used for the phylogenetic analysis, as reported in Table 1. Geographic distribution of *Podarcis latastei* is also reported at the top right.

reconstruct phylogenetic relationships we used a Bayesian coalescent framework implemented in BEAST v.1.8 (Drummond et al., 2012). To calibrate the tree in absolute time we used two vicariant calibration points: the separation between the Peloponnesus (P. peloponnesiacus) and the islands of Crete and Pori (P. cretensis and P. levendis); and the separation between the islands of Menorca and Mallorca (P. lilfordi) and the Pytiusic Islands (P. pytiusensis). Both episodes occurred following the Messinian Salinity Crisis (MSC, at about 5.2 Mya) yielding the sudden separation of these landmasses (Poulakakis et al., 2003; Brown et al., 2008). A normal distribution using the mean in real space option ( $\mu = 5.325$ ; SD = 0.2) has been incorporated for each of the aforementioned nodes. We used a Yule process in a linked tree partition and a lognormal relaxed model maintaining unlinked clock partitions. As substitution models we used GTR+I+G for 16s and cytb; TVM+I+G for nd4 and mc1r; HKY for pod15b and HKY+I for pod55. We performed three independent runs of 10<sup>8</sup> generations sampling every 10<sup>4</sup> steps. Convergence was checked using the software TRACER v 1.5 (Rambaut and Drummond, 2007) and after combining the trees using LogCombiner, the final consensus tree was computed in TreeAnnotator (Drummond et al., 2012).

## Morphology

We used the measurements and scale counts published by Mertens (1967) for diagnosing the subspecific taxa of *P. sicu-*

lus recognized by him and compared them with our own data taken from the holdings deposited in the Florence Museum (MZUF). We measured and counted the scales of 151 specimens (60 females and 91 males) from the main islands of the Pontine Archipelago preserved at the Natural History Museum of the University of Florence (MZUF) (see Table 2). Specimens previously studied by Lanza (1952, 1967) and used for his descriptions of P. s. patrizii and P. s. pasquinii were also included. We analyzed sex, snout-vent length (SVL), and the following meristic characters: a) number of mid-body dorsal scales (DORS); b) number of ventral plates counted longitudinally along the intermediate row (VENT); c) number of gular scales counted along the throat mid-line from the collar to the confluence of maxillaries (GUL); d) number of collar scales (COLL); e), number of femoral pores on the right leg (PORF).

To test for significance of differences between sexes and islands, we used a two-way analysis of variance (ANOVA). An additional two-way ANOVA was performed to test differences between Ventotene Island and Santo Stefano Island sampled in 1954 and 1966, and the Western Pontine and Santo Stefano Island sampled in 1878.

#### RESULTS AND DISCUSSION

The final alignment of 3117 bp included 27 taxa (Supplementary Information). The three independent runs

**Table 1.** Currently accepted *Podarcis* species and their original description name and reference. The geographic localities are shown in Fig. 1.

Loc.	Species (Author and year of description)	Described as	Reference		
1	P. hispanicus (Steindachner, 1870)	Lacerta oxycephala var. hispanica	Geniez et al. 2007		
2	P. carbonelli Pérez-Mellado, 1981	Podarcis bocagei carbonelli	Sá-Sousa and Harris, 2002		
3	P. bocagei (Lopez-Seoane, 1885)	Lacerta murals bocagei	Sá-Sousa et al., 2000		
5	P. liolepis (Boulenger, 1905)	Lacerta muralis var. liolepis Lacerta muralis atrata	Geniez et al., 2014		
6	P. vaucheri (Boulenger, 1905)	P. hispanicus vaucheri	Oliverio et al., 2000		
7a, 7b	P. guadarramae (Boscá, 1916)	Lacerta muralis guadarramae, Podarcis hispanicus "type 1A, 1B"	Geniez et al., 2014		
8	P. virescens (Geniez et al., 2014)	Podarcis hispanicus "type 2"	Geniez et al., 2014		
9	P. muralis (Laurenti, 1768)	Lacerta muralis			
10	P. lilfordi (Günther, 1874)				
11	P. pityusensis (Boscá, 1883)	Lacerta muralis var. pityusensis			
12	P. tiliguerta (Gmelin, 1789)	Lacerta tiliguerta			
13a, 13b	P. siculus (Rafinesque-Schmaltz, 1810)	Lacerta sicula			
14	P. latastei (Bedriaga, 1876)				
15	P. waglerianus (Gistel, 1868)	Podarcis muralis var. wagleriana			
16	P. raffoneae (Mertens, 1952)	Lacerta sicula raffonei	Capula, 1994		
17	P. filfolensis (Bedriaga, 1876)				
18	P. melisellensis (Braun, 1877)				
19a, 19b	P. tauricus (Pallas, 1814)				
20	P. gaigeae (Werner, 1930)	Lacerta taurica gaigeae			
21	P. milensis (Bedriaga, 1882)	Lacerta muralis fusca var. milensis			
22	P. peloponnesiacus (Bibron and Bory, 1833)				
23	P. erhardii (Bedriaga, 1882)	Lacerta muralisfusca var. erhardii			
24	P. cretensis (Wettstein, 1952)	Lacerta erhardii cretensis			
25	P. levendis (Lymberakis et al., 2008)				

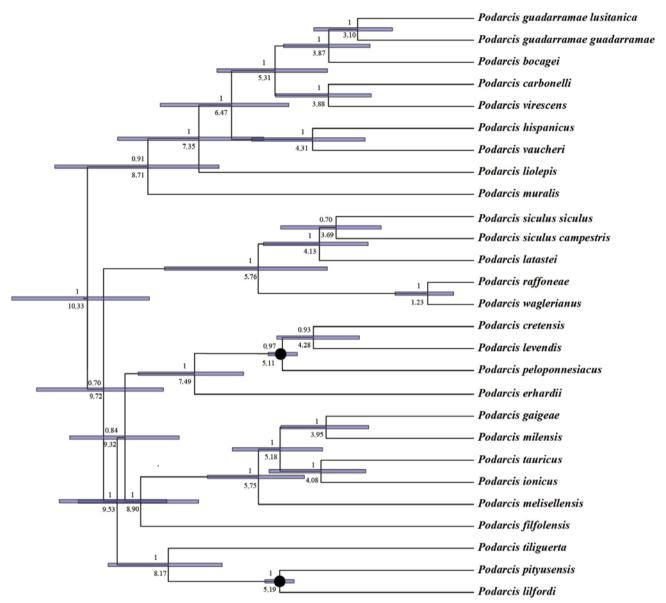
**Table 2.** Population number and relative sample size for both males and females for each island. \*Individuals collected in Santo Stefano Island in 1954/1966.

N°	Island	Females	Males
1	Ponza	18	22
2	Gavi	3	9
3	Palmarola	11	21
4	Zannone	6	6
5	Santo Stefano (1878)	5	5
	Santo Stefano*	5	14
6	Ventotene	8	12
7	Scoglio Cappello	4	2
	Tot.	60	91

showed Effective Sample Size (ESS) for each parameter of more than 200. The phylogenetic tree obtained is shown in Fig. 2. The tree topology is rather well supported (most of the nodes showed posterior probabilities higher than 0.95) and the relationships among species only partly cor-

responds to previous phylogenetic reconstructions. Within the *Podarcis* radiation we found five principal groups with biogeographic consistency (Fig. 1-2).

- 1 The *Podarcis hispanicus* complex currently includes seven species distributed from North Africa to the Iberian Peninsula and south-western France. All species from the *P. hispanicus* complex were first described as intraspecific taxa of the collective species *P. muralis* and later raised to species rank in order to resolve paraphyly (see Table 1) (Oliverio et al., 2000; Sá-Sousa and Harris, 2002; Geniez et al., 2007, 2014). Our phylogenetic analysis support a similar phylogenetic relationships among species as previously reported, and suggested, albeit with moderate support (0.91), *P. muralis* as the sister species of all the Iberian *Podarcis*.
- 2 The "erhardii" group comprises species of the Balkan Peninsula and the Greek islands. Because of a paraphyletic relationship between *P. erhardii* (Bedriaga, 1882) and *P. peloponnesiacus* (Bibron and Bory, 1833), two new insular endemics *P. cretensis* (Wettstein, 1952) and *P. levendis* (Lymberakis et al., 2008) were raised to



**Fig. 2.** Bayesian phylogenetic tree based on multilocus data (*cytb*, 16s, nd4, mc1r, pod15b and pod55) using BEAST v. 1.8. Black filled circles indicate nodes used to calibrate phylogeny (Poulakakis et al.,

2003; Brown et al., 2008). The times of the most recent common ancestor are reported for each node as well as the posterior probability.

the species rank (Poulakakis et al., 2003; 2005a; Lymberakis et al., 2008).

3 – The "tauricus" group includes two species *P. tauricus* (Pallas, 1814) and *P. melisellensis* (Braun, 1877) distributed over a large part of the Balkans and two endemic insular species: *P. gaigae* (Werner, 1930) from Skyros and surrounding islands, and *P. milensis* (Bedriaga, 1882) from Milos and surrounding islands (Poulakakis et al., 2005a, 2005b). However, a recent species delimitation approach (Psonis et al., 2017), suggested the presence of nine species within the *tauricus* group: *P. melisellensis*, *P.* 

gaigeae, *P. milensis*, and six in the *P. tauricus* complex. Based on the absence of support to the monophyly of *P. tauricus*, the authors proposed to raise the subspecies *P. t. ionicus* (Lehrs, 1902) to the species rank (Psonis et al., 2017). Our phylogenetic analysis confirms this scenario indicating an ancient divergence between *P. ionicus* and *P. tauricus* (Fig. 2).

It is interesting to note that although the geographic distribution of *P. filfolensis* (Bedriaga, 1876) would suggest a close relationship with the other two endemic species of the Siculo-Maltese area, *P. waglerianus* (Gistel,

**Table 3.** Scale counts after Mertens (1965) (minimum – mean – maximum) of the insular populations of *P. latastei* (the six left columns) and *P. siculus* (the two right columns). DORS = no. of mid-body dorsal scales; VENT = no. of ventral plates; COLL = no. of collar scales; PORF = no. of femoral pores on the right leg; m. = males; f. = females.

		Ponza	Gavi	Zannone	Palmarola	Sc. Cappello	S. Stefano 1878	S. Stefano 1963	Ventotene
DORS	m	68- <b>70.4</b> -75	71- <b>76.3</b> -81	66- <b>72.8</b> -78	69- <b>76.6</b> -86	72- <b>73.2</b> -76	72- <b>75.8</b> -79	60- <b>65.6</b> -72	61- <b>66.8</b> -78
	f	62- <b>67.7</b> -73	70- <b>73.2</b> -78	63- <b>68.0</b> -74	66- <b>68.7</b> -71	66- <b>68.7</b> -71	71- <b>75.3</b> -79	59- <b>61.2</b> -63	60- <b>60.3</b> -68
VENT	m	25- <b>26.1</b> -27	26- <b>26.3</b> -27	25- <b>26.7</b> -28	24- <b>25.2</b> -26	25- <b>25.7</b> -26	25- <b>26.3</b> -27	24- <b>24.8</b> -26	22- <b>24.6</b> -26
	f	27- <b>28.1</b> -29	27- <b>28.0</b> -30	27- <b>28.4</b> -30	27- <b>28.2</b> -29	28- <b>28.7</b> -30	27- <b>28.1</b> -30	27- <b>28.0</b> -29	25- <b>26.9</b> -29
COLL.	m	9- <b>10.8</b> -12	9- <b>10.0</b> -11	9- <b>10.5</b> -12	9- <b>10.4</b> -13	10- <b>10.5</b> -11	12- <b>12.1</b> -13	8- <b>9.1</b> -11	9- <b>10.6</b> -12
	f	10- <b>10.7</b> -11	9- <b>10.2</b> -11	9- <b>10.5</b> -11	10- <b>10.7</b> -11	11- <b>11.0</b> -11	10- <b>11.0</b> -12	7- <b>8.2</b> -09	8- <b>9.8</b> -11
PORF.	m	22- <b>24.8</b> -29	22- <b>24.3</b> -26	22- <b>25.1</b> -28	21- <b>24.9</b> -29	22- <b>24.7</b> -28	24- <b>25.3</b> -28	19- <b>23.8</b> -26	20- <b>23.5</b> -27
	f	21- <b>23.8</b> -28	22- <b>24.7</b> -26	19- <b>23.0</b> -25	22- <b>24.1</b> -26	23- <b>24.5</b> -26	22- <b>24.8</b> -27	20- <b>21.6</b> -24	20- <b>22.0</b> -23

**Table 4.** Snout-vent length (SVL) and scale counts (minimum – **mean** – maximum) of specimens preserved at the Natural History Museum of the University of Florence (MZUF). DORS = no. of mid-body dorsal scales; VENT = no. of ventral plates; GUL = no. of gular scales; COLL = no. of collar scales; PORF = no. of femoral pores on the right leg; m. = males; f. = females. \*Individuals collected in Santo Stefano Island in 1954/1966.

		Ponza	Gavi	Zannone	Palmarola	Sc. Cappello	S. Stefano 1878	S. Stefano*	Ventotene
SVL	m.	58- <b>68.6</b> -78.8	70.5- <b>73.2</b> -78	70.4- <b>67.1</b> -76.2	58- <b>67</b> -75	62.5- <b>65</b> -67.5	69- <b>76.1</b> -81.5	67- <b>73.5</b> -81.6	60- <b>70.7</b> -77
	f.	50- <b>58.6</b> -68.6	61- <b>63.5</b> -67	52.6- <b>62.7</b> -76.1	57.8- <b>52</b> -63	56.5- <b>57.9</b> -60	55- <b>63.1</b> -69	59- <b>63.5</b> -70	53.5- <b>60.4</b> -66
DORS	m.	67- <b>70.1</b> -76	73- <b>74.3</b> -77	69- <b>70.1</b> -73	68- <b>72.4</b> -76	72	68- <b>71-</b> 74	59- <b>64.1</b> -69	62- <b>66</b> -70
	f.	62- <b>68.2</b> -74	67- <b>72</b> -75	63- <b>67.3</b> -74	63- <b>68-</b> 74	65- <b>67-</b> 69	69- <b>71.8</b> -75	55- <b>58</b> -63	57- <b>61.4</b> -67
VENT	m.	18- <b>19.9</b> -21	22 <b>-23</b> -24	19- <b>21.3</b> 20	18- <b>19.3</b> -21	20- <b>20.</b> 5-21	20- <b>20.3</b> -21	17- <b>18.</b> 9-21	17- <b>19.2</b> -20
	f.	22- <b>22.7</b> -24	18- <b>19.9</b> -23	22- <b>22.2</b> -23	21- <b>22.4</b> -24	24	19- <b>21-</b> 23	20- <b>21.4</b> -23	21- <b>21.6</b> -23
COLL	m.	11- <b>12.7</b> -14	11- <b>12.3</b> -13	10- <b>12.1</b> -13	10- <b>12.4</b> -15	12-13-14	13-14-15	9- <b>12.3</b> -16	10- <b>12.6</b> -15
	f.	11- <b>13</b> -15	11- <b>13</b> -15	10- <b>11.5</b> -13	11- <b>12.8</b> -14	12- <b>12.8</b> -13	12- <b>13.4</b> -15	9- <b>11.2</b> -12	11- <b>12.9</b> -16
GUL	m.	28- <b>32.4</b> 37	31-34 <b>.8</b> -38	31- <b>33.7</b> -40	27- <b>33</b> 39	31	34- <b>34.3</b> -35	23- <b>26.8</b> -32	27- <b>30.1</b> -34
	f.	27- <b>31.2</b> 35	32-33.3-35	31-33-36	27 <b>-33</b> 36	23- <b>24</b> -25	33- <b>36.4</b> -40	23- <b>25.4</b> -28	25- <b>27</b> -29
PORF	m.	22-24.5-26	23- <b>24.7</b> -26	23- <b>25</b> -26	21- <b>24.8</b> -28	25- <b>25.5</b> -26	26- <b>26.5</b> -27	21- <b>22.2</b> -24	21- <b>23.7</b> -27
	f.	21- <b>23.9</b> -27	22- <b>24.4</b> -27	21- <b>23.3</b> -27	21- <b>22.8</b> -26	23- <b>24</b> -25	23- <b>27.4</b> -30	20- <b>20.8</b> -21	20- <b>22</b> -25

1868) and *P. raffoneae* (Mertens, 1952), previous molecular analysis has resulted in contrasting phylogenies regarding the position of these three species (Harris et al., 2005; Psonis et al., 2017; Salvi et al., 2017). Our phylogenetic reconstruction supports a tangled evolutionary history indicating *P. filfolensis* as the sister species of the *Podarcis* "tauricus" group (Fig. 2).

4 – Podarcis species from the Western Mediterranean islands include P. tiliguerta (Gmelin, 1789), P. lilfordi (Günther, 1874) and P. pityusensis (Boscá, 1883). Podarcis tiliguerta distributed in Sardinia, Corsica and surrounding islands, has also been argued to be a species complex showing very deep phylogeographic discontinuities (Harris et al., 2005; Rodriguez et al., 2017; Salvi et al., 2017; Senczuk et al., 2019). On the other hand, P. lilfordi and P. pityusensis from the Balearic and Pityusic islands showed closer phylogenetic relationship as a consequence of vicariance following the Messinian Salinity Crisis (Brown et al., 2008). The phylogenetic reconstruction reported here, confirms the close relationship of these endemic Western Mediterranean species.

5 – Podarcis species from the Italian Peninsula, Sicily and surrounding islands forms a monophyletic assemblage that includes *P. siculus*, *P. waglerianus* and *P. raffoneae*. The last of these was raised to the species rank on the basis of allozyme analysis although further studies showed relatively low genetic distances from *P. waglerianus* (3.3% at cytochrome b), far lower than those observed between many other *Podarcis* species (Capula, 1994; Harris et al., 2005). Based on our data, the lineage including *P. waglerianus* and *P. raffoneae* is sister to *Podarcis siculus* and the lizards of the Western Pontine Archipelago. The Western Pontine *Podarcis* are separated from *P. siculus* by approximately 4 Mya based on our results. The genetic distinctiveness of these insular populations is comparable or even greater than several other

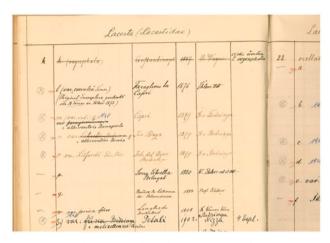
**Table 5.** Analysis of variance (ANOVA) for SVL and meristic characters of the MZUF specimens. Significant *p*-value at 0.05 are marked in bold. Degrees of freedom (d.f.) are also reported. In the last column, ANOVA results using the endemic insular taxon (*P. latastei* + the extinct *P. s. sanctistephani*) and introduced *P. siculus* as factors, are reported. SVL = snout-to-vent length; DORS = no. of mid-body dorsal scales; VENT = no. of ventral plates; GUL = no. of gular scales; COLL = no. of collar scales; PORF = no. of femoral pores. \*Individuals collected in Santo Stefano Island in 1954/1966.

		SEX	Islands	S. Stefano 1878 + W. Pontine/ S. Stefano* + Ventotene
	d.f.	1	7	2
SVL	F	152.96	8.73	4.54
	p	<0.001	< 0.001	<0.05
DORS.	F	40.73	27.15	57.42
	p	<0.001	< 0.001	<0.001
VENT.	F	259.4	9.88	5.4
	p	< 0.001	< 0.001	< 0.01
COLL.	F	1.74	2.9	4.44
	p	0.18	< 0.01	<0.05
GUL.	F	5.71	24.86	62.13
	p	< 0.05	< 0.001	<0.001
PORF.	F	15.41	10.71	57.42
	p	<0.001	<0.001	<0.001

pairs of *Podarcis* sister species (i.e., *P. bocagei/P. guadarramae*, *P. carbonelli/P. virescens*, *P. cretensis/P. levendis*, *P. gaigeae/P. milensis*, *P. tauricus/P. ionicus*).

Our morphological analysis substantially confirms what Bedriaga (1879a) and Mertens (1965) already observed. Indeed, we found significant differences comparing the specimens of the Western Pontine Islands and the Santo Stefano Island collected in 1878, with those collected in Santo Stefano in 1954/1966 and Ventotene Island (Tables 3, 4 and 5; Fig. A1). Furthermore, we also found significant differences when considering sexes and islands as factors (Tables 3, 4 and 5; Fig. A1). Smaller dorsal scales (resulting in higher dorsal scales counts) were already reported by Bedriaga (1879a) to characterize his new taxon latastei. Slight discrepancies between the scale counts taken by Mertens (1967) as compared with ours (Tables 3 and 4) are likely due to a different counting method, which was not precisely defined in Mertens' (1967) paper, e.g., in the number of oblique ventral rows which is dependent on whether only complete or also incomplete rows are counted.

Based on multiple sources of evidence from genetics (herein and Senczuk et al., 2018a), morphology (herein and in Senczuk et al., 2018b) we believe that this insular endemic taxon deserves specific rank and should be referred to as *Podarcis latastei* (Bedriaga, 1879). We propose to adopt as common name "Lataste's lizard" for this



**Fig. 3.** Detail of the entry of a *P. latastei* specimen from Ponza collected by J. v. Bedriaga, in the catalogue of the Göttingen Zoological Museum.

species, following Bedriaga, (1979b).

In accepting the specific status for the lizards of the Western Pontine Islands, under the oldest name available Podarcis latastei (Bedriaga, 1879), type locality Ponza Island, we nevertheless accept the infraspecific subdivisions within the Western Pontine Islands assigned by earlier authors to P. siculus. This means that the former subtaxa of the latter taxon, viz. patrizii, pasquinii, lanzai etc. now become subspecies of P. latastei. The various island populations of *Podarcis latastei* in the Western Pontine Archipelago exhibit variable color patterns. The patterned color morphs often show a tendency for longitudinal stripes to dissolve into oblique bands, thus forming a reticulate pattern with light ocelli included (Fig. 4, 5 and 6). In other individuals, particularly from Gavi Island (Fig. 5a, 5b) there is a strong tendency for a reduction of black-pigmented color pattern elements, corresponding to the "concolor" mutation that also occurs in other Podarcis species. These differences in body dimensions, scalation and color pattern justify, in our opinion, the maintenance of their subspecific names, at least for conservation purposes (Senczuk et al., 2018a).

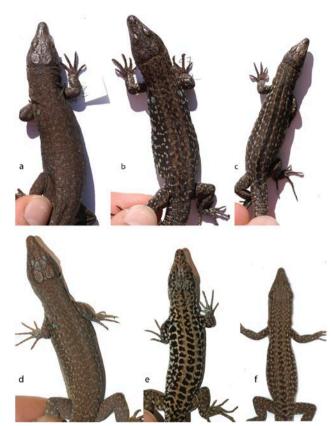
Bedriaga (1879a) based his nomen *latastei* on an unknown number of individuals – "in Anzahl" which means "in a certain quantity" – collected by himself on Ponza Island in Summer 1878, plus one individual from a rock west off Ponza which he called Faraglioni of Ponza. Obviously, he kept all specimens in a cage alive during his travel and brought them via Nice (Nizza), France, from where he sent a part of them to F. Lataste to Paris, to his residential town of Heidelberg, Germany, where he continued to observe them in life, mainly in respect to colour change phenomena (Bedriaga, 1879a). In 1879 and 1902 he sent preserved specimens to some German museums,



**Fig. 4.** Detail of plate IX. (Bedriaga, 1879b) with a specimen (right) of his "*Lacerta muralis* var. *latastei* (= *Podarcis latastei*).

including Frankfurt and Munich as well as the Zoological Museum of the University of Göttingen (whose herpetological holdings have been in Bonn since 1977), and one specimen of his Ponza lizard is still documented in the old Göttingen catalogue, although unfortunately it was lost some time before 1968 (Böhme, 2014, Fig. 3). We failed to retrieve any of these old syntypes in any of the mentioned collections. So, there seems to be no extant type material of this taxon, and the single colour image provided by Bedriaga (1879b), can be regarded as the figure of the individual that could have been chosen as a lectotype if it would be still extant (Fig. 4). A neotype selection, however, seems presently to be unnecessary in this case.

According to the genetic and geometric morphometric data published by Senczuk et al. (2018a, b) and to our data, the wall lizards of the Western Pontine Islands, so far classified as belonging to *Podarcis siculus*, clearly merit their own specific status und should be treated under the oldest



**Fig. 5.** Examples of living representatives of the Pontine Islands populations. Gavi: a, b, c; Ponza: d, e; Palmarola: f.



Fig. 6. Two different color morphs from Zannone Island: a "quasi" concolor individual above and a dark reticulated individual below.

available name for these Western Pontine populations, i.e., *Podarcis latastei* (Bedriaga, 1879). Because of the marked morphological differences between these populations, their former insular subspecific names (Ponza: *latastei*, Gavi: *lanzai*, Zannone: *patrizii*, Palmarola: *palmarolae*, and Scoglio Cappello: *pasquinii*) which were ranked as subspecies of *P. siculus* before, should be maintained but now attached as subspecific names to *Podarcis latastei*. Each of these island populations has its own characteristics and may well turn out to be a distinct conservation unit.

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#### SUPPLEMENTARY MATERIAL

Supplementary material associated with this article can be found at <a href="http://www.unipv.it/webshi/appendix">http://www.unipv.it/webshi/appendix</a> manuscript number 25159.

# REFERENCES

- Bedriaga, J. von (1879a): Herpetologische Studien (Fortsetzung). Arch. f. Naturges. 45: 234-339.
- Bedriaga, J. von (1879b): Mémoire sur les variétés européennes du Lézard des murailles. Bull. Soc. zool. France 4: 194-228.
- Böhme, W. (2014): Herpetology in Bonn. Mertensiella 21: 1-256.
  Boulenger, G.A. (1887): Catalogue of the lizards in the British Museum (Natural History). III. (Lacertidae, Gerrhosauridae, Scincidae, Anelytropsidae, Dibamidae, Chamaeleontidae). Trustees of the British Museum, London.
- Boulenger, G.A. (1905): A contribution to our knowledge of the varieties of the wall lizard (*Lacerta muralis*). Trans. Zool. Soc. London 17: 351-436.
- Boulenger, G.A. (1913): Second contribution to our knowledge of the varieties of the wall lizard (*Lacerta muralis*). Trans. Zool. Soc. London **20**: 135-231.

- Boulenger, G.A. (1920): Monograph of the Lacertidae. Vol. 1. Trustees of the British Museum, London.
- Brown, R.P., Terrasa, B., Pérez-Mellado, V., Castro, J.A., Hoskisson, P.A., Picornell, A., Ramon, M.M. (2008). Bayesian estimation of post-Messinian divergence times in Balearic Island lizards. Mol. Phylogenet. Evol. **48**: 350-358.
- Capula, M. (1994): Genetic variation and differentiation in the lizard, *Podarcis wagleriana* (Reptilia: Lacertidae). Biol. J. Linn. Soc. **52**: 177-196.
- Corti C., Biaggini M., Capula M. (2010): *Podarcis siculus* (Rafinesque-Schmaltz, 1810). In: Fauna d'Italia. Reptilia, pp. 407-417. Corti C., Capula M., Luiselli L., Razzetti E., Sindaco R., Eds, Edizioni Calderini, Bologna, Italy.
- Darriba, D., Taboada, G.L., Doallo, R., Posada, D. (2012): jModelTest 2: more models, new heuristics and parallel computing. Nat. Methods **9:** 772-772.
- Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A. (2012): Bayesian phylogenetics with BEAUti and the BEAST 1.7. Molecular Biology and Evolution **29**: 1969-1973.
- Geniez, P., Cluchier, A., Sa-Sousa, P., Guillaume, C.P., Crochet, P.A. (2007): Systematics of the *Podarcis hispanicus* complex (Sauria, Lacertidae) I: Redefinition, morphology and distribution of the nominotypical taxon. Herpetol. J. 17: 69-80.
- Geniez, P., Sa-Sousa, P., Guillaume, C.P., Cluchier, A., Crochet, P.A. (2014): Systematics of the *Podarcis hispanicus* complex (Sauria, Lacertidae) III: valid nomina of the western and central Iberian forms. Zootaxa 3794: 1-51.
- Hall, T.A. (1999): BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp. Ser. 41: 95-98.
- Harris, D.J., Arnold, E.N. (1999): Relationships of Wall Lizards, *Podarcis* (Reptilia: Lacertidae) based on mithocondrial DNA sequences. Copeia **1999**: 749-754.
- Harris, D.J., Pinho, C., Carretero, M.A., Corti, C., Böhme, W. (2005): Determination of genetic diversity within the insular lizard *Podarcis tiliguerta*, using mtDNA sequence data, with a reassessment of the phylogeny of *Podarcis*. Amphibia-Reptilia 26: 401-407.
- Harris, D.J., Sà-Sousa (2002): Molecular phylogenetics of Iberian wall lizards (*Podarcis*): is *Podarcis hispanica* a species complex? Mol. Phylogenet. Evol. **23**: 75-81.
- Henle, K., Klaver, C.J.J. (1986): *Podarcissicula* Rafinesque-Schmaltz, 1810 Ruineneidechse. In: Handbuch der Reptilien und Amphibien Europas, vol. 2/II (Echsen III, *Podarcis*), pp. 254-342. Böhme, W., Ed., AULA Verlag, Wiesbaden, Germany.
- Lanza, B. (1952): Note critiche su alcune lucertole italiane e diagnosi preliminare di una nuova razza insulare. Riv. Sci. Nat., Natura 43: 69-82.

Lanza, B. (1967): Su due nuove razze insulari di *Lacerta sicula* e di *Lacerta tiliguerta*. Arch. Zool. Ital. **51**: 511-522.

- Lanza, B., Corti, C. (1996). Evolution of the knowledge on the Italian herpetofauna during the 20th century. Boll. Mus. civ. St. Nat. Verona **20**: 373-436.
- Lymberakis, P., Poulakakis, N., Kaliontzopoulou, A., Valakos, E., Mylonas, M. (2008): Two new species of *Podarcis* (Squamata; Lacertidae) from Greece. Syst. Biodiv. **6**: 307-318.
- Méhely, L. v. (1907): Zur Lösung der "*Muralis*-Frage". Vorläufige Mitteilung. Ann. Mus. Natl. Hungar. 5: 84-88.
- Méhely, L. v. (1909): Materialien zu einer Systematik und Phylogenie der *muralis*-ähnlichen Lacerten. Ann. hist.-nat. Mus. Natl. Hungar. 7: 409-621.
- Mertens, R. (1926): Zwei neue Inselrassen der Gattung *Lacerta*. Zool. Anz. **68**: 319-322.
- Mertens, R. (1965): Das Rätsel der Eidechsen von Santo Stefano. Zool. Jahrb., Abt, Syst. **92**: 91-102.
- Mertens, R. (1967): Unterlagen zu einer "Herpetologia tyrrhenica" VIII. Die Reptilien der Pontinischen Inseln. Senckenberg. biol. 44: 125-144.
- Mertens, R., Wermuth, H. (1960): Die Amphibien und Reptilien Europas (Dritte Liste nach dem Stand von vom 1. Januar 1960). Kramer, Frankfurt am Main.
- Oliverio, M., Bologna, M.A., Mariottini, P. (2000): Molecular biogeography of the Mediterranean lizards *Podarcis* Wagler, 1830 and *Teira* Gray, 1838 (Reptilia, Lacertidae). J. Biogeogr. **27**: 1403-1420.
- Podnar, M., Mayer, W., Tvrtković, N. (2005): Phylogeography of the Italian wall lizard, *Podarcis sicula*, as revealed by mitochondrial DNA sequences. Mol. Ecol. **14**: 575-588.
- Poulakakis, N., Lymberakis, P., Antoniou, A., Chalkia, D., Zouros, E., Mylonas, M., Valakos E. (2003): Molecular phylogeny and biogeography of the wall-lizard *Podar*cis erhardii (Squamata: Lacertidae). Mol. Phylogenet. Evol. 28: 38-46.
- Poulakakis, N., Lymberakis, P., Valakos, E., Pafilis, P., Zouros, E., Mylonas, M. (2005): Phylogeography of Balkan wall lizard (*Podarcis taurica*) and its relatives inferred from mitochondrial DNA sequences. Mol. Ecol. **14**: 2433-2443.
- Poulakakis, N., Lymberakis, P., Valakos, E., Zouros, E., Mylonas, M. (2005b): Phylogenetic relationships and biogeography of *Podarcis* species from the Balkan Peninsula, by Bayesian and maximum likelihood analyses of mitochondrial DNA sequences. Mol. Phylogenet. Evol. 37: 845-857.
- Psonis, N., Antoniou, A., Kukushkin, O., Jablonski, D., Petrov, B., Crnobrnja-Isailović, J., Poulakakis, N. (2017): Hidden diversity in the *Podarcis tauricus* (Sauria, Lacertidae) species subgroup in the light of multi-

- locus phylogeny and species delimitation. Mol. Phylogenet. Evol. **106**: 6-17.
- Rambaut, A., Suchard, M., Xie, D., Drummond, A. (2014): Tracer v1. 6. http://beast.bio.ed.ac.uk/Tracer/ [accessed on 29 May 2015]
- Rodríguez, V., Buades, J.M., Brown, R.P., Terrasa, B., Pérez-Mellado, V., Corti, C., Delaugerre, M., Castro, J. A., Picornell, A., Ramon, C. (2017): Evolutionary history of *Podarcis tiliguerta* on Corsica and Sardinia. BMC Evol. Biol., **17**: 27.
- Salvi, D., Pinho, C., Harris, D.J. (2017): Hotspot of genetic diversity: decoupled mito-nuclear histories in the evolution of the Corsican-Sardinian endemic lizard *Podarcis tiliguerta*. BMC Evol. Biol. **17**: 63.
- Sà-Sousa, P., Harris, D.J. (2002): Podarcis carbonelli Pérez-Mellado, 1981 is a distinct species. Amphibia-Reptilia 23: 459-468.
- Senczuk, G., Colangelo, P., De Simone, E., Aloise, G., Castiglia, R. (2017): A combination of long term fragmentation and glacial persistence drove the evolutionary history of the Italian wall lizard *Podarcis siculus*. BMC Evol. Biol. 17: 6.
- Senczuk, G., Havenstein, K., Milana, V., Ripa, C., De Simone, E., Tiedemann, R., Castiglia, R. (2018a): Spotlight on islands: on the origin and diversification of an ancient lineage of the Italian wall lizard *Podarcis siculus* in the western Pontine Islands. Sci. Rept. 8: 15111.
- Senczuk, G., Colangelo, P., Avramo, V., Castiglia, R. Böhme, W., Corti, C. (2018b): A study in scarlet: incipient speciation, phenotypic differentiation and conservation implications of the *Podarcis* lizards of the western Pontine Islands, Italy. Biol. J. Linn. Soc. 125: 50-60.
- Senczuk, G., Castiglia, R., Colangelo, P., Delaugerre, M., Corti, C. (2019): The role of island physiography in maintaining genetic diversity in the endemic Tyrrhenian wall lizard (*Podarcis tiliguerta*). J. Zool. 309: 140-151.
- Sindaco, R, Venchi, A, Grieco, C. (2013): The reptiles of the western Palearctic, Volume 2 Annotated checklist and distributional atlas of the snakes of Europe, North Africa, Middle East and Central Asia, with an update to Volume 1. Edizioni Belvedere, Latina, Italy.
- Speybrock, J., Beukema, W., Crochet, P.-A. (2010): A tentative species list of the European herpetofauna (Amphibia and Reptilia) an update. Zootaxa **2492**: 1-27.
- Taddei, A. (1949): Le Lacerte (*Archaeolacerta e Podar-cis*) dell'Italia peninsulare e delle isole. Coment. Pont. Acad. Sci. Vaticano **13**: 197-174.
- Woldstedt, P. (1958): Das Eiszeitalter. Grundlinien einer Geologie des Quartärs, II. Europa, Vorderasien und Nordafrika im Eiszeitalter, 2nd Edition. Enke, Stuttgart, Germany.