
First record of bluish *Podarcis muralis* (LAURENTI, 1768)

Lizard coloration depends on the combined action of three classes of pigment or light-reflecting cells (i.e., chromatophores) located in the dermal layer of the skin. The xanthophores are the most superficial and contain pigments (i.e., pteridines and/or carotenoids) that absorb short-wavelength light and reflect long wavelengths. Iridophores contain intracellular guanine platelets that scatter the incident light. Melanophores occupy a basal position in the dermis and contain eumelanin that absorbs all light transmitted by the xanthophores and the iridophores (COOPER & GREENBERG 2002; GRETHER et al. 2004). Variation in the abundance and in the spatial arrangement of these cell types can produce the great array of skin colors found in lizards (e.g., SAENKO et al. 2013).

Blue coloration has long attracted the attention of researchers and herpetoculturists due, among other reasons, to the fact that blue pigments are almost absent in nature (BAGNARA 2007; UMBERS 2013; but see GODA & FUJI 1995). In vertebrates, blue is generally thought to be a structural color that results from selective light scattering by nanoscale elements that differ in refractive index (BAGNARA 2007). In particular, short-wavelength colors (blue and ultraviolet-blue) in lizards are structural colors produced by light scattering in the iridophores, although these colors also depend on interactions with xanthophores and the underlying layer of melanophores (MENTER et al. 1979; KURIYAMA et al. 2006; BAGNARA et al. 2007). In *Anolis carolinensis* VOIGT, 1832, the isolated iridophores appear blue-green under reflected light, and the color intensifies if a layer of melanophores is added under the iridophores (presumably due to absorption of longer wavelengths, ROHRLICH & PORTER 1972; ROHRLICH 1974). The addition of xanthophores containing yellow pigments results in the normal brown-green skin color of the species. These results suggest that blue colors are produced when xanthophores contain few or no pigments (allowing almost all wavelengths of the incident light to interact directly with the iridophores). Consequently, the term axan-

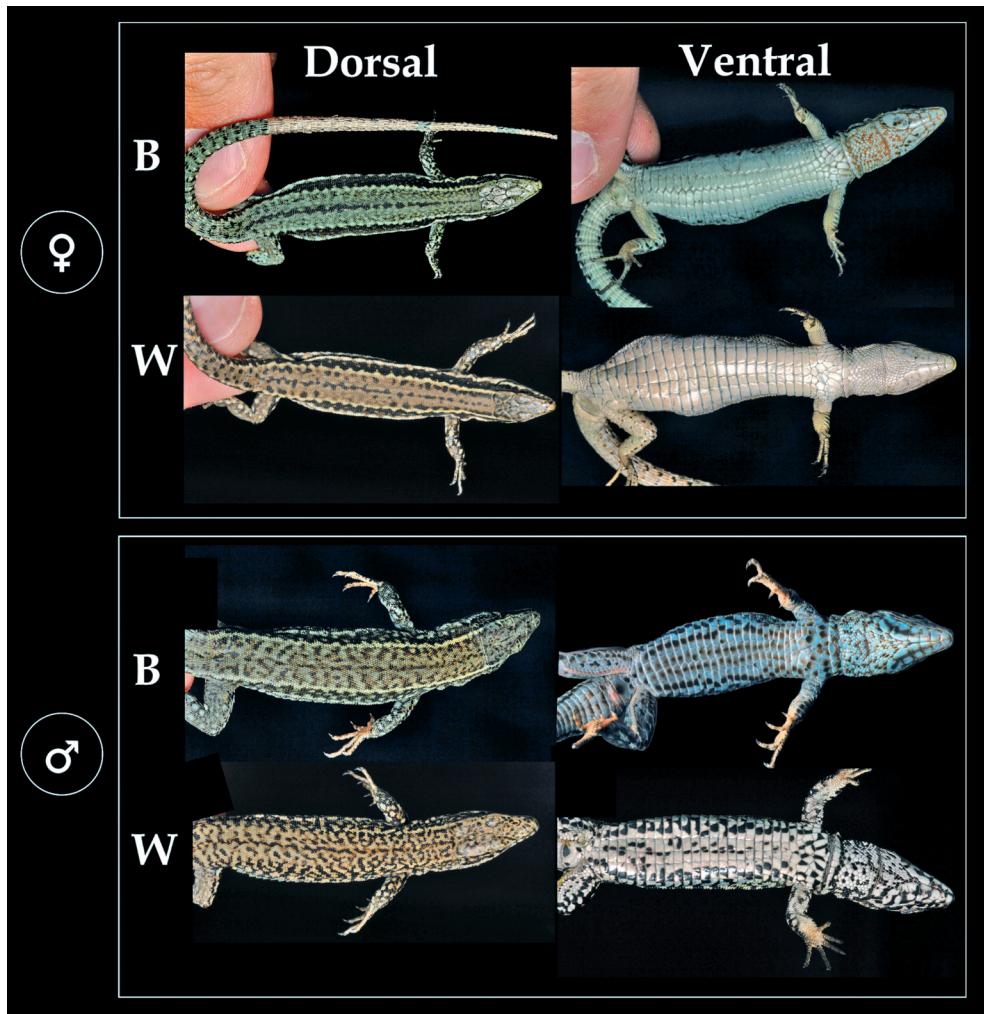


Fig. 1: Dorsal and ventral views of the bluish (B) *Podarcis muralis* (LAURENTI, 1768), and of same-sex and same location individuals showing white (W) ventral background coloration for comparison.
 Above – bluish female from Porta (Languedoc-Roussillon, Département Pyrénées Orientales, France; 42°31'38"N, 1°49'36"E); note orange scales on the throat.
 Below – bluish male from Latour de Carol (Languedoc-Roussillon, Département Pyrénées Orientales, France; 42°27'57"N, 1°53'23"E).

thism (i.e., lacking yellow pigment) is used to designate individuals exhibiting abnormal bluish coloration (BAGNARA et al. 1978, 2007). Although the mechanisms of color production are often unclear, blue coloration in lacertids is generally attributed to lack of pigments in the xanthophores (e.g., *Ibero-*

lacerta martinezricai (ARRIBAS, 1996), ARRIBAS et al. 2008). Alternatively, it has been suggested that the blue coloration of some insular populations of *Podarcis siculus* (RAFINESQUE-SCHMALTZ, 1810), may be caused by an increase in the concentration of dermal melanin and is therefore consid-



Fig. 2: A – Bluish male *Podarcis muralis* (LAURENTI, 1768), perched in its place of capture.
B – Close-up of the head.

ered a type of melanism (RAIA et al. 2010; NOVOSOLOV et al. 2013; see also QUINN & HEWS 2003).

In June 2015, during fieldwork in the eastern Pyrenees (France; for locality details see caption of Fig. 1), the authors found two individuals of *Podarcis muralis* (LAURENTI, 1768) with an unusual blue coloration in two localities ca. nine km apart. One was an adult female (snout-vent length, SVL: 59 mm, body mass: 4.3 g) with a light blue coloration over all her body (especially in the ventral surface), and some orange scales in the throat (Fig. 1). The other was an adult male (SVL: 61 mm, body mass: 5.5 g) showing a darker, more saturated blue coloration than the female, also affecting the entire body surface (Fig. 1). Only these two

individuals from a total of 1,118 lizards captured during this field season presented this abnormal blue coloration (< 0.18 %) and none were observed during previous field campaigns (2005–2014). Both animals were found basking on stone walls (Fig. 2). The animals were captured by noosing, put inside individual cloth bags, and transferred to a dark room for spectrometric measurements. Reflectance spectra were obtained with a portable USB-2000 spectrometer and a PX-2 Xenon strobe light (Ocean Optics Inc., Dunedin, Fl. U.S.A.) using standard spectrophotometric techniques (FONT et al. 2009; PÉREZ I DE LANUZA & FONT 2011). Measurements extended over the 300–700 nm range, which encompasses the entire visual spectrum of lacertids (PÉREZ I DE LANUZA & FONT 2014; MARTIN et al. 2015). To further characterize the unusual coloration, the reflectance spectra of the bluish lizards were compared to the mean reflectance curve of a sample of males ($N = 14$) and females ($N = 13$) with normal coloration captured at the same localities (Fig. 3). For this comparison the authors used animals having exclusively white ventral coloration as this phenotype is the most common in this area. Both lizards were released at their capture sites after measurements. The male was again sighted in May 2016, at the same location where it was originally captured.

Reflectance spectra (Fig. 3) underscore the singularity of the blue coloration exhibited by the individuals reported in this study. Spectra from the throat and belly of normal-colored white individuals rise steeply toward long wavelengths, peaking at ~660 nm. In contrast, these spectra are rather flat in the blue male and female, and peak at lower wavelengths (ca. 420 nm in the male, ca. 590 nm in the female). Spectra of the two blue individuals differ both in hue (i.e., spectral peak location) and brightness, the female having a less chromatically pure blue than the male. Blue coloration in normal-colored *P. muralis*, as in other lacertids, is restricted to the outer ventral scales (PÉREZ I DE LANUZA et al. 2013). Some of these scales, particularly in males, display conspicuous blue patches which, upon spectrophotometric examination, have their reflectance peak in the ultraviolet (UV) range (ca. 370 nm). These UV-blue patches

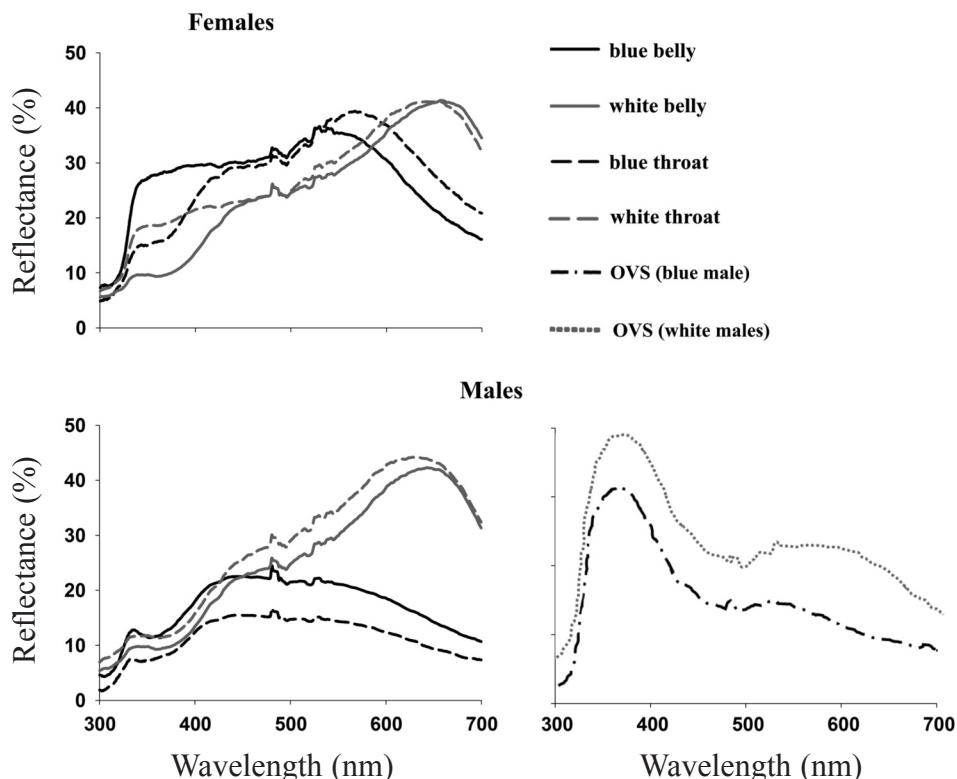


Fig. 3: Reflectance spectra for the bluish male and female *Podarcis muralis* (LAURENTI, 1768), reported in this study. Mean reflectance spectra of normal-colored individuals (14 males and 13 females) from the same localities are included to illustrate the difference. OVS – outer ventral scales.

are the focus of recent work because they seem to function as honest signals of individual male quality used in intraspecific communication (PÉREZ I DE LANUZA et al. 2014). Interestingly, the reflectance spectra of the UV-blue patches of the blue male lizard reported here is very similar to those of normal-colored lizards (Fig. 3).

Blue body coloration is described in continental lacertids, e.g., *Dalmatolacerta oxycephala* (SCHLEGEL, 1839), *Omanosaura cyanura* (ARNOLD, 1972), and *Scelarcis perspicillata* (DUMÉRIL & BIBRON, 1839), and in the insular *Podarcis* species *P. lilfordi* (GÜNTHER, 1874) and *P. pityusensis* (BOSCÁ, 1883) in the Balearic Islands, *P. milensis* (BEDRIAGA, 1882) in some Aegean Islands,

P. tiliguerta (GMELIN, 1789), in the Molarotto islet, and *P. siculus* from the Faraglioni islets near Capri – RAIA et al. 2010; PÉREZ I DE LANUZA et al. 2011) but, to our knowledge, this is the first record of a blue phenotype in any continental population of *Podarcis*. However, individuals showing abnormal blue ventral coloration are known in some continental populations of *Anguis fragilis* LINNAEUS, 1758 (FILÍPEK 2005), *Anguis colchica* (NORDMANN, 1840) (JABLONSKY & MEDUNA 2010; KACZMAREK et al. 2016), *Lacerta agilis* LINNAEUS, 1758 (STRIJBOSCH 1994), *Iberolacerta martinezraca* (ARRIBAS et al. 2008) and *Iberolacerta monticola* (BOULENGER, 1905) (ARRIBAS et al. 1996; GALÁN 2006, 2010).

The occurrence of sporadic blue specimens in mainland populations of a lacertid species suggests the transition to blueish phenotypes could be produced by a rather simple mutation (FROST & MALACINSKI 1979; BUKOWSKI et al. 1990). This mutation would reduce the concentration of short wavelength-absorbing pigments in the xanthophores or cause dermal melanisation, making the lizards appear blue. In continental populations natural selection may eliminate blue mutants, but in insular populations the selective regime may be different (FULGIONE et al. 2008; see also MACEDONIA et al. 2009), which could help the mutation to become fixed. This may explain why blue individuals are hardly found on the continent but are relatively frequent in islands.

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REFERENCES: ARRIBAS, O. J. (1996): Taxonomic revision of the Iberian "Archaeolacertae" I: A new interpretation of the geographical variation of "*Lacerta*" *monticola* BOULENGER, 1905, and "*Lacerta*" *cyreni* MÜLLER & HELLMICH, 1937.- Herpetozoa, Wien; 9: 31-56. ARRIBAS, O. & CARBONERO, J. & LIZANA, M. (2008): Sobre el dicromatismo ventral verde/azul en la lagartija batueca, *Iberolacerta martinezricai* (ARRIBAS, 1996).- Boletín de la Asociación Herpetológica Española, Madrid; 19: 51-54. BAGNARA, J. T. & FERNANDEZ, P. J. & FUJII, R. (2007): On the blue coloration of vertebrates.- Pigment Cell Research, Oxford; 20: 14-26. BAGNARA, J. T. & FROST, S. K. & MATSUMOTO, J. (1978): On the development of pigment patterns in amphibians.- American Zoologist, Lawrence; 18: 301-312. BUKOWSKI, L. & ERICKSON, K. & LYERLA, T. A. (1990): Characterization of the yellow pigment in the axanthic mutant of the Mexican axolotl, *Ambystoma mexicanum*.- Pigment Cell Research, Oxford; 3: 123-125. COOPER Jr., W. E. & GREENBERG, N. (1992): Reptilian coloration and behavior; pp. 298-422. In: GANS, C. & CREWS, D. (Eds.): Biology of the reptilia. Volume 18. Physiology E : Hormones, brain and behavior. Chicago, London (University of Chicago Press). FILÍPEK, M. (2005): Neobvykly sfarbený slepúch lámavý.- Živa, Praha; 1: 36. [Unusually coloured Slow Worm - in Czech]. FONT, E. & PÉREZ I DE LANUZA, G. & SAMPEDRO, C. (2009): Ultraviolet reflectance and cryptic sexual dichromatism in the ocellated lizard, *Lacerta (Timon) lepida* (Squamata: Lacertidae).- Biological Journal of the Linnean Society, Oxford; 97: 766-780. FROST, S. K. & MALACINSKI, G. M. (1979): The developmental genetics of pigment mutants in the Mexican axolotl.- Developmental Genetics, New York; 1: 271-294. FULGIONE, D. & GUGLIELMI, S. & ODIERRA, G. & RIPPA, D. & CALIENDO, M. F. & RASTOGI, R. K. (2008): Morphological differentiation and genetic structure in island lizard populations.- Zoological Science, Tokyo, Kawaguchi; 25: 465-474. GALÁN, P. (2006): Coloración azul atípica en machos de *Iberolacerta monticola* del extremo norte de Galicia.- Boletín de la Asociación Herpetológica Española, Madrid; 17: 96-99. GALÁN, P. (2010): Dicromatismo ventral verde-azul en una población de *Iberolacerta monticola*.- Boletín de la Asociación Herpetológica Española, Madrid; 21: 49-52. GODA, M. & FUJII, R. (1995): Blue chromatophores in two species of callionymid fish.- Zoological Science, Tokyo, Kawaguchi; 12: 811-813. GREATHER, G. F. & KOLLURU, G. R. & NERSISSIAN, K. (2004): Individual colour patches as multicomponent signals.- Biological Reviews, Oxford; 79: 583-610. JABLONSKI, D. & MEDINA, P. (2010): Blue colour of the ventral body part of Eastern Slow Worm *Anguis colchica* (NORDMANN, 1840).- Herpetology Notes, Braunschweig; 3: 295-296. KACZMAREK, P., SKAWIŃSKI, T., & SKORZEWSKI, G. (2016): Blue venter in the slow worm (*Anguis fragilis*): review and new data.- Herpetological Review, New York; 47: 375-377. KURIYAMA, T. & MIYAJI, K. & SUGIMOTO, M. & HASEGAWA, M. (2006): Ultrastructure of the dermal chromatophores in a lizard (Scincidae: *Plestiodon latiscutatus*) with conspicuous body and tail coloration.- Zoological Science, Tokyo, Kawaguchi; 23: 793-799. MACEDONIA, J. M. & LAPPIN, A. K. & LOEW, E. R. & MCGUIRE, J. A. & HAMILTON, P. S. & PLASMAN, M. & BRANDT, Y. & LEMOS-ESPINAL, J. A. & KEMP, D. J. (2009): Conspicuousness of Dickerson's collared lizard (*Crotaphytus dickersonae*) through the eyes of conspecifics and predators.- Biological Journal of the Linnean Society, Oxford; 97: 749-765. MARTIN, M. & LE GALLIARD, J. F. & MEYLAN, S. & LOEW, E. R. (2015): The importance of ultraviolet and near-infrared sensitivity for visual discrimination in two species of lacertid lizards.- Journal of Experimental Biology, Cambridge; 218: 458-465. MENTER, D. G. & OBILKA, M. & TCHEH, T. T. & TAYLOR, J. D. (1979): Leucophores and iridophores of *Fundulus heteroclitus*: biophysical and ultrastructural properties.- Journal of Morphology, Hoboken; 160: 103-119. NOVOSOLOV, M. & RAIA, P. & MEIRI, S. (2013): The island syndrome in lizards.- Global Ecology and Biogeography, Oxford; 22: 184-191. PÉREZ I DE LANUZA, G. & FONT, E. (2011): Lizard blues: Blue body colouration and ultraviolet polychromatism in lacertids.- Revista Española de Herpetología, Madrid; 24: 67-84. PÉREZ I DE LANUZA, G. & CARAZO, P. & FONT, E. (2014): Colours of quality: structural (but not pigment) coloration informs about male quality in a polychromatic lizard.- Animal Behaviour, Amsterdam, Oxford; 90: 73-81. PÉREZ I DE LANUZA, G. & FONT, E. (2014): Ultraviolet vision in lacertid lizards: evidence from retinal structure, eye transmittance, SWS1 visual pigment genes and behaviour.- Journal of Experimental Biology, Cambridge; 217: 2899-2909. PÉREZ I DE LANUZA, G. & FONT, E. & MONTERDE, J. L. (2013): Using visual modelling to study the evolution of lizard coloration: sexual selection drives the evolution of sexual dichromatism in lacertids.- Journal of Evolutionary Biology, Oxford; 26:

1826-1835. QUINN, V. S. & HEWS, D. K. (2003): Positive relationship between abdominal coloration and dermal melanin density in phrynosomatid lizards.- Copeia, Washington; 2003: 858-864. RAIA, P. & GUARINO, F. M. & TURANO, M. & POLESE, G. & RIPPA, D. & CAROTENUTO, F. & MONTI, D. M. & CARDI, M. & FULGIONE, D. (2010): The blue lizard spandrel and the island syndrome.- BMC Evolutionary Biology, London : BioMed Central, Berlin, Heidelberg; 10: 289. ROHRLICH, S. T. (1974): Fine structural demonstration of ordered arrays of cytoplasmic filaments in vertebrate iridophores. A comparative survey.- Journal of Cell Biology, New York; 62: 295-304. ROHRLICH, S. T. & PORTER K. R. (1972): Fine structural observations relating to the production of color by the iridophores of a lizard, *Anolis carolinensis*.- Journal of Cell Biology, New York; 53: 38-52. SAENKO, S. V. & TEYSSIER, J. & VAN DER MAREL, D. & MILINKOVITCH, M. C. (2013): Precise colocalization of interacting structural and pigmentary elements generates extensive color pattern variation in *Phelsuma* lizards.- BMC Evolutionary Biology, London : BioMed Central, Berlin, Heidelberg; 11: 105. STRIJbosch, H. (1994): Een blauwe Zandhagedis (*Lacerta agilis*).- Lacerta, 's-Gravenhage; 52 (6): 147-148. UMBERS, K. D. (2013): On the perception, production and function of blue colouration in animals.-Journal of Zoology, London; 289: 229-242.

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