

The Black Aesculapian Snake *Zamenis longissimus* (Serpentes: Colubridae): characters and possible origin of the *subgrisea* morphotype

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Abstract

The Black Aesculapian Snake, *Zamenis longissimus* (Serpentes: Colubridae): characters and possible origin of the *subgrisea* morphotype. New data acquired on the biology of the Aesculapian snake *Zamenis longissimus* shed light on a widespread specific morphotype in this species: the *subgrisea* form. Through captive breeding of groups of individuals for several generations, it was established that this morphotype is caused by a recessive mutation. The presence and combination of several traits indicate that this form is not from a single genetic mutation, such as melanoticism or axanthism but from a morphotype more complex than previously considered. The expression of this form in several specimens from different European and Middle Eastern countries suggests that the origin of the morphotype is common and ancient, not random. From genetic analyses, fossil records, and the recent observations of wild individuals, it is probable that this form originated in the Balkan peninsula, where it is more common, and spread to central Europe during the species expansion and recolonization in the late Pleistocene after the last glaciation. *Zamenis longissimus* could therefore be considered a polymorphic species.

Keywords: Balkans, Phenotype, Polymorphism, Recessive gene, Snakes.

A serpente-negra-de-esculápio, *Zamenis longissimus* (Serpentes: Colubridae): caracteres e possível origem do morfotipo *subgrisea*. Novos dados adquiridos sobre a biologia de *Zamenis longissimus* lançam luz sobre um morfotipo específico amplamente difundido nessa espécie: a forma *subgrisea*. Por meio da criação em cativeiro de grupos de indivíduos durante várias gerações, foi estabelecido que esse morfotipo é causado por uma mutação recessiva. A presença e a combinação de vários caracteres indicam que essa forma não provém de uma única mutação genética, como o melanismo ou o axantismo, mas sim de um morfotipo mais complexo do que considerado anteriormente. A expressão dessa forma em vários exemplares de diferentes países da Europa e do Oriente Médio sugere que a origem do morfotipo é comum e antiga, não aleatória. A partir de análises genéticas, registros fósseis e observações recentes de indivíduos selvagens, é provável que essa forma tenha-se originado na península dos Balcãs, onde é mais comum, e se espalhado para a Europa Central durante a expansão e a recolonização da espécie no final do Pleistoceno, após a última glaciação. *Zamenis longissimus* poderia, portanto, ser considerada uma espécie polimórfica.

Palavras-chave: Balcãs, Fenótipo, Gene recessivo, Polimorfismo, Serpentes.

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Introduction

Melanism and melanoticism are conditions in which an individual is characterized by an excess of melanin compared to the normal phenotype of intraspecific individuals (Majerus 1998). This form represents the most common and highly variable mutation among ophidians and can express itself in multiple forms, affecting an individual partially or totally or being congenital or ontogenetic; multiple melanotic forms can be present within the same species (Senczuk *et al.* 2021, Fănar *et al.* 2022, Jablonski *et al.* 2023, Storniolo *et al.* 2023, Meier *et al.* 2024). In snakes, mutations such as melanoticism, melanism, amelanism, leucism, xanthism/axanthism, and erythrism/anerythrism can randomly occur in any individual of any species in any location (Schulz 1996, Bruni 2017, Meier *et al.* 2021, Jablonski *et al.* 2022), leading to the possibility that characters may become fixed within some populations (Tokunaga and Ono 1991, Andrén 2004). Studies on melanistic/melanotic populations of snakes are abundant in the literature, as are reports of a single or a few individuals (Andrén and Nilson 1981, Kuriyama *et al.* 2013, Bury *et al.* 2020).

In this study, the “melanotic” morphotype of the Aesculapian snake, *Zamenis longissimus* (Laurenti, 1768), was examined. Previously, such dark/black individuals have been treated as “simple” or sporadic chromatic mutations, involving single individuals or small populations described in single reports from several Central European, Balkan, and Middle Eastern countries (Fitzinger 1826, 1832, De Betta 1853, Massalongo 1859). In these works, following Schulz (1996) and others (Edgar and Bird 2006, Kreiner 2007), this form is identified by the name designated by Werner (1897) as “var. *subgrisea*.”

Data from the literature, together with observations published on online platforms, were used to define a spatial map in which this morphotype is found. Published genetic and phylogenetic research about populations of *Zamenis longissimus* was considered to

hypothesize the most probable origin of the morphotype and how it spread to the locations where it is currently found. This information was combined with a seven-year project in which individuals of the *subgrisea* phenotype were kept and bred in a controlled environment, and several captive-bred generations were produced to determine the genetic nature of this morphotype.

Materials and Methods

Two pairs of the *subgrisea* form born in captivity were donated to OPHIS, Museo Paleontologico e Centro Erpetologico in 2017 and 2023. The most recently received pair consisted of two adult individuals from Montenegro, while the other consisted of two young specimens born in 2017 from parents originating from two Balkan locations (male from Croatia and female from Montenegro). The specimens remain at OPHIS, where they have reproduced for two generations. The adult specimens were raised in terraria with dimensions of 100 × 60 × 50 cm (length, height, and depth, respectively). Their offspring were housed in terraria appropriate to their size and moved to larger ones during growth.

After being collected and measured, the eggs were placed in an incubator (38 × 58 × 36 cm) that had the temperature regulated by an electronic thermostat and digital probes. Each clutch was positioned in a plastic box with a transparent lid filled with moist vermiculite as a medium.

Photographs were obtained with Sony α6000 and Nikon Coolpix P510 digital cameras. Comparative or geographical data were obtained from the literature and from the GPS data provided in the reports on the iNaturalist.org platform.

Results

During the growth of the *subgrisea* specimens, as in the classic phenotype, the juvenile dorsal pattern fades, replaced by a uniform color ranging from solid black to dark grey with very

small white flecks (Figure 1A, B). The scales of both black and grey individuals are iridescent, and blue pigmentation may be present in the contact areas of black and white. In some individuals, four longitudinal dorsal lines may be visible. The ventral coloration is black, with white spots at the lateral margins of the ventral scales. These white spots form a longitudinal white stripe along the lower portion of the flanks. The chin and labial scales are white, and the subocular black spot disappears completely in adults. Scattered yellow spots appear on the ventral, subcaudal, and labial scales of adults (Figure 1A, B).

Juveniles of the *subgrisea* form exhibit a dorsal pattern of spots arranged in four longitudinal rows that distinguish all young *Zamenis longissimus* (Figure 1C, D). Unlike the more widespread phenotype, however, longitudinal rows are dark grey on a lighter grey background. As in adults, the belly is completely black with small white dots located on the lateral edges of the ventral scales. The chin and neck are white ventrally with small symmetrical black spots. The labial scales are white, the fourth and fifth with a black tear-shaped spot below the eye. A black line extends along the postocular and temporal scales. The head shields are dark grey, almost black. The iris is dark; in some individuals, the pupil is difficult to distinguish.

Three clutches were produced by the female born in 2017: in 2019, 2021, and 2022. These clutches consisted of 6, 2 and 6 fertilized eggs (plus an infertile egg), respectively (Figure 2A). The elongate white eggs featured irregular concretions on the shell (Figure 2B). Egg length ranged from 50–59 mm and diameter from 20–24 mm; eggs weighed 9–14 g.

Following an incubation of 51–56 days at temperatures between 26 and 28°C, the clutches hatched completely (Figure 2B). The hatchlings measured 30–33 cm and weighed 12–14 g. In the 2019 clutch, half of the specimens exhibited the *subgrisea* form and the other half the classic phenotype (two males and one female for each phenotype; Figure 2B). In the 2021 clutch, both

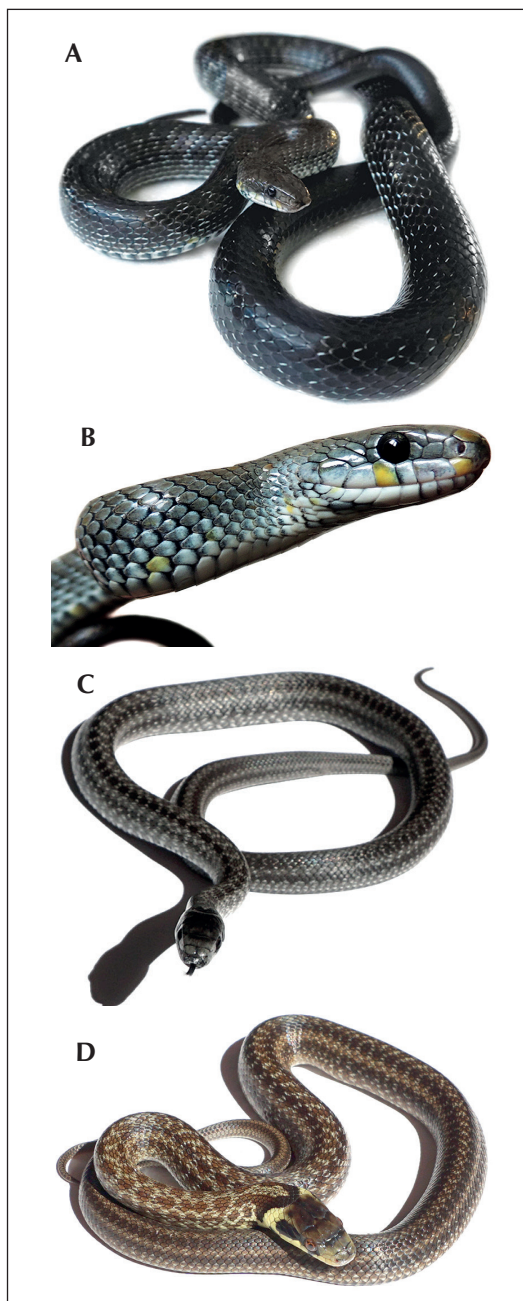


Figure 1. Specimens from the breeding program of *Zamenis longissimus*: (A) adult male *subgrisea* from Montenegro; (B) adult female *subgrisea*; (C) hatchling of the *subgrisea* morphotype; (D) hatchling of the dominant morphotype from *subgrisea* parents.



Figure 2. Specimens from the breeding program of *Zamenis longissimus*: (A) adult female *subgrisea* with eggs; (B) hatchlings from both morphotypes pipping the eggs; (C) juvenile female of the dominant morphotype showing black ventral coloration; (D) juvenile male showing characters of both dominant and *subgrisea* morphotypes.

hatchlings were of the *subgrisea* form. In 2022, four individuals exhibited the *subgrisea* form, and two were the classic phenotype. At hatching, the individuals of the classic phenotype from the mating of the *subgrisea* specimens exhibited a darker coloration than the hatchlings of *Z. longissimus* from other localities bred by the author and those observed by the author in the wild in Central Europe. The darker coloration becomes paler as the snakes grow. These offspring also exhibit a very bright orange iris (Figure 1D) that contrasts with the dark ground color.

Some chromatic “anomalies” occurred among the captive-bred specimens. One of the snakes born in 2023 (second generation bred in captivity) from heterozygous specimens (first generation in captivity) exhibits typical dorsal

coloration but is black ventrally (Figure 2C). A specimen born in 2022 from the original *subgrisea* pair exhibits coloration intermediate between the two morphotypes: hypoxanthistic with darker head shields and a greyish/bluish background dorsal coloration. The black pattern of this individual, if exposed to light, produces the same iridescence typical of the dorsal scales of *subgrisea* individuals (Figure 2D), possibly caused by a variation of concentration of iridophores and xanthophores compared to the classic phenotype.

Discussion

For many years, several authors have reported their observations of dark or “melanistic” individuals of *Zamenis longissimus*, naming this

variety/form *nigra*, or *nigrescens* (Fitzinger 1826, 1832, De Betta 1853, Massalongo 1859, Boulenger 1913). The first detailed information for identifying the morphotype, the object of this study, with those described in past literature was by Werner (1897). This author provided precise references to some characters, such as the dark belly and the longitudinal white line generated by the succession of spots located on the external portion of each ventral scale. This particular character was also confirmed by Angel (1946) and Cattaneo (1975), who even specified that this line terminates at the cloaca and is not present on the subcaudal scales.

The *subgrisea* form has been documented in France, Italy, Austria, Hungary, Croatia, Montenegro, Greece, Romania, Bulgaria, and the Caucasus (Werner 1897, Cattaneo 1975, Kreiner 2007, Schulz 1996, 2013). Most reports consist of observations of single individuals, although cases in which this form appears widespread are

known (Werner 1897, Cattaneo 2017). This latter situation appears to be more frequent in Balkan localities, where individuals of the classic and *subgrisea* phenotypes share the same habitats. Photos portraying these subjects appear in recent texts (Schulz 1996, 2013, Kreiner 2007), where details and localities are reported. Photographs of the *subgrisea* morphotype of *Z. longissimus* are on online platforms such as iNaturalist, with specific localities of the observations. Both literature and online records point out a high concentration of *subgrisea* sightings in the Balkan peninsula, and the online data confirm the distribution area in literature records (Figure 3). Most of the specimens have been documented in Greece, Bulgaria, Romania, Serbia, and Croatia, with records also in Hungary and Slovakia. The easternmost records reconfirm the presence of such morph in Russia and Turkey, and the westernmost in Italy, France, and Spain (Figure 3).

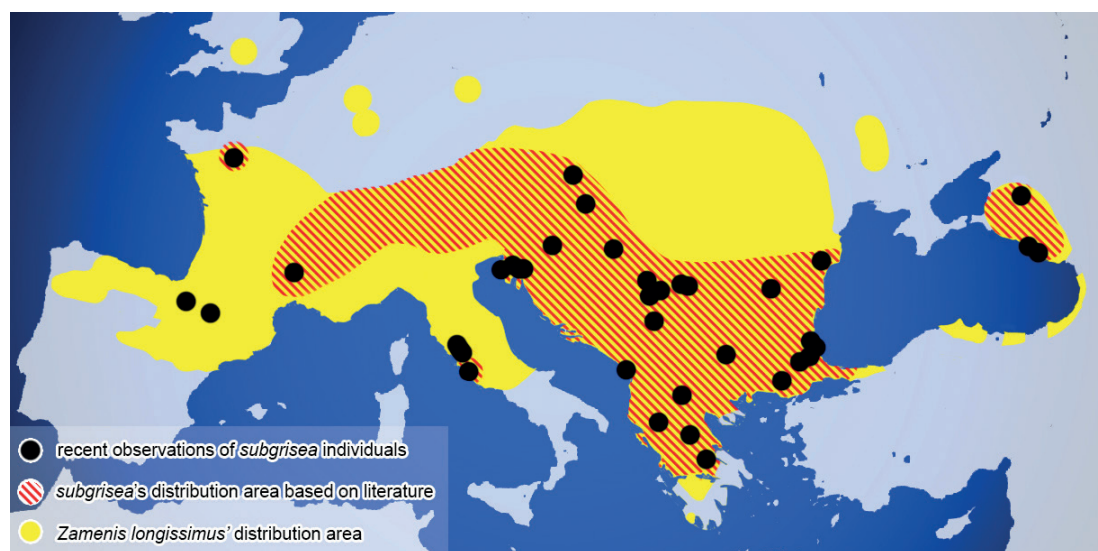


Figure 3. Distribution and observations of individuals of the *subgrisea* form. The yellow area indicates the distribution of *Zamenis longissimus*. Diagonal red lines indicate the predicted area of occurrence of the *subgrisea* form, based on information provided in the literature (Werner 1897, Cattaneo 1975, Kreiner 2007, Schulz 1996, 2013). Black dots correspond to recent observations of individuals of the *subgrisea* form from specific localities (Cattaneo 1975, Kreiner 2007, Schulz 1996, 2013, Zadavec and Lauš 2011) and from the iNaturalist platform (to April 2024).

In the literature, this morphotype has often been treated as melanic or axanthic (Zadavec and Lauš 2011, Cattaneo 2015, 2017). The results obtained by reproduction in captivity highlight the presence of several traits for which this form cannot be considered a single chromatic mutation. A character uniformly present in the *subgrisea* specimens is the black belly. This character is not found in the classic phenotype, in which the chin, belly, and tail are all colored with the same cream/yellowish shade. Pure melanic individuals are completely black, lacking even the small white spots between the dorsal scales, and any axanthistic specimen would have a white or light-grey venter, as in *subgrisea* juveniles, in which labials and the most anterior dorsal scales on the neck are white. Dark grey specimens with uniform white venters have been documented and are present on the iNaturalist platform. The same concept can be verified in the known axanthic/anerythristic forms of other colubroids (Fankhauser and Cumming 2008, Borteiro *et al.* 2021) and in the closely related species *Zamenis lineatus* (Russo *et al.* 2020).

A character not described in the literature is the presence of yellow pigment, which appears in some scales of *subgrisea* subjects. This pigmentation may affect any scale on the body, usually covering part of the scale. The yellow coloration is more evident in larger scales, such as the head shields, ventrals, and subcaudals but is also found on the dorsals. Yellowing scales in adults also occur in other species, such as the sympatric *Elaphe quatuorlineata* Lacépède, 1789 (pers. obs.). The presence of yellow pigmentation contradicts the hypothesis of axanthism and melanism because xanthophores are absent or rare in purely melanic colubrids (Kuriyama *et al.* 2013, 2016). The absence of iridophores was also reported in melanic individuals of the formerly congeneric *Elaphe quadrivirgata* (Boie, 1826) (Kuriyama 2013).

The white line on the external margins of the ventral scales is present in specimens of the classic phenotype. In the typically colored

individuals, it is present although barely visible against the light venter.

The data obtained from breeding show that the genetics of this morphotype are recessive. The results shed light on the genetics of the original pair. One of the two *subgrisea* parents that generated the individuals born in 2017 was heterozygous because among the offspring of the second generation (obtained from the mating of the 2017 *subgrisea* specimens) some of the hatchlings exhibit the classic/dominant phenotype. Furthermore, in the third generation produced by individuals of the classic phenotype, all of the hatchlings exhibited the same coloration as the parents. Confirmation of the recessive nature of this morphotype is noted by Cattaneo (1975), where a pregnant *subgrisea* female, captured near Rome in a limited and mixed *subgrisea* colony (possibly now extinct), laid eggs producing offspring of both forms.

Anomalies in the livery appeared in two hatchlings of the classic phenotype (Figure 2 C, D). These anomalies involved typical characteristics of the *subgrisea* form, demonstrating that some characters of this morphotype may appear individually in heterozygous specimens. This may be a case of incomplete dominance of the alleles but would need to be further investigated in future generations.

Conclusion

The results obtained from breeding suggest that the *subgrisea* form is a recessive mutation. Within the groups raised in a controlled environment, specimens manifesting partial traits of such morphotypes were born. An individual born in the third generation, obtained from the mating of recessive heterozygous specimens exhibiting the dominant classic coloration, featured the black belly. This trait is characteristic of the *subgrisea* form, which does not exist in the classic phenotype, as darker iridescent dorsal tones manifested in a second individual. This would likely mean that this

morphotype expresses itself in a combination of multiple traits and would be consequently not linked to a single gene, representing a more complex form than a single chromatic mutation.


The fact that such combine traits can be found in the same form in different sites greatly distant from each other suggests that the observed specimens in the wild may not be the result of individual/occasional mutations, but instead these specimens have an ancient common origin that continues to be actively transmitted by recessive homozygous and heterozygous individuals within populations in which the classic phenotype appears to be the dominant one.

Recent genetic analyses and fossil records could help determine the origins of this form. It is supposed that in the last glacial period, the northern and central European populations of *Z. longissimus* became extinct, and these areas were subsequently repopulated in the Holocene, mainly by populations surviving in Balkan refuges (Musilová *et al.* 2010, Allentoft *et al.* 2018). Most of the observations of individuals or small populations of the *subgrisea* morphotype come from the Balkans. It is conceivable that this form was already present in the Pleistocene of southeastern Europe, and that it has survived to this day in certain central European populations that were recolonized by individuals with the genetics of the eastern clade. Further studies focused on dermal chromatophores could indicate where this form would have been advantaged and more functional during the glacial period (King 1988, Forsman 1995, Trullas *et al.* 2007, Geen and Johnston 2014, Monahan *et al.* 2022). The appearance of the *subgrisea* form could even be backdated because records of this morph come from the Caucasus and Greece (Schulz 1996, 2013, iNaturalist data), of which populations present profound genetic differences from the European and Transcaucasian ones (Musilová *et al.* 2007, 2010), suggesting that these southern-oriental groups remained isolated even longer and did not contribute to the colonizing expansion of Central Europe following the last glacial phase.

The *subgrisea* individuals and populations have been reported from coastal areas in Montenegro, Croatia, Italy, and Russia to mainland forests of the central and eastern European countries (Werner 1897, Cattaneo 1975, Kreiner 2007, Schulz 1996, 2013, Zadravec and Lauš 2011, iNaturalist data). Such differences both in altitudes and biotopes suggest that the presence of this form may not depend exclusively on environmental factors. The occurrence of the *subgrisea* form could not be selected by a switch of an environmental nature but would mainly depend *in primis* on the genetic pool of the micropopulation in question.

Considering the analyzed evidence, the Aesculapian snake could be considered a polymorphic species that expresses (at least) two forms: the dominant classic one and the recessive *subgrisea*, which occurs in several countries within the entire distribution of this colubrid.

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