



Citizen Science, taxonomy and grass snakes: iNaturalist helps to clarify variation of coloration and pattern in *Natrix natrix* subspecies

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Abstract

We used a dataset of georeferenced photos of 5,751 grass snakes from iNaturalist to evaluate subspecific variation of *Natrix natrix* in coloration and pattern. Our results provide evidence that all four genetically delineated subspecies differ morphologically, although unstriped individuals of *N. n. vulgaris* are difficult to tell apart from the nominotypical subspecies. The iNaturalist dataset shows that the frequency of dark body coloration increases from south to north and from west to east. This trend is both concordant with taxonomic variation (the easternmost subspecies, *N. n. scutata*, being the darkest taxon) and variation within the same subspecies (in *N. n. natrix* and *N. n. scutata* more northern populations harbor more dark or melanistic individuals than more southern populations). Although available characters were limited to coloration and pattern traits, our study suggests that photo material from iNaturalist and similar platforms can be a valuable data source for studies on morphological variation. However, investigations using such databases can only supplement, but not replace, studies using museum material because only then measurable, meristic and genetic characters will be accessible.

Keywords

Colubridae, hybridization, morphology, Natricidae, *Natrix helvetica*, *Natrix natrix moreotica*, *Natrix natrix natrix*, *Natrix natrix scutata*, *Natrix natrix vulgaris*, *Natrix tessellata*

Introduction

Online Citizen Science projects, like iNaturalist (www.inaturalist.org), became popular platforms for the broad-scale involvement of the public in science. In particular, the knowledge of the spatial distribution of animal and plant taxa (Seltzer 2019; Unger et al. 2021), but also animal-plant interactions (Gazdic and Groom 2019), phenology (e.g., Di Cecco and Hurlbert 2022) and daily activity patterns (e.g., Blais and Shaw 2018), may profit from these endeavors.

In the present study we harvested the iNaturalist database for georeferenced photographic records of the common grass snake, *Natrix natrix* (Linnaeus, 1758), to investigate how geographic variation of coloration and pattern correspond to its genetically redefined subspecies (Asztalos et al. 2021a).

Subspecific variation of grass snakes has been contentious for decades and represents a classical example for the splitter-lumper conflict in taxonomy (Simpson 1945).

Hecht's (1930) highly controversial study opened the debate and recognized no fewer than 20 different subspecies within '*Tropidonotus natrix*.' Significant progress was made with Mertens' (1947) and Thorpe's (1979) seminal studies with nine versus four accepted subspecies. Nevertheless, later up to 14 morphologically defined subspecies were recognized by some authors (see review in Kabisch 1999), before genetic investigations (Kindler et al. 2013, 2017, 2018; Pokrant et al. 2016; Asztalos et al. 2020, 2021a, b; Schultze et al. 2020) substantially enhanced and fundamentally modified grass snake taxonomy.

These recent studies concluded that there are three distinct and largely parapatric species of grass snake. Their abutting distribution ranges are connected across narrow hybrid zones in which hybrids co-occur with the parental species (Pokrant et al. 2016; Kindler et al. 2017; Schultze et al. 2019, 2020; Asztalos et al. 2020, 2021b). The two western grass snake species, the red-eyed grass snake *N. astreptophora* (Seoane, 1884) and the barred grass snake *N. helvetica* (Lacépède, 1789), are beyond the scope of the present investigation. Here we focus on the widely distributed eastern species, the common grass snake (*N. natrix*). It occurs from western Germany in Central Europe to Lake Baikal in Central Asia, i.e., across a region spanning approximately 6,300 km from west to east.

According to the recent genetic assessment of its taxonomy (Asztalos et al. 2021a), *N. natrix* comprises four subspecies. The nominotypical subspecies lives in the northwestern part of the distribution range (Central Europe, Scandinavia) and is replaced in southern Central Europe and the northern Balkans by *N. n. vulgaris* Laurenti, 1768. *Natrix natrix moreotica* (Bedriaga, 1882) is distributed in the southern Balkans, western Anatolia and Cyprus, whereas *N. n. scutata* (Pallas, 1771) occurs in the vast eastern part of the distribution range, from eastern Poland and central Anatolia to Lake Baikal. The morphological differences between these four taxa remain to be examined. The present study contributes to this task using a dataset of georeferenced photos of more than 5,750 grass snakes available from iNaturalist to evaluate how variation in coloration and pattern matches the genetically delineated subspecies.

Materials and Methods

All photos identified as common grass snakes (*Natrix natrix*) present in the iNaturalist database by December 31, 2021 were inspected and, as far as informative, classified using a predefined scheme for coloration and pattern characters. In the three regions where hybridization between common grass snakes (*N. natrix*) and barred grass snakes (*N. helvetica*) is known to occur (Rhine and Lake Constance regions, southern Bavaria and adjacent Austria, northeastern Italy; Thorpe 1979; Kindler et al. 2017; Schultze et al. 2019, 2020; Asztalos et al. 2021b), all photos were scrutinized for misidentified *N. helvetica* or putative hybrids using the following traits: The head

pattern of grass snakes typically includes a conspicuous light occipital marking, which can be bordered by an anterior and a posterior dark element. In contact zones of *N. natrix* and *N. helvetica*, the presence (*N. natrix*) or absence (*N. helvetica*) of the anterior dark element and the shape of the posterior dark element (narrow in *N. natrix*, posteriorly conspicuously elongated in *N. helvetica*) are species-diagnostic. However, the entire head can alternatively be dark or black colored in both species. Common grass snakes typically show a light colored crescent on each side of the head, whereas in *N. helvetica* the light occipital markings tend to fuse to a closed collar, which is frequently paler than the crescents in *N. natrix*. In aged *N. helvetica*, the collar frequently fades, so that it has the same color as the body flanks. In addition, in Central Europe the body pattern of *N. natrix* is frequently inconspicuous, entirely absent or consists only of small dark elements. In contrast, *N. helvetica* has more pronounced dark streaks, spots or prominent lateral bars on a typically lighter primary coloration (Meyer 2020). In northeastern Italy, many *N. natrix* bear light longitudinal back stripes, a character never recorded in pure *N. helvetica*. It turned out that in northeastern Italy the majority of grass snakes reclassified as hybrids were originally misidentified as *N. natrix* on iNaturalist because of the presence of back stripes, although these specimens displayed otherwise characteristic traits of *N. helvetica*.

Even though we are confident that our assessment of iNaturalist photos improved previous determinations significantly, overlooked hybrids and the recently reported unexpected hybridization of common grass snakes and the widely sympatric dice snake (*N. tessellata*; Asztalos et al. 2021a) still may have blurred our results to some extent (see Discussion).

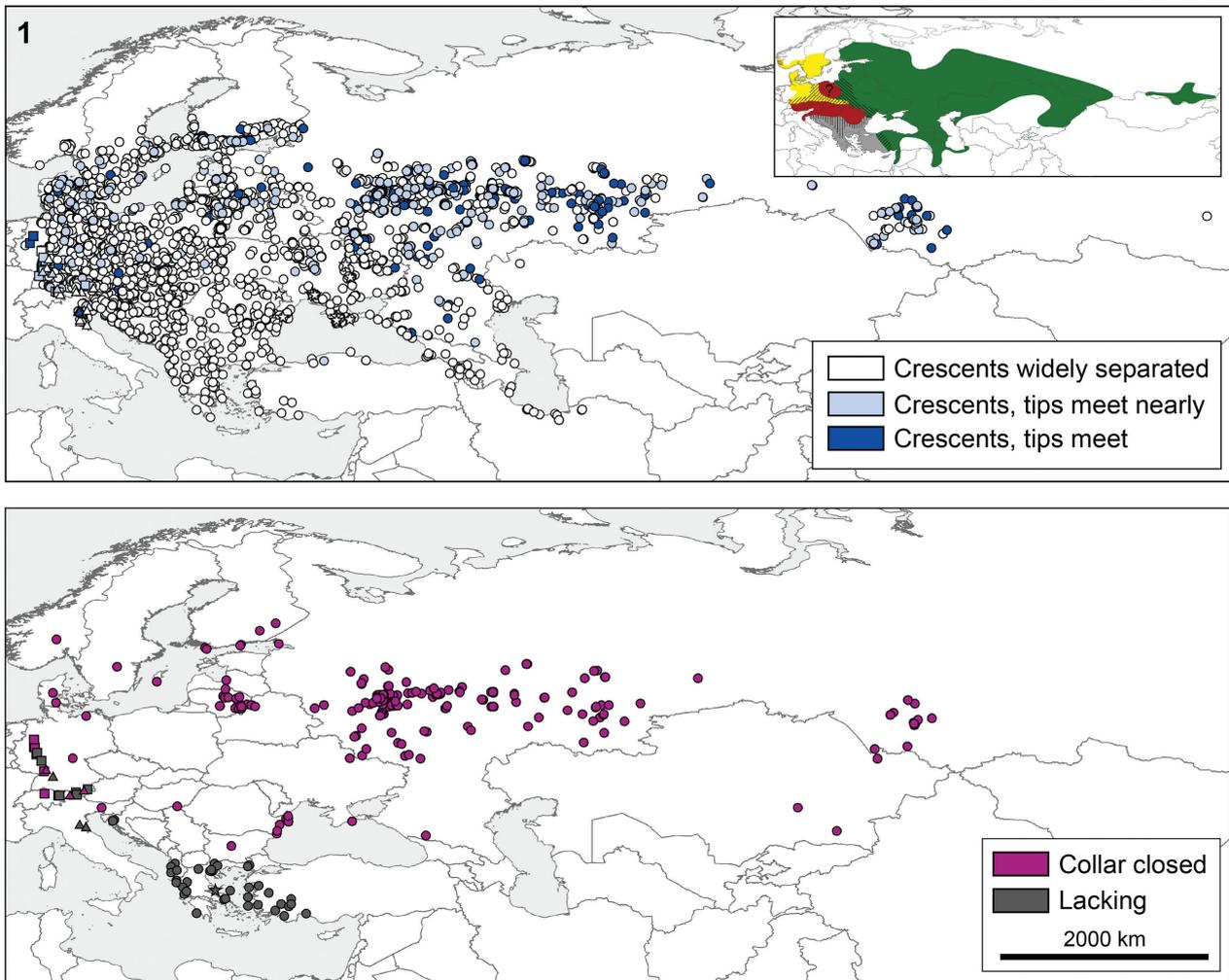
For examining geographic variation in *N. natrix*, only such traits were utilized that are easily quantifiable in non-standardized photographs, preventing the use of any meristic traits. This does not imply that geographically significant variations might not exist in meristic traits. The following coloration and pattern characters were recorded and plotted in seven maps using ArcGIS 10.8 (Figs 1–7):

Light occipital markings

- (a) absent or
- (b) present; if present
 - (b1) as distinct lunar marks on each side of the head, if yes
 - (b1') widely separated
 - (b1'') tips nearly meet medially
 - (b1''') tips meet medially
- (b2) as completely closed collar.

Primary coloration of the light occipital markings (melanistic snakes disregarded)

- (a) whitish to pale yellow
- (b) yellow
- (c) pale orange
- (d) orange
- (e) pale grey
- (f) like body.



● *Natrix natrix* ■ *Natrix helvetica* ▲ *Natrix natrix* x *Natrix helvetica* ★ *Natrix natrix* x *Natrix tessellata*

Figure 1. Variation in the occipital color pattern of grass snakes based on iNaturalist records. Small inset map (top) shows subspecies distribution according to Asztalos et al. (2021a): *Natrix natrix natrix* – yellow, *N. n. vulgaris* – red, *N. n. moreotica* – grey, *N. n. scutata* – green. Hybrid zones hatched. Note that the occurrence of closed collars is largely restricted to the range of *N. n. scutata* and to the hybrid zones between *N. natrix* and *N. helvetica* in the very west. Grass snakes with lacking occipital pattern occur in the southwest, within the distribution range of *N. n. moreotica*, and again in the hybrid zones of *N. natrix* and *N. helvetica*. It is well known that the collar may fade and disappear in aged *N. helvetica* (cf. Kabisch 1999; Meyer 2020). According to the photo material, the same is true for *N. n. moreotica*.

Primary coloration of the body

- (a) grey
- (b) dark grey
- (c) black (including melanistic individuals)
- (d) brownish.

In dark grey snakes the occipital markings are still visible and darker than the body, whereas in black snakes the occipital markings are invisible because of the black primary color of the body. In melanistic grass snakes the head is entirely black.

Body pattern (except for absence/presence of back stripes and absence/presence of lateral bars)

- (a) large dark spots
- (b) dark and/or light spots
- (c) small dark and/or light spots
- (d) mottled

- (e) marbled
- (f) uniform (including melanistic individuals).

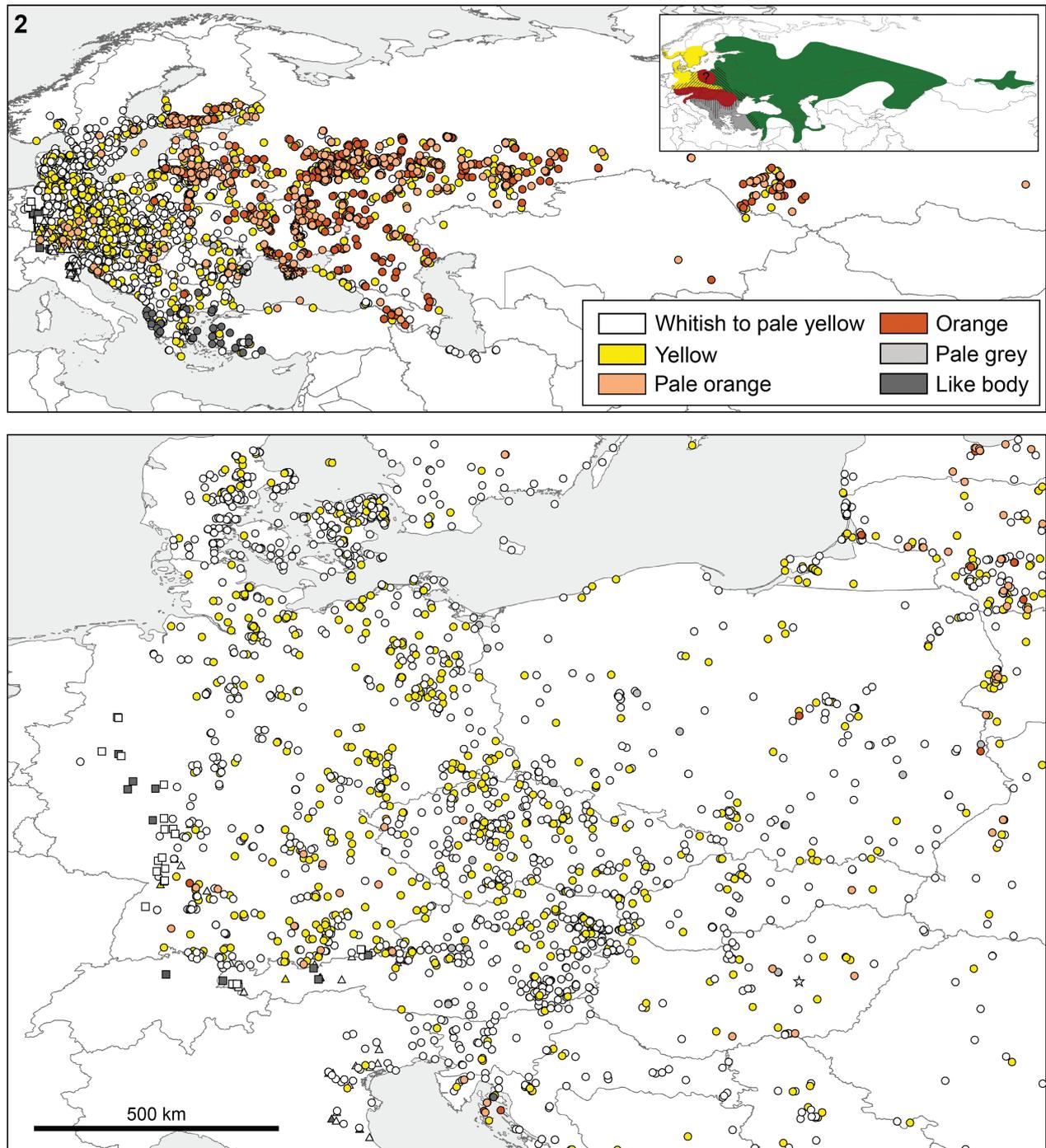
Two back stripes

- (a) absent or
- (b) present; if present
 - (b1) well defined
 - (b2) weakly defined.

Side bars

- (a) present
- (b) absent.

In addition, partially or completely melanistic individuals and two rare coloration variations, the ‘*picturata* morphotype’ and the spotted ‘*schweizeri* morphotype,’ were recorded and plotted.

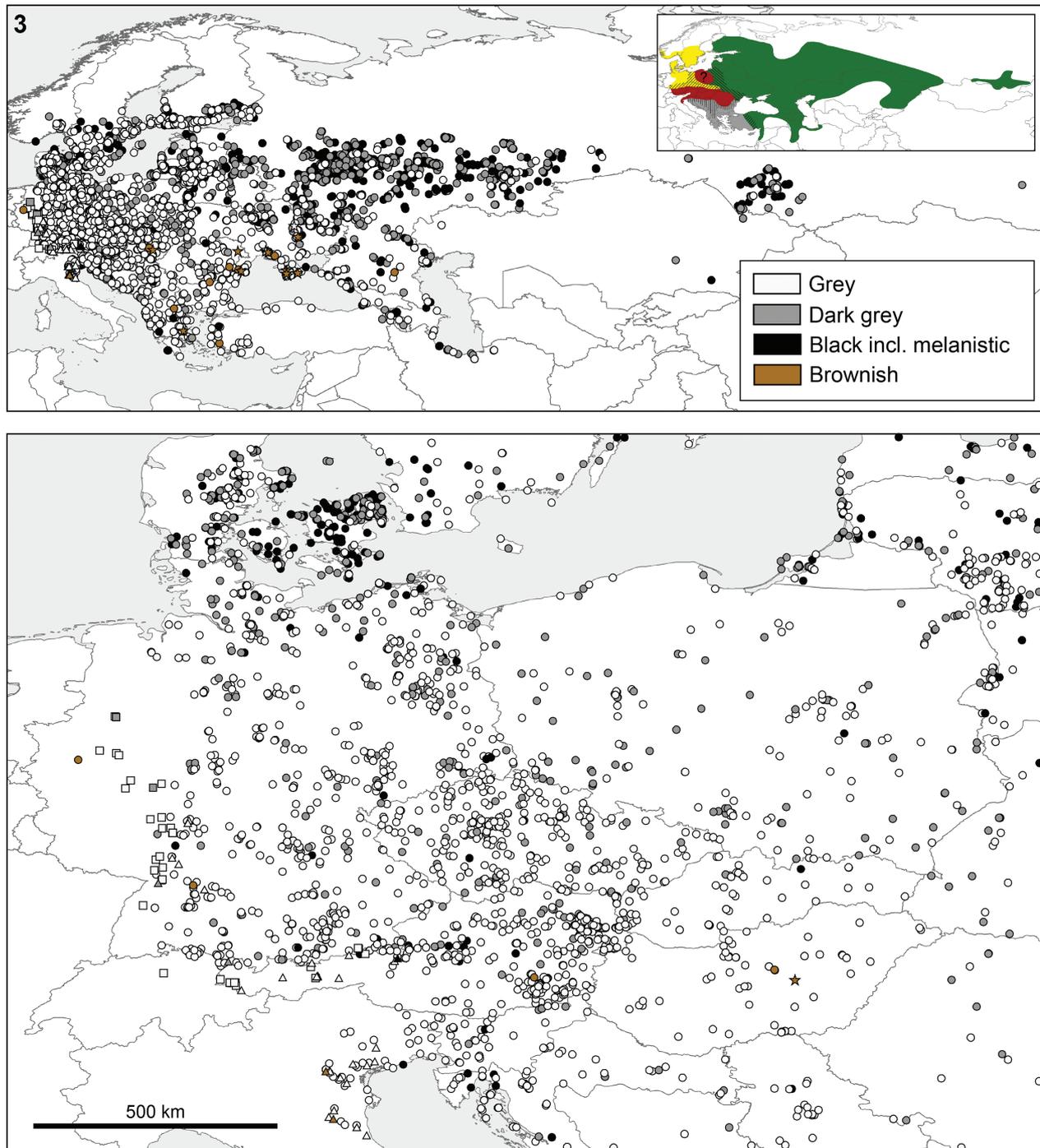


● *Natrix natrix* ■ *Natrix helvetica* ▲ *Natrix natrix* x *Natrix helvetica* ★ *Natrix natrix* x *Natrix tessellata*

Figure 2. Variation in the coloration of the light elements in the occipital region of grass snakes based on iNaturalist records. Densely documented western part enlarged in bottom map. Small inset map (top) shows subspecies distribution according to Asztalos et al. (2021a): *Natrix natrix natrix* – yellow, *N. n. vulgaris* – red, *N. n. moreotica* – grey, *N. n. scutata* – green. Hybrid zones hatched. Note that pale orange and orange coloration is largely restricted to two regions: the northeast (range of *N. n. scutata*) and the southwest (range of *N. n. vulgaris*, where coloration is mostly less intense). When the crescents or collars fade completely in aged snakes, pale grey or body-like coloration types occur (range of *N. n. moreotica* and hybrid zones of *N. natrix* and *N. helvetica*).

Melanistic grass snakes and the ‘*picturata* morphotype’ are known both from *N. natrix* and *N. helvetica* (Fritz and Schmidler 2020). The ‘*picturata* morphotype’ was originally described by Jan (1864) as *Tropidonotus natrix* var. *picturata* for grass snakes from Azerbaijan and perhaps Switzerland showing this coloration variant. Such snakes have a black primary color and bear many

small light speckles. The ‘*picturata* morphotype’ was later illustrated by Jan and Sordelli (1868), making Jan’s (1864) earlier description unambiguous. Nevertheless, Gredler (1882) created some years later another name for the same coloration variant (*Tropidonotus natrix* var. *bulsanensis*), based on a barred grass snake from South Tyrol. For the present study, snakes of the ‘*picturata*



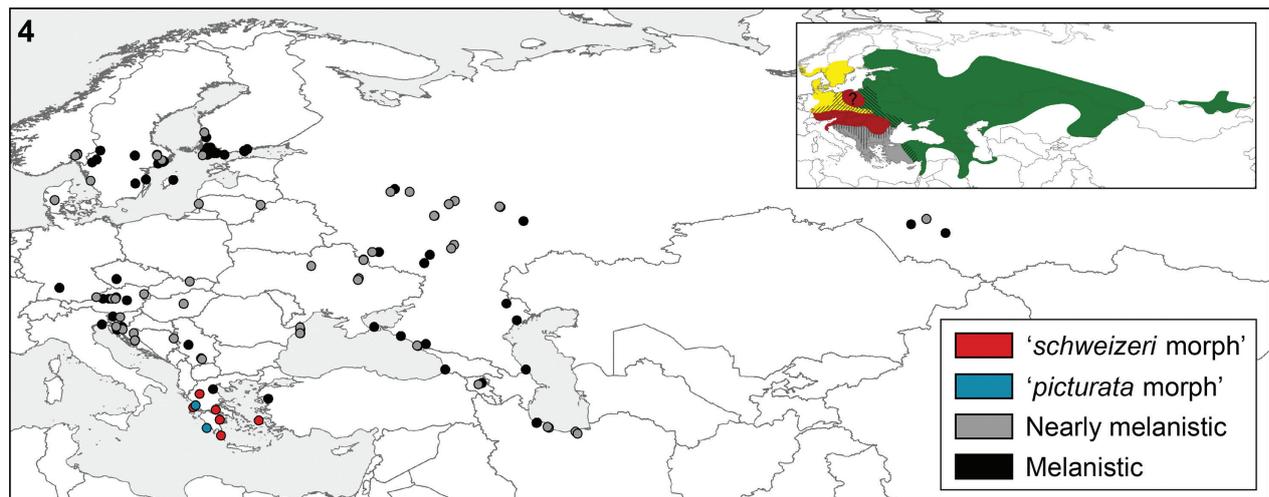
● *Natrix natrix* ■ *Natrix helvetica* ▲ *Natrix natrix* × *Natrix helvetica* ★ *Natrix natrix* × *Natrix tessellata*

Figure 3. Variation in the body coloration of grass snakes based on iNaturalist records. Densely documented western part enlarged in bottom map. Small inset map (top) shows subspecies distribution according to Asztalos et al. (2021a): *Natrix natrix natrix* – yellow, *N. n. vulgaris* – red, *N. n. moreotica* – grey, *N. n. scutata* – green. Hybrid zones hatched. Note that dark coloration types prevail in the north and northeast of the range. *Natrix natrix* × *N. tessellata* hybrids are often characterized by a brownish coloration.

morphotype’ and fully melanistic individuals from contact zones of *N. natrix* and *N. helvetica* were excluded, because their identity could not be clarified.

The second coloration variant, the ‘*schweizeri* morphotype,’ is only known from *N. natrix*. Snakes of the ‘*schweizeri* morphotype’ have been mentioned or depicted for Milos and other Cycladic islands as well as for Cyprus (Müller 1932; Kreiner 2007; Baier et al. 2009; Geniez 2015). This morphotype is characterized by very

large dark spots on a light grey body. Light back stripes do not occur and the occipital region can have the same color as the body. The name of this coloration variant is derived from the subspecies name *N. n. schweizeri* Müller, 1932, which was coined for such spotted grass snakes from Milos. This name is now to be synonymized under *N. n. moreotica* (cf. Fritz and Schmidtler 2020; Asztalos et al. 2021a).



● *Natrix natrix* ■ *Natrix helvetica* ▲ *Natrix natrix* × *Natrix helvetica* ★ *Natrix natrix* × *Natrix tessellata*

Figure 4. Distribution of melanistic grass snakes and rare color pattern morphotypes based on iNaturalist records. Small inset map shows subspecies distribution according to Asztalos et al. (2021a): *Natrix natrix natrix* – yellow, *N. n. vulgaris* – red, *N. n. moreotica* – grey, *N. n. scutata* – green. Hybrid zones hatched. The ‘schweizeri morphotype’ was previously only known from some Cyclades islands (including Milos) and from Cyprus (Kabisch 1999; Baier et al. 2009), from where no photos are on iNaturalist.

Excluding non-informative pictures on iNaturalist, we used photos of a total of 5,751 snakes for our investigation. As far as possible, photos showing the same snake, but uploaded by different users, were dismissed. For some snakes, not all traits could be observed.

We examined photos showing 5,663 *N. natrix*, 40 *N. helvetica*, 34 putative *N. natrix* × *N. helvetica* hybrids, and 14 putative *N. natrix* × *N. tessellata* hybrids. At the time of our study, all of these snakes were identified as *N. natrix* on iNaturalist (quality rank ‘Research Grade’). We included in our maps data for all of these snakes, but made no efforts to review photos identified as *N. helvetica* or *N. tessellata* or those that were only assigned to the genus *Natrix*. However, we show in our maps our conclusions about the identity of the evaluated snakes, i.e., we assign them to *N. helvetica* or one of the hybrid combinations if we classified them as such.

According to countries, we studied the following numbers of *N. natrix*: Albania (19), Armenia (11), Austria (396), Azerbaijan (9), Belarus (58), Bosnia and Herzegovina (9), Bulgaria (34), Croatia (86), Czech Republic (305), Denmark (418), Estonia (17), Finland (215), Georgia (12), Germany (752), Greece (89), Hungary (67), Iran (14), Italy (43), Kazakhstan (5), Kosovo (4), Latvia (33), Lithuania (294), Montenegro (19), North Macedonia (4), Norway (26), Poland (201), Romania (114), Russia (1,725), Serbia (31), Slovakia (95), Slovenia (35), Sweden (209), Switzerland (7), Turkey (27), and Ukraine (280).

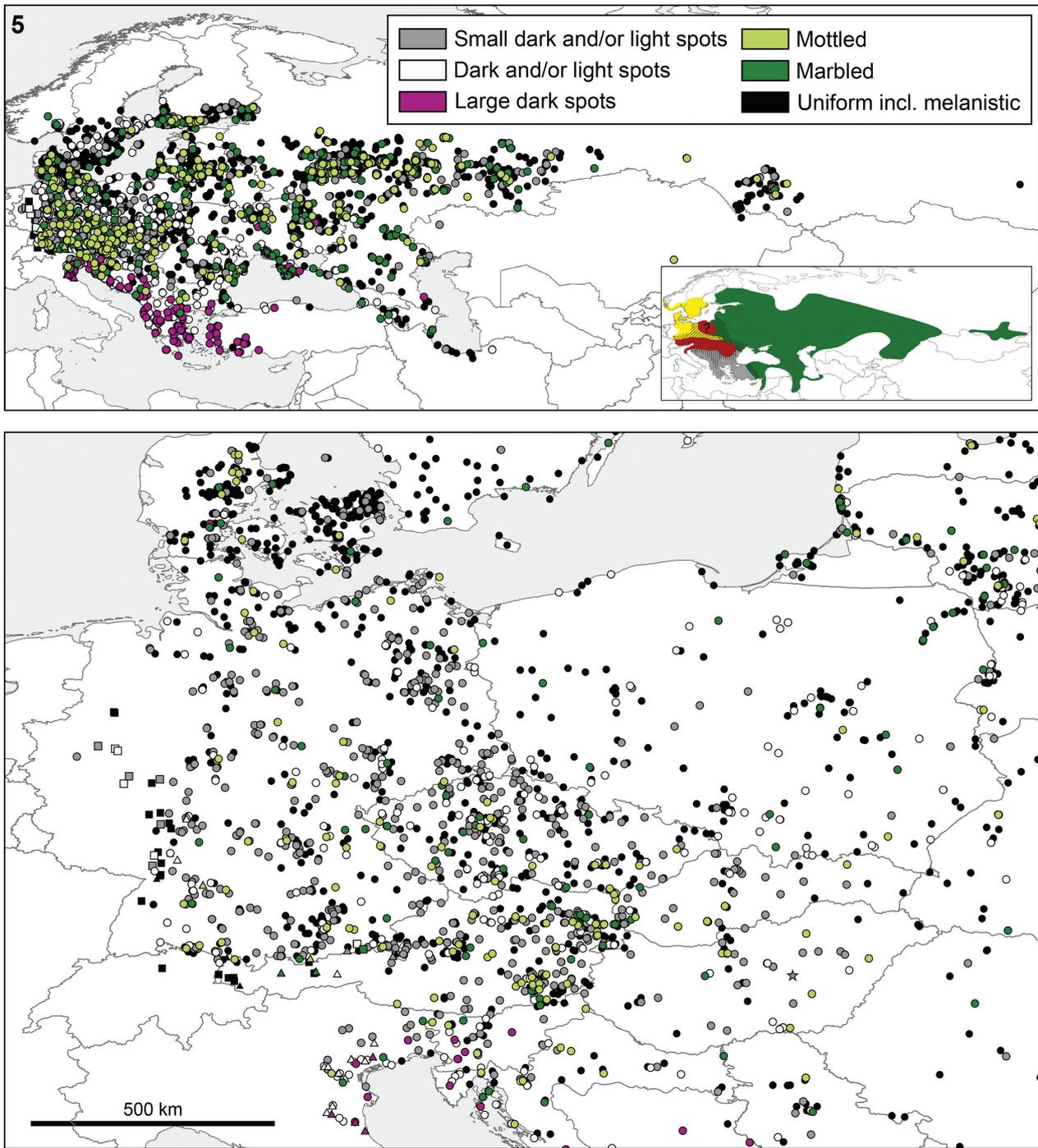
The studied *N. helvetica* or putative *N. natrix* × *N. helvetica* hybrids were from Austria (9 *N. helvetica*/7 putative hybrids), Germany (30/12), Italy (0/15), and Switzerland (1/0). The snakes tentatively identified as *N. natrix* × *N. tessellata* hybrids came from Greece (1), Hungary (1), Moldova (1), Romania (1), and Ukraine (10).

Results

With respect to head pattern and head coloration, some geographic differences emerge. Except for some *Natrix helvetica* and putative *N. natrix* × *N. helvetica* hybrids which were identified on iNaturalist as *N. natrix*, there are in the western part of the distribution range of *N. natrix* only a few individuals in which the light crescents are so extended that their tips meet or nearly meet medially or which possess closed light collars (Fig. 1). This is markedly different in the eastern part of the distribution range, i.e., from the Baltic countries and Finland to Central Asia. This latter region corresponds to the distribution range of the subspecies *N. n. scutata*. Here, many snakes occur that either have widely extended crescents that nearly meet or meet medially or that have completely closed collars.

Except for misidentified *N. helvetica* and putative *N. natrix* × *N. helvetica* hybrids, snakes lacking light crescents (or completely closed collars) are nearly completely confined to the southern Balkan Peninsula and western Asia Minor. These individuals are apparently all aged snakes in which the coloration has faded. The occurrence of this coloration variant matches the distribution range of the subspecies *N. n. moreotica*.

The variation of the coloration of the crescents and collars parallels these observations (Fig. 2). In the north-western part of the distribution range of *N. natrix*, a less intense coloration occurs, with most snakes having whitish to pale yellow or yellow colored crescents. A pale orange coloration of the crescents is confined to an area matching well with the distribution range of *N. n. vulgaris* (southern Central Europe, adjacent Balkans), whereas within the range of *N. n. natrix* (northern Central Europe,



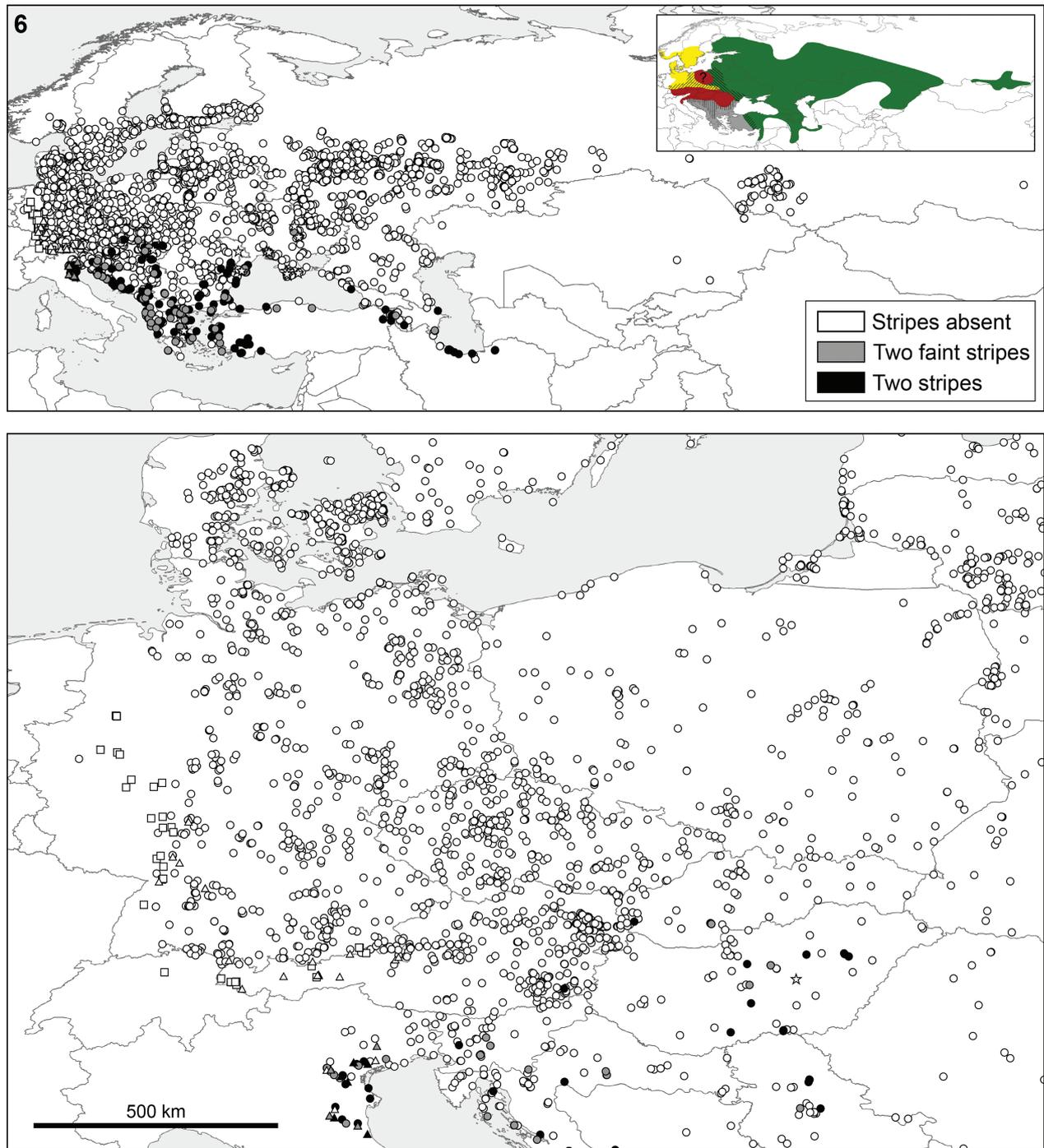
● *Natrix natrix* ■ *Natrix helvetica* ▲ *Natrix natrix* × *Natrix helvetica* ★ *Natrix natrix* × *Natrix tessellata*

Figure 5. Distribution of different body coloration types in grass snakes based on iNaturalist records. Densely documented western part enlarged in bottom map. Small inset map (top) shows subspecies distribution according to Asztalos et al. (2021a): *Natrix natrix natrix* – yellow, *N. n. vulgaris* – red, *N. n. moreotica* – grey, *N. n. scutata* – green. Hybrid zones hatched. Note that large dark spots are largely restricted to the Balkans and western Asia Minor (approximately matching the range of *N. n. moreotica*), where grass snakes with uniform, marbled or mottled body are virtually lacking.

Scandinavia) mainly grass snakes with whitish or yellow crescents were recorded. To the east, from eastern Poland, the Baltic countries and Finland eastwards, the number of grass snakes with pale orange or orange crescents or collars substantially increases. This region again corresponds with the distribution range of *N. n. scutata*. A pale grey or body-like coloration of the crescents or collars in the west is largely confined to misidentified *N. helvetica*

or putative *N. natrix* × *N. helvetica* hybrids. However, in the southern Balkans and western Turkey, i.e., within the distribution range of *N. n. moreotica*, many aged snakes have instead of a lighter coloration a body-like coloration in the places where normally light crescents are present. Younger individuals show whitish or yellow crescents.

With respect to the primary body coloration (Fig. 3), there is an obvious trend from south to north, and espe-



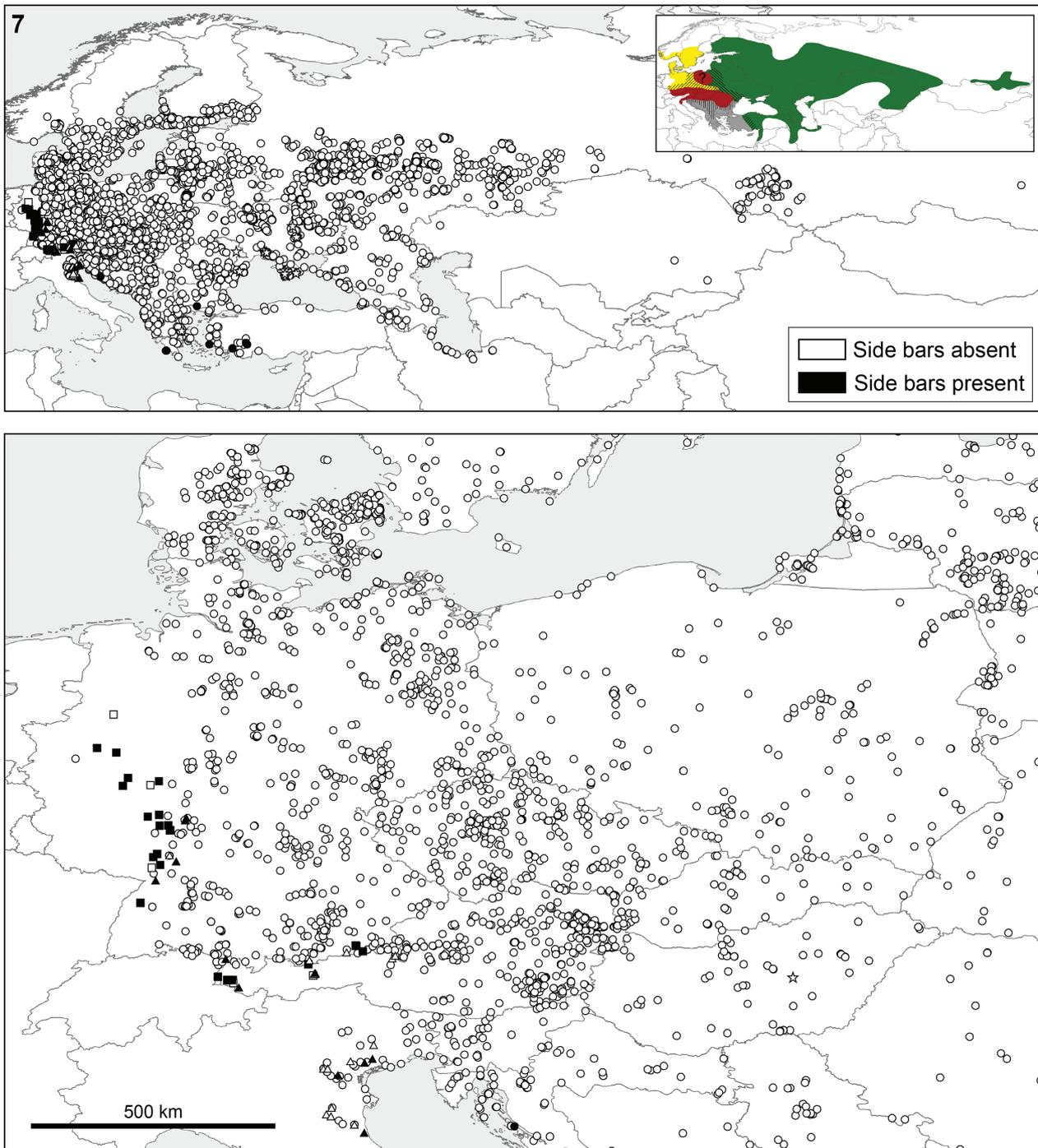
● *Natrix natrix* ■ *Natrix helvetica* ▲ *Natrix natrix* x *Natrix helvetica* ★ *Natrix natrix* x *Natrix tessellata*

Figure 6. Distribution of light back stripes in grass snakes based on iNaturalist records. Densely documented western part enlarged in bottom map. Small inset map (top) shows subspecies distribution according to Asztalos et al. (2021a): *Natrix natrix natrix* – yellow, *N. n. vulgaris* – red, *N. n. moreotica* – grey, *N. n. scutata* – green. Hybrid zones hatched. Back stripes are restricted to two regions, the Balkan Peninsula plus adjacent Central Europe and Transcaucasia plus northern Iran.

cially from west to east, towards darker variants. This concerns two subspecies, *N. n. natrix* and *N. n. scutata*. Within the distribution range of *N. n. scutata*, grass snakes with a dark grey and black body prevail, especially in the more northern populations. This is not explained by the occurrence of nearly completely or completely melanistic grass snakes, which do not occur here more frequently than in other parts of the range (Fig. 4). In contrast to melanistic grass snakes, which tend to be entirely black,

dark grey or black *N. n. scutata* have well pronounced, contrasting crescents or collars. In the west, however, there is an increasing frequency of dark and melanistic grass snakes in Scandinavia (Figs 3 and 4), i.e., within the distribution range of *N. n. natrix* and, with respect to southern Finland, in the westernmost part of the distribution range of *N. n. scutata*.

Besides grass snakes with grey or black body coloration, there are also individuals with a brownish body



● *Natrix natrix* ■ *Natrix helvetica* ▲ *Natrix natrix* x *Natrix helvetica* ★ *Natrix natrix* x *Natrix tessellata*

Figure 7. Distribution of side bars in grass snakes based on iNaturalist records. Densely documented western part enlarged in bottom map. Small inset map (top) shows subspecies distribution according to Asztalos et al. (2021a): *Natrix natrix natrix* – yellow, *N. n. vulgaris* – red, *N. n. moreotica* – grey, *N. n. scutata* – green. Hybrid zones hatched. The occurrence of side bars is largely restricted to the hybrid zones between *N. natrix* and *N. helvetica* along the western range border of *N. natrix* and to the range of *N. n. moreotica*.

coloration, which has not been recorded from any northern population on iNaturalist (Fig. 3). Many snakes with brownish body coloration share some morphological traits with dice snakes (*N. tessellata*), like the eponymous dice pattern or the head shape, so that we tentatively identified such snakes as hybrids.

Among the recorded traits for the body pattern, there are some trends visible: In the southwest, within the

distribution range of *N. n. moreotica* and in part within the distribution range of *N. n. vulgaris*, there is a high frequency of grass snakes with large dark spots (Fig. 5), and in the same region, but also in the Transcaucasus and northern Iran, back stripes may occur (Fig. 6). Large dark spots also occur in the southwestern range of *N. n. scutata*. On the other hand, mottled, marbled and plain-colored grass snakes seem to be rare or entirely lacking in the



Figure 8. Coloration and pattern of *Natrix natrix natrix* documented by photos from iNaturalist. **A** Individual with plain dark grey body; Biosphärenreservat Schorfheide-Chorin, Germany; photo: cloudya. **B** Individual with spotted grey body; Bernau near Berlin, Germany; photo: kohal. **C** Individual with black body; Lillerød, Denmark; photo: petersc. **D** Nearly melanistic individual; Solängen, Mölndal, Sweden; photo: Janne Asp. **E** Individual with marbled grey body; Garstedt, Germany; photo: vasquez. **F** Individual with marbled dark grey body; Ebeltoft, Denmark; photo: Oskar Liset Pryds Hansen.

range of *N. n. moreotica* (Fig. 5). Side bars, as typical for *N. helvetica*, were recorded only rarely and, with a few exceptions from Greece and western Turkey (*N. n. moreotica*), only concerned misidentified *N. helvetica* or putative *N. natrix* × *N. helvetica* hybrids (Fig. 7).

With respect to rare coloration variants (Fig. 4), only two *N. natrix* on iNaturalist represented the ‘*picturata* morphotype,’ whereas six individuals from Greece (including one record from Ikaría off the Turkish coast) represented the ‘*schweizeri* morphotype.’ None of the Greek

snakes came from one of the islands where this coloration variant was known to occur.

How coloration and pattern match subspecific differentiation

According to the iNaturalist data, the four genetically redefined subspecies of *N. natrix* (Asztalos et al. 2021a) show the following coloration and pattern characters:



Figure 9. Coloration and pattern of *Natrix natrix vulgaris* documented by photos from iNaturalist. **A** Individual with plain grey body, note the weak dark spot in front of the yellow crescent; Gossendorf, Austria; photo: Andrea Bregar. **B** Striped individual with pale orange crescents; Nagykováta, Hungary; photo: Tamara Szentiványi. **C** Individual with pale yellow crescents and mottled body coloration; Eslarn, Germany; photo: novastorm. **D** Individual with pale yellow crescents and marbled body coloration; Nußdorf, Austria; photo: fabi-henne. **E** Individual with pale orange crescents and mottled body coloration; Garmisch-Partenkirchen, Germany; photo: carmen1988. **F** Melanistic individual; Liezen, Austria; photo: Harald Komposch.

***Natrix natrix natrix* (Linnaeus, 1758)**

The nominotypical subspecies is characterized by widely separated, whitish to yellow crescents, which are present throughout life. The body is typically grey-colored, with an increasing tendency to dark and melanistic coloration variants to the north of the distribution range. The body is typically either plain-colored or with small spots; back stripes or side bars do not occur. Figure 8 gives an over-

view of the variation in coloration and pattern in *N. n. natrix*.

***Natrix natrix vulgaris* Laurenti, 1768**

This only recently recognized subspecies (Fritz and Schmidler 2020; Asztalos et al. 2021a, b) resembles in coloration and pattern *N. n. natrix*, but the body coloration tends to be lighter. In addition, the crescents are



Figure 10. Coloration and pattern of *Natrix natrix moreotica* documented by photos from iNaturalist. **A** Striped individual with pale yellow crescents and side bars; Thrace, Greece; photo: Wolfgang Wüster. **B** Striped individual with faded crescents and large body spots, the elongated black occipital element resembles *N. helvetica*; Lesvos, Greece; photo: Paul Cools. **C** Variation in color pattern in three juveniles; Thessaly, Greece; photo: Neil Balchan. **D** Weakly striped individual with side bars and completely disappeared crescents; photo: Claudine Delmas. **E** Very weakly striped individual with side bars and completely disappeared crescents; Samos, Greece; photo: rgm95. **F** Individual of the 'picturata morphotype,' Peloponnese, Greece; photo: Manuel Ruedi. **G** Individual of the 'schweizeri morphotype' feeding on a fire salamander (*Salamandra salamandra*); Metsovo, Greece; photo: Joost de Moor.



Figure 11. Coloration and pattern of *Natrrix natrrix scutata* documented by photos from iNaturalist. **A** Dark individual with orange collar; Nizhny Novgorod Oblast, Russia; photo: Evgenii Iaitskii. **B** Black individual with yellow collar; Bashkortostan, Russia; photo: Evgenii Samarin. **C** Marbled dark individual with pale orange collar; Tatarstan, Russia; photo: Denis Tishin. **D** Couple with yellow and pale orange crescents and mottled dark bodies; Kharkiv region, Ukraine; photo: Yehor Yatsiuk. **E** Grey individual with orange crescents; Simferopol region, Crimea, Ukraine; photo: Vyacheslav Luzanov. **F** Striped individual with whitish occipital coloration; Mazandaran, Iran; photo: Parham Beyhaghi.

more frequently pale orange colored than in the nominotypical subspecies. Furthermore, two light back stripes may be present, while *N. n. natrrix* is always unstriped. Figure 9 gives an overview of the variation in coloration and pattern in *N. n. vulgaris*.

***Natrrix natrrix moreotica* (Bedriaga, 1882)**

Until recently, this subspecies was lumped together with other subspecies of *N. natrrix* in which back stripes can occur (Asztalos et al. 2021a). *Natrrix natrrix moreotica* is

characterized by widely separated white to yellow crescents that increasingly fade with age, so that the coloration of the neck does not differ from the general body coloration in old snakes. Furthermore, it seems that *N. n. moreotica* often lacks the dark coloration element in front of the light occipital marking, otherwise characteristic for *N. natrrix*, even though we could not quantify this for the whole dataset. Two light back stripes are frequently present in *N. n. moreotica*, and the body typically shows large dark spots. Plain, mottled or marbled body colorations are exceptions. In rare cases, side bars resembling



Figure 12. Putative hybrids of *Natrix natrix vulgaris* × *N. helvetica sicula*: **A** Baricella near Bologna, Italy; photo: morganaphoto. **B** Veneto, Italy; photo: Daniele Seglie. Note in both individuals the weak back stripes (never occurring in *N. helvetica*), the lacking anterior dark element in the occipital region and in (A) the much elongated posterior element in the occipital region (characteristic for *N. helvetica*). The snake from the Veneto also shows weak side bars (characteristic for *N. helvetica*). Putative hybrids of *N. natrix scutata* × *N. tessellata* from iNaturalist, see text for further explanation: **C** Skvortsove, Crimea, Ukraine; photo: Denis Davydov. **D** Dnipro, Ukraine; photo: Anna Nikolenko.

N. helvetica may be present. Figure 10 gives an overview of the variation in coloration and pattern in *N. n. moreotica*. Only for *N. n. moreotica* both the ‘*picturata*’ and the ‘*schweizeri*’ morphotype are documented on iNaturalist (Fig. 10F, G). Notably, the ‘*schweizeri*’ morphotype was recorded on iNaturalist exclusively from outside of its known distribution range (Milos and other Cycladic islands, Cyprus).

***Natrix natrix scutata* (Pallas, 1771)**

This subspecies is frequently darker than others; the body is typically plain-colored. Except for the Caucasus region and northern Iran, *N. n. scutata* has no light back stripes. The crescents are generally either extended, with tips frequently meeting in the occipital region, or a closed collar is present. Crescents or collars are often orange-colored. However, in the Caucasus region and northern Iran, crescents seem to be more frequently separated and often paler than in the north. Like in *N. n. natrix*, more northern populations of *N. n. scutata* tend to

harbor more dark-colored individuals than more southern populations, even though in *N. n. scutata* melanistic individuals seem to contribute less to this trend than in the nominotypical subspecies. Figure 11 gives an overview of the variation in coloration and pattern in *N. n. scutata*.

Asztalos et al. (2021a) only hesitantly identified the easternmost grass snake populations from the border regions of eastern Kazakhstan, western Mongolia, western China and Siberia as *N. n. scutata* because from these regions no material could be studied genetically. For the present study, only a single iNaturalist record was available for the Lake Baikal region, while from eastern Kazakhstan and adjacent Siberia substantially more photos could be studied (Figs 1–7). These data show, together with the photos and descriptions of grass snakes from the Lake Baikal region published by Mertens (1966) and Litvinchuk et al. (2013), that these eastern populations morphologically match *N. n. scutata*, so that the assignment of all eastern populations to *N. n. scutata* is corroborated.

Discussion

Compared to ethanol-preserved museum specimens that are typically compromised by fading, in particular by the loss of yellowish and reddish colors, photo records of animals in the wild have an advantage because they illustrate their natural live coloration. On the other hand, there always remains some subjectivity using non-standardized photos, especially with respect to color tones. Also, many traits that are easily recorded from museum material are not accessible in photos. This includes measurements and meristic characters, but also certain traits of the color pattern. For instance, due to difficulties in taking standardized notes from photos in different perspectives, we could not examine shape and size of the dark elements bordering the light occipital spots, even though it was obvious that geographic variation exists. Nevertheless, our iNaturalist dataset allowed identifying some clear differences between the genetically redefined subspecies of *Natrix natrix*.

In this context, however, we have to discuss records of single striped grass snakes from Germany, at first glance contradicting our conclusions about subspecific variation. Günther and Völkl (1996) reported that a few striped grass snakes are known from the regions of Berlin, Leipzig, Perleberg and Stuttgart and believed that such individuals represent rare natural coloration variants. Among our 752 iNaturalist records from Germany was not a single striped individual, supporting their rarity both within the range of *N. n. natrix* (northern Germany) and within the range of *N. n. vulgaris* (southern Germany). Yet, in contrast to Günther and Völkl (1996), we doubt that striped grass snakes are native to Germany because all records are associated with larger towns or cities. This suggests that these snakes were introduced, a conclusion explicitly confirmed for Leipzig by Grosse (2011). Thus, we are confident that *N. n. natrix* is generally unstriped, a conclusion also supported by the absence of striped grass snakes in other parts of the distribution range of the subspecies (Denmark, Norway, Sweden), whereas striped individuals definitely occur in *N. n. vulgaris* (Fig. 6).

In any case, telling *N. n. natrix* and *N. n. vulgaris* apart remains challenging. *Natrix natrix moreotica* and *N. n. scutata* are much easier to distinguish by coloration and pattern traits.

Within *N. n. scutata*, the occurrence of striped grass snakes in two parts of the distribution range (Transcaucasus inclusive of northern Iran and northwestern Black Sea coast) is remarkable. The presence of striped *N. n. scutata* in the Transcaucasus and northern Iran correlates with the occurrence of distinct mtDNA lineages. *Natrix natrix scutata* is generally characterized by mtDNA lineage 8 (sensu Kindler et al. 2013). However, in the Transcaucasus and northern Iran occur two endemic mtDNA lineages (lineages 1 and 2 sensu Kindler et al. 2013), which are not sister to lineage 8 in phylogenetic analyses. This suggests the survival of distinct genetic lineages in local refugia in the Caucasus and the southern Caspian Sea regions that were genetically ‘swamped’ during

range expansions (cf. the lacking genotypic differentiation of Transcaucasian and Iranian grass snakes; Asztalos et al. 2021a). The occurrence of striped grass snakes in these regions could represent an idiosyncratic footprint of their temporarily independent evolutionary trajectory. In a similar vein, the striped grass snakes along the northwestern Black Sea coast are from a region bordering the distribution range of *N. n. vulgaris*, a subspecies in which back stripes are known to occur. This suggests that the back stripes in this region may be caused by hybridization between *N. n. scutata* and *N. n. vulgaris*. On the other hand, it can be speculated that the absence of back stripes in *N. n. vulgaris* from the northwesternmost part of the distribution range of this subspecies (southern Germany) results from hybridization with the generally unstriped nominotypical subspecies. Although southern German grass snakes genotypically match *N. n. vulgaris*, many individuals bear mitochondrial haplotypes of *N. n. natrix* and show nuclear genomic admixture (Schultze et al. 2019; Asztalos et al. 2021b).

Our data also reveal that the frequency of dark body coloration increases from south to north and from west to east. This trend concerns both variation concordant with taxonomy (the easternmost subspecies, *N. n. scutata*, being generally the darkest) and variation occurring within the same subspecies (in *N. n. natrix* and in *N. n. scutata* more northern populations harbor more dark or melanistic individuals). This suggests that dark coloration types are advantageous in the north and in regions with a continental climate.

Noteworthy is that iNaturalist photos document the occurrence of the ‘*schweizeri* morphotype’ outside of its previously known distribution (Cycladic Islands, Cyprus), in particular from the Greek mainland (Figs 4 and 10). Compared to the ‘*schweizeri* morphotype,’ there are very few records of the ‘*picturata* morphotype’ on iNaturalist. The only two unambiguous records of this morphotype for *N. natrix* refer to *N. n. moreotica* (Figs 4 and 10); a third record on iNaturalist from Innsbruck, Austria, represents most likely a *N. h. sicula*, i.e., two taxa from which this coloration variant was already known (*N. n. moreotica*: Müller 1932 and Kreiner 2007 for the Cycladic Islands and Baier et al. 2009 for Cyprus; *N. h. sicula*: Gredler 1882 and Glaser et al. 2008 for South Tyrol). However, the lack of additional records on iNaturalist does not imply that the ‘*picturata* morphotype’ does not occur in additional taxa. Jan (1864) included in his description of *Tropidonotus natrix* var. *picturata* material from the distribution range of *N. n. scutata* (Azerbaijan), so that this morphotype definitely occurs at least also in *N. n. scutata*. This underlines that even the large iNaturalist dataset may not completely cover the entire variation in coloration and pattern of grass snakes. Nevertheless, it allows a major step forward in morphologically characterizing the subspecies of *N. natrix*.

Furthermore, our results suggest that iNaturalist is also a valuable source for studying the geographic extent and frequency of hybridization between the parapatric grass snake species and between *N. natrix* and *N. tessellata*. Putative hybrids often show coloration and pattern charac-

ters of both parental species combined. This is particularly obvious in northeastern Italy, where hybrids between *N. n. vulgaris* and *N. helvetica sicula* may show a head coloration and side bars typical for *N. helvetica* (cf. Meyer 2020) combined with more or less distinct back stripes (Fig. 12A, B). Some of these hybrids may even resemble in coloration and pattern *N. n. moreotica* (Fig. 10), a subspecies which occurs further south on the Balkan Peninsula. Hybrids between *N. natrix* and *N. tessellata* often seem to be characterized by a brownish body coloration that can be combined with a ‘dice pattern’ typical for *N. tessellata* or an intermediate body and head coloration (Fig. 12C, D). With respect to hybridization of distinct grass snake species, future studies should focus on the geographic contact zones of the individual species. Such investigations should then include photo records for both species involved in the hybrid zones to ensure that all misidentified photos, including putative hybrids, are considered.

In summary, our study on *N. natrix* shows exemplarily that iNaturalist and similar platforms are a valuable data source for studies using coloration and pattern traits. Automated information extraction algorithms using Artificial Intelligence obviously have the power to accelerate data processing. However, due to the limitations of non-standardized photo material, such investigations can only supplement, but not replace, studies using museum material because only then measurable and meristic characters will be available. In addition, the increasing accessibility of genetic information of collection material (Raxworthy and Smith 2021) currently begins to open a true treasure vault that cannot be replaced by any photographic dataset.

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